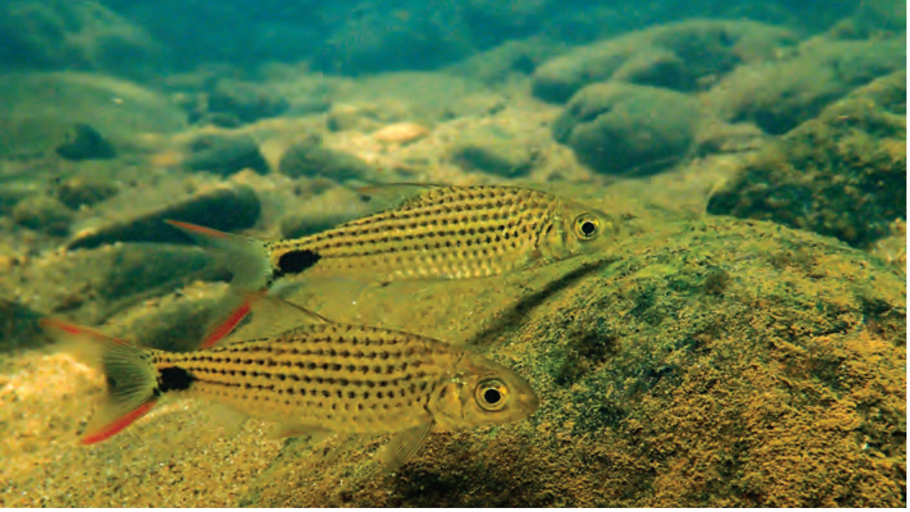

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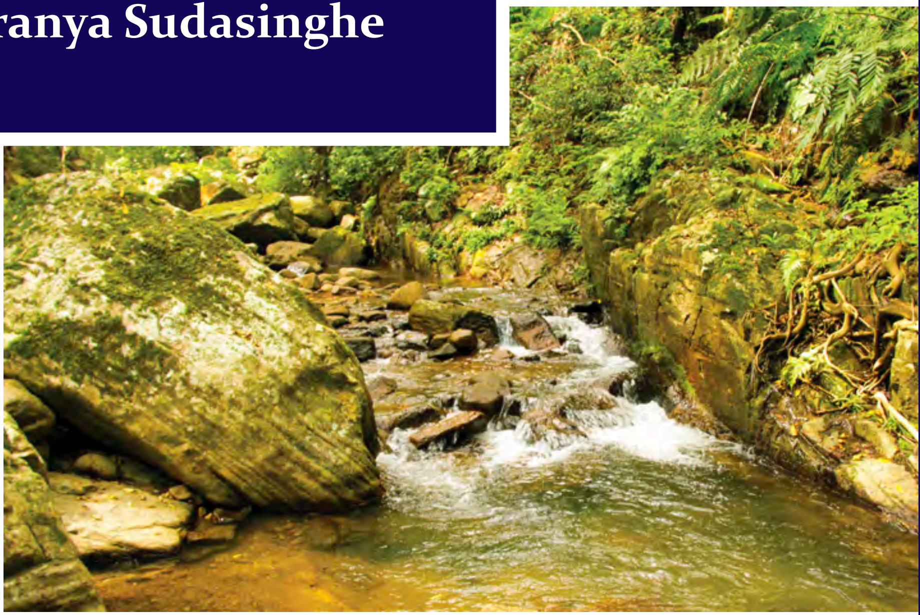
A context for freshwater fishes

Rohan Pethiyagoda & Hiranya Sudasinghe



THE ECOLOGY AND BIOGEOGRAPHY OF SRI LANKA

A CONTEXT FOR FRESHWATER FISHES

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ROHAN PETHIYAGODA & HIRANYA SUDASINGHE

WHT
LITTERAE SCRIPTAE MANET

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Title page: *Systomus pleurotaenia* and *S. asoka*.

Frontispiece: *Schismatogobius deraniyagalai.*

Contents

Foreword

In 2000 the ecologist Norman Myers and colleagues introduced the concept of biodiversity hotspots for conservation priorities, defining these as biogeographic regions that host exceptional biotic diversity and are under a high threat from anthropogenic activity. At that time, they identified 25 hotspots. Although these encompassed only 1.4% of Earth's land surface, they harboured an astonishing 44% of all vascular plant species as well as 35% of the known amphibians, reptiles, birds and mammals. Today, 35 terrestrial biodiversity hotspots are recognised.

When that paper was published, I was fresh out of graduate school and the idea of biodiversity hotspots struck a chord with me. I find the uneven distribution of biotic diversity both across the globe and across taxonomic groups infinitely captivating, particularly when freshwater fishes—my passion since my early school days—are involved. I started my career as an evolutionary biologist working on the adaptive radiation of cichlids in Lake Tanganyika in Africa, but the hotspot paper opened my eyes to the fascinating biotic diversity of Asia, especially in the Sundaland, Indo-Burma, Himalaya and Western Ghats-Sri Lanka biodiversity hotspots. I was intrigued; but there was also the obvious question: Why were my beloved freshwater fishes excluded from the analyses of biodiversity hotspots? The authors of the paper gave the following reason: "The other vertebrate group, fishes, is excluded because data are generally poor (there could well be at least 5,000 species waiting to be discovered, or more than all mammals)." This was a call for action and an excellent reason to go East, so I took the challenge.

Later on, in 2004, I was working on two groups of Asian freshwater fishes, the fighting-fish genus *Betta* and the Badidae, the chameleon fishes, when I came across a paper titled "Local endemism within the Western Ghats-Sri Lanka biodiversity hotspot" by herpetologist Franky Bossuyt and colleagues. Using molecular phylogenies of several invertebrate and vertebrate groups, they demonstrated that Sri Lanka has a large number of endemic species, often the result of extensive radiation on the island. And yes, the authors of this study did include freshwater fishes: small barbs of the genus *Puntius*, with species now assigned to the genera *Dawkinsia, Pethia* and *Systomus*. Furthermore, this study showed that Sri Lanka harbours a fauna that is notably distinct from that of the Indian mainland.

This result was surprising. Sri Lanka is a continental island separated from the Indian subcontinent by the Palk Strait, a narrow, approximately 10-metre-deep shelf sea. Global sea level reconstructions suggest that during extensive periods in the past, and for almost all of the Pleistocene, Sri Lanka was connected to the Indian mainland through a broad isthmus, called the Palk Isthmus. The expectation was that Sri Lanka's biota would be but a subset of the richness found in the Western Ghats. However, here was a study showing that many sister-group relationships between Indian and Sri Lankan taxa pre-date the Pleistocene and its sea-level fluctuations. Clearly, there was more to Sri Lanka's evolutionary history than had been previously assumed.

How can we explain the unique nature of Sri Lanka's biota? Some of the answers, of course, are hidden in hundreds of scientific articles, old and new, which need to be screened painstakingly. Finding the answers also requires the interested person to become a taxonomic expert for many different groups including plants, invertebrates and vertebrates. One would need to understand the evolutionary history of the biota of Sri Lanka as well as the island's complex geological and climatological history. Better however, would be to start by thoroughly reading *The ecology and biogeography of Sri Lanka – a context for freshwater fishes*, by Rohan Pethiyagoda and Hiranya Sudasinghe.

From this book we learn about the complex interplay between geology and climate in the formation of the Western Ghats-Sri Lanka biodiversity hotspot. The short story is that the break-up of Gondwana and the 70 My-long northward journey of the Indian plate, of which Sri Lanka is a part, ended with the collision with Eurasia around 50 Mya, triggering a major biotic exchange between India and Asia. This exchange, however, was affected by climate changes that caused India to become more arid until rainforests remained confined to south-western Sri Lanka. Thus, climate change modulated biotic interchange between Southeast Asia and India and, more importantly, between southern India and Sri Lanka.

In the Preface, the authors write "Despite this wealth of new knowledge, it is still too early for a synthesis—an overarching narrative that explains how exactly the island's plants and animals came to be as they are." I think this statement is unduly modest. It is true that there are frustrating gaps in our understanding of the biogeographic history of the Western Ghats-Sri Lankan biodiversity hotspot, in particular regarding the exact timing of geological events, the details of past connectivity between different tectonic plates, or tectonic plates and island arcs, or the influence of past climate. But Rohan and Hiranya have succeeded in giving us readers the most complete synthesis possible at this time. And it is not only about freshwater fishes! With *The ecology and biogeography of Sri Lanka…* we, for the first time, have an authoritative overview of Sri Lanka's staggering terrestrial diversity: Roughly 25% of the 3500 vascular plants, over 65% of the 78 species of freshwater fishes, over 60% of the 233 reptiles, over 80% of the roughly 250 species of land snails, and all 51 species of freshwater crabs, are endemic.

As the exploration of Sri Lanka's evolutionary history continues, *The ecology and biogeography of Sri Lanka…* will serve as an essential beacon guiding it. More importantly, the biogeographic connections and disjunctions it reveals will inspire future generations. But aside from its great scientific value, this book is a labour of love and dedication to Sri Lanka's majestic natural beauty. It is beautifully illustrated with maps, figures and wonderful photos of landscapes, animals and plants. A photo says so much more than a thousand words. How wonderful it would be if we had comparable books dedicated to the other biodiversity hotspots in Asia! Sri Lanka is very privileged indeed to have Rohan and Hiranya, two passionate ambassadors of their country's stunning natural heritage.

As I have been working with Asian freshwater fishes for several years, I've had the good fortune to meet both Rohan and Hiranya. Rohan is well known as an ichthyologist and conservationist who in 1991 published the widely acclaimed book *Freshwater Fishes of Sri Lanka*. And yes, he was one of the authors of that important paper on "Local endemism within the Western Ghats-Sri Lanka biodiversity hotspot". As the founder of the Wildlife Heritage Trust of Sri Lanka and as a recipient of the Rolex Award for Enterprise in 2000, he is a relentless champion for Sri Lanka's biodiversity and above all a dedicated mentor who continues to inspire young researchers to get involved with the exploration and conservation of Sri Lanka's natural diversity. Hiranya is one of these, a remarkable, young ichthyologist with expertise in both taxonomy and molecular systematics. Many of the insights we gain from *The ecology and biogeography of Sri Lanka – a context for freshwater fishes* regarding the distribution and phylogeographic patterns of Sri Lanka's ichthyofauna and its historic connections to the Indian mainland are derived from Hiranya's recently published molecular phylogenetic studies on a variety of cyprinid groups including the genera *Dawkinsia, Devario, Garra, Laubuka, Pethia, Rasbora,* and *Systomus*, as well as the snakehead genus *Channa*, amongst others. His research is largely based on his own fieldwork in Sri Lanka, conducted between 2014 and 2019. It is noteworthy that Hiranya is not only an ichthyologist with a strong background in fieldwork, but also an expert naturalist and nature photographer. Many of the photos in this book are his, including all the stunning underwater shots of freshwater fishes, many of them photographed in their natural habitats for the first time.

After reading *The ecology and biogeography of Sri Lanka – a context for freshwater fishes*, Sri Lanka, with its natural beauty and unique freshwater fish diversity, moved to the top of my travel bucket list. I can't wait to embark on a journey of discovery to The Resplendent Isle.

Lukas Rüber, PhD
Natural History Museum Bern, Switzerland, and
Aquatic Ecology and Evolution, Institute of Ecology
and Evolution, University of Bern, Switzerland.

Preface

Why we wrote this book

Despite Sri Lanka being positioned within a Global Biodiversity Hotspot and its fauna and flora being among the best explored in Asia, the island's biogeography has yet to be reviewed in a single work. We discovered this in the course of working on the evolutionary and biogeographic relationships of Sri Lankan freshwater fishes. Chapters 3 and 4 of this book represent a first attempt at joining the dots formed by hundreds of studies of varying scope and focus, and thereby trying to discern the patterns and processes that gave rise to the island's present-day fauna and flora.

Why hasn't this been done before? In a way, it has, in the form of *Ecology and biogeography in Sri Lanka* (1984), edited by Herbert Fernando. The focus of that volume, however, was largely on ecology, with relatively little attention paid to biogeography except in the case of mayflies. This is understandable, given that much of the information needed to construct a narrative of the island's biogeographic story simply did not exist at the time. Although yawning gaps still remain, the past few decades have seen huge advances in key fields associated with biogeographic understanding: tectonics, geology, historical sea levels, past continental connections, climatic history, phylogenetic analyses, molecular clocks, and comprehensive regional species-inventories based on an ever more reliable taxonomy. The rate of progress is evident from the ~800 publications on which the present review is based (listed in References). Almost three-quarters of these were published after 2000, and more than half after 2010.

Despite this wealth of new knowledge, it is still too early for a synthesis—an overarching narrative that explains how exactly the island's plants and animals came to be as they are. There are simply too many gaps. Nevertheless, some patterns are becoming clear, and we draw attention to the ones we have spotted. Yet others present intriguing lines of inquiry: we mention them only as hypotheses. So rapidly is the field evolving that we suspect this book will be out of date almost as soon as it is published.

Why then, do we write it in the first place?

We do so in order to bring together in a single volume the diverse body of evidence there is from multiple disciplines. We needed this to aid our own research. Besides, colleagues who think about similar problems will likely benefit from it, too. Hence this book is written in the hope that it will stimulate more studies of the historical and geographic relationships of Sri Lanka's extraordinary fauna and flora, and the processes that gave rise to these. While most of our current knowledge derives from vertebrate groups, it is clear that the plants and invertebrates too, offer huge opportunities for research. Despite the much greater ease with which plant material can be collected for molecular analysis, DNA-based studies of relationships among vertebrates outnumber those of plants by at least an order of magnitude. This must change, and if this book helps instigate that change, our work will have been done.

We recognize two audiences for a book such as this. A scientific one, which demands a technically coherent text that is extensively referenced so that every datum can be verified; and a general readership composed of those interested in Sri Lankan natural history. We recognize that one size does not fit both. For a fine example of the former approach, see Heads' (2019) review of New Caledonian biogeography. The latter readers, however, arguably prefer a book which presents an illustrated, broad-strokes account of the island's biotic story. We hope that general readers who do not want to be overloaded with technical details can still get an idea of the broad narrative. To make this easier, we provide a non-technical summary in Chapter 1 and conclusions in Chapter 6. In order to make the text more accessible to non-specialist readers, we have also illustrated it extensively. But, most of all, we decided to publish this book because a small number of scientists and students may find the stories we tell and examples we cite inspiring enough to pursue biogeographic inquiries of their own.

Given that our primary interest is in ichthyology, two chapters are devoted to fishes. Chapter 4 reviews the wider relationships of a few groups of fishes for which information is available; Chapter 5 reviews the distribution of fishes within the island and, for the first time for any substantial group of Sri Lankan plants or animals, provides an account of the distribution of genetically distinct populations of several species.

Limitations and significance

Phylogenetic and phylogeographic studies in Sri Lanka

Many new species of freshwater fishes are described from South Asia each year. In most cases, these descriptions are based on samples from only a single locality and based wholly on morphology. Although increasing numbers of taxonomic studies report on the *cox1* barcoding gene, the utility of a single gene marker in illuminating phylogenetic relationships is limited (Mallo & Posada, 2016). Despite these advances, studies of evolutionary relationships between species—and especially diversity within species—are still in their infancy. In the case of Sri Lanka, almost all studies prior to those of Sudasinghe *et al*. (listed in the Literature Cited) were based only on morphology and constrained by limited geographic sampling. In Chapter 5, however, we explore for the first time, across a substantial number of Sri Lankan freshwater fishes, evolutionary relationships derived from the *cytb* and *cox1* mitochondrial markers and the *rag1* and *irbp* nuclear markers. These studies have allowed us to evaluate intraspecific variation, in both morphology and genetics, based on large sample sizes while also helping to delineate the geographic distributions of the various species and lineages.

Mitochondrial markers are maternally inherited and usually not associated with recombination. They also have a higher substitution rate compared with nuclear markers and are hence useful in detecting genetic structure among closely related species and populations. Hence, mitochondrial markers are widely used in phylogeographic studies (Beheregaray, 2008; Hickerson *et al*., 2010). Meanwhile, *rag1* (among many others), a paralog-free gene, is extensively used to elucidate higher level relationships in teleost phylogenetics (Hughes *et al*., 2018, 2021).

While phylogeographic studies have been advancing rapidly in developed countries (Beheregaray, 2008), there is a clear deficiency of such research in most developing countries such as Sri Lanka, particularly given that it lies within a Global Biodiversity Hotspot. Nevertheless, the field of evolutionary biology is advancing rapidly, with genomic data now becoming more and more readily available for comparative population-genomic and phylogenomic studies. Inferences made from genomics data are substantially more informative than those using a few molecular markers, as in our studies. Thus, we are the first to acknowledge the limitations of the results we report in Chapter 5: this is only a starting point.

Despite this, even phylogeographic studies that are thus constrained help us to understand evolutionary patterns and processes, and to test hypotheses on the geographical distribution of lineages of a species by using genetic data (Avise, 2000; Avise *et al*., 1987).

In many cases, we objectively explored species boundaries using a combination of criteria: morphology, genetic data, and geographic distributions following a general lineage concept of species (de Queiroz, 1998). While clarifying the taxonomy of the concerned species—which no one disputes is the starting point for conservation planning and management—these studies are additionally handicapped by limited comparative data from India.

Nevertheless, these studies have, for the first time, detected evolutionary dynamics that have not hitherto been reported: drought refugia in the southern basins, unexpected barriers to dispersal among adjacent river basins, instances of dispersal by river capture, and historical extinction events. We show also that climate has been a major driver in shaping Sri Lanka's biodiversity. This becomes increasingly relevant given the rapid changes to climate that we are now witnessing.

RP & HS, October 2021.

Dawkinsia srilankensis.

Dedications

HS
To my parents, Shantha and Nirmala: for their endless love, and giving me the freedom to explore and discover.

RP
To my mother, Mary, and the memory of my late father, T.B. — for those idyllic early years.

A stream in Kottawa Forest.

Acknowledgements

The idea of this book was first suggested to us by Nimal and Savitri Gunatilleke in 2015. We thank them for commenting on parts of the text and also for several discussions relating to Sri Lankan biogeography over the years. Their work on the community ecology of the rainforest flora of Sri Lanka inspired lines of inquiry we followed in the phylogeographic studies summarized in Chapter 5.

We are grateful to those of our colleagues who commented on various versions of the text and gave us valuable suggestions for its improvement: Lukas Rüber, Madhava Meegaskumbura, Jaap de Vlas, and Michael and Nancy van der Poorten. We alone are responsible for the errors that remain.

This book would not have been possible if not for the many images that illuminate the text. We thank our many colleagues who helped by contributed photographs. They are acknowledged alongside the respective images. In addition to providing us with dozens of images of difficult-to-photograph plants, Himesh Jayasinghe generously shared with us his encyclopaedic knowledge of the Sri Lankan flora.

We are grateful to Lalith Ekanayake and David J. Krishnapillai for advice on improving the quality of print.

RP acknowledges several colleagues who, over the years, contributed ideas and literature that helped improve the text, including (alphabetically) Suresh Benjamin, S. D. Biju, Pruthu and Jenny Fernando, the late K. C. Jayaram, the late Rodney Jonklaas, Rahul Kumar, Ian Lockwood, Kelum Manamendra-Arachchi, the late A. G. K. Menon, Sudath Nanayakkara, Rajeev Raghavan, Nancy and Michael van der Poorten, Dinarzarde Raheem, K. Rema Devi, Ruchira Somaweera, Gothamie Weerakoon, Siril Wijesundera, and Mendis Wickramasinghe.

HS thanks (alphabetically) Dhanushka Lakshan, Tharindu Ranasinghe, Charana Widuranga, Kumudu Wijesooriya and many other friends and colleagues who joined and assisted in numerous field expeditions. HS is grateful to the Director General, Department of Wildlife Conservation, Sri Lanka, and the Conservator General, Forest Department, Sri Lanka, for providing all the necessary permits to carry out fieldwork. He also thanks the Director and the Assistant Director of Zoology of the National Museum, Colombo, and their staff for providing access to specimens in their care.

HS thanks (alphabetically) Neelesh Dahanukar, Unmesh Katwate, Rahul Kumar, and Rajeev Raghavan for making Indian material from their collections available for study and for useful discussions and generous hospitality during visits to India; and also (alphabetically) Ralf Britz, Kalana Maduwage, Lukas Rüber, and Tan Heok Hui for useful discussions.

HS takes pleasure in thanking Madhava Meegaskumbura for his support, guidance and inspiration over the past several years.

Being a review, this book relies heavily on the published literature. Our text distils the discoveries and conclusions made by hundreds of authors over several decades. While they are cited where relevant, we hope we have abstracted their work accurately and in context.

Finally, we thank our wives, Janaki Pethiyagoda and Dayesha Sudasinghe, for allowing us to be distracted from our connubial responsibilities during the writing of this book.

Units, abbreviations, terms, notes

~ approximately.

asl above sea level.

CI confidence interval.

cox1 cytochrome c oxidase subunit 1.

cytb cytochrome b.

DH Deutsche Härte, a unit of water hardness.

Dry zone: Region in which rainfall < 1.8 $m \cdot y^{-1}$ (see Figure 2.6).

Gondwanan: Here applied to taxa whose ancestors inhabited the Sri Lanka-India-Seychelles-Madagascar plate prior to the former rifting from Madagascar *ca* 90 Mya, as well as other elements of the Gondwana supercontinent prior to that.

HPD highest posterior density

Intermediate zone: region in which rainfall is 1.8–2.5 $m \cdot y^{-1}$ (see Figure 2.6).

irbp interphotoreceptor retinoid binding protein

ky thousand years.

kya thousands of years ago.

LGM Last Glacial Maximum.

µm one millionth of a metre

µS micro-Siemens [per cm]: unit of electrical conductivity

My million years.

Mya millions of years ago.

NMSL: National Museum of Sri Lanka, Colombo.

PCA principal component analysis.

Peninsular India: mainland India south of ~21°N.

pH potential of hydrogen: a scale used to indicate the acidity or basicity of an aqueous solution.

Photographs: almost all the photographs of Sri Lankan freshwater fishes in this volume were taken by HS. For consistency, some have been laterally inverted so that the specimen faces left, as is the convention in ichthyology.

rag1 nuclear recombination activating protein 1.

Rain forest: forest occurring in perhumid tropical climates. In Sri Lanka, 'rain forest' includes the Mixed Dipterocarp Forests of the lowland wet zone as well as the tropical montane forests of the highest hills. We recognize such forests primarily on the aseasonality of rainfall rather than floristics.

Rivers: Sri Lankan river names are binomial, the second word of which is of the many local-language words for the different kinds of waterways, such as *ara, aru, ela, ganga* and *oya*. For the convenience of non-native readers, we translate all these as 'River'.

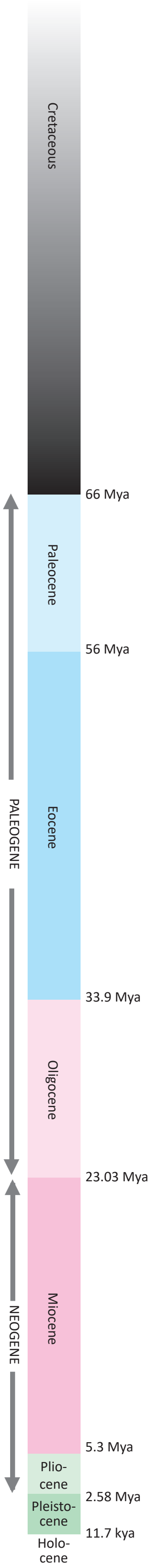
Species: species names change over time, as taxonomy is revised. When referencing the earlier literature, we have updated species names to those currently in use, noting where the identity of a species cannot be inferred with certainty.

sp. abbreviation of 'species', singular. Plural: spp.

Wet zone: region in which rainfall is >2.5 $m \cdot y^{-1}$ (see Figure 2.6).

y year.

ya years ago.



1

Précis

A broad-brush summary of the principal biogeographic ideas presented in Chapters 3–5.

1.1 External relationships

Except for fragments of teeth and bones recovered from cave middens and ancient riverbeds while mining for precious stones, Sri Lanka lacks a fossil record of vertebrate animals. While these fragments give us an idea of the large mammals such as elephants, rhinoceroses, hippopotamuses and big cats that inhabited the island during the past few tens of thousands of years, there is almost nothing from the millions of years before that. In the past decade or so, however, DNA from ever more Sri Lankan animals has been sequenced, allowing us, in some cases, to make estimates of their history using molecular clocks. These, however, are only as reliable as the means by which they are calibrated, which involves many assumptions and hence, substantial uncertainty. Nevertheless, molecular-clock methods allow us to time-calibrate phylogenetic trees and hence to infer the timing of lineage divergence.

Until about 130 million years ago (Mya), Sri Lanka and India were part of the supercontinent of Gondwana, attached to Antarctica, in Earth's southern hemisphere. As the supercontinent continued to break up, Sri Lanka-India remained attached to Madagascar and the Seychelles. Around 90 Mya, however, the Sri Lanka-India-Seychelles plate broke away from Madagascar and began drifting north, passing through the humid equatorial region into Earth's northern hemisphere. Sri Lanka was at that time a part of India, not yet separated from the subcontinent by a marine barrier.

Around 66 Mya, while the subcontinent continued its northward transit across the Tethys Sea, the impact of an asteroid near eastern Mexico caused the Cretaceous-Paleogene (K-Pg) extinction event. This coincided with an extended period of volcanism around present-day Maharashtra in India, resulting in the Deccan Trap lava flows, which exacerbated the crisis facing biodiversity as a result of the K-Pg upheaval*. These events had devastating consequences for the plants and animals of India and Sri Lanka. Also, at about the same time, the Seychelles micro-plate rifted from India-Sri Lanka, which continued drifting north.

We know of no surface-dwelling vertebrate lineages that survived the extinctions associated with the K-Pg cataclysm and Deccan-volcanism on India or Sri Lanka. In Sri Lanka, only the burrowing blind-snakes of the family Gerrhopilidae have been shown to pre-date to the rifting from Madagascar 90 Mya. Several insect, scorpion, spider and mollusc lineages, however, appear to have survived the extinction event; they persist in the island even now. In India, however, at least two further vertebrate groups survived, both of them below the earth's surface: the aenigmachannid snakehead fishes and the nasikabatrachid frogs, both of which occur in the humid southern region of the Western Ghats.

The Western Ghats and Sri Lanka are now recognized as a Global Biodiversity Hotspot (Figure 1.1). To qualify as a Hotspot, the unit must have at least 1,500 vascular plants endemic to it (Sri Lanka alone has around 1000, and the Western Ghats more than a further 1700: Jagtap, 1994); and, importantly, it must retain 30 percent or less of its original natural vegetation. These criteria make hotspots centres of high conservation concern.

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* This episode of volcanism resulted in the deposition of more than 700,000 km^3 of basalt on an area of about 500,000 km^2 of continental India. The volcanism itself lasted several million years (Jain *et al.*, 2020).

Figure 1.1. The Western Ghats-Sri Lanka Biodiversity Hotspot (in green).

Current geological models show the Sri Lanka-India-Seychelles plate as an island in the Tethys Sea between 90 and 66 Mya. There is, however, evidence from plant and animal studies that suggests that this plate had terrestrial contact with Africa and Madagascar at some points during this interval. There seems to have been an ephemeral land bridge between Southeast Asia and Madagascar too, during this time. However, evidence from the earth sciences is yet to be offered to support such a model.

In one of many posited scenarios, by at latest 57 Mya, India had its first contacts with Asia, in the region of what is now Sumatra. Several such contacts followed before the subcontinent finally accreted with Asia in the region of what is now the Himalayan mountain chain. These early contacts with Asia lay within the equatorial humid zone, allowing for the exchange of tropical biota (Figure 1.2).

We have only a scant idea of the plants and animals that inhabited Sri Lanka prior to the immigration of Asian lineages adapted to an ever-wet climate following the final India-Asia contact around 50 million years ago. The earliest (albeit indirect) evidence we have for a vertebrate group dispersing into the island is of the ancestor of the endemic frog genus *Lankanectes,* which arrived sometime after India-Asia contact. It is possible, however, that these amphibians in fact dispersed to Sri Lanka as late as 31 Mya, concurrently with the ancestor of the diversification of *Pseudophilautus* shrub frogs that now dominate the island's amphibian fauna.

Lowered sea levels since then, however, gave rise to a wide isthmus ('the Palk Isthmus'[*]) connecting Sri Lanka to India, allowing plants and animals to disperse between the two landmasses. If not already by the late Eocene, between 30 Mya and 20 Mya, a large number of Asian plant and animal lineages dispersed across the isthmus to colonize Sri Lanka, almost all of them associated with rain forests. Among these were the ancestors of the island's oldest freshwater-fish lineages: *Rasboroides + Horadandia, Malpulutta, Belontia* and the endemic diversification of *Systomus*.

By 20 Mya, however, northern India (broadly, the Ganges-Brahmaputra basin) was experiencing a prolonged annual dry season, leading to the loss of rain forests there. As a result, the dispersal of plants and animals associated with rain forests between India and Southeast Asia gradually declined. Meanwhile, the climate of the Indian Peninsula too, was becoming increasingly seasonal and arid (Figure 1.3). By about 6 Mya, rain forests disappeared from the peninsula, except in the southernmost part of the Western Ghats. Thus, the rain forests of south-western Sri Lanka and the southern Western Ghats have been biotically isolated from each other for about the past 6 My.

In Sri Lanka, rain forests were confined to the south-western quadrant, including the western and southern slopes of the central and Knuckles hills. The island's southwestern rain forests became, in effect, an island within an island, insu-

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[*] Palk Bay and Palk Strait are named after Sir Robert Palk (1717–1798), from 1755–1763 governor of the East India Company's Madras Presidency. We followed this usage by naming the land bridge between India and Sri Lanka the Palk Isthmus for reasons of convenience in referring to existing maps of the region (Sudasinghe *et al.*, 2018b).

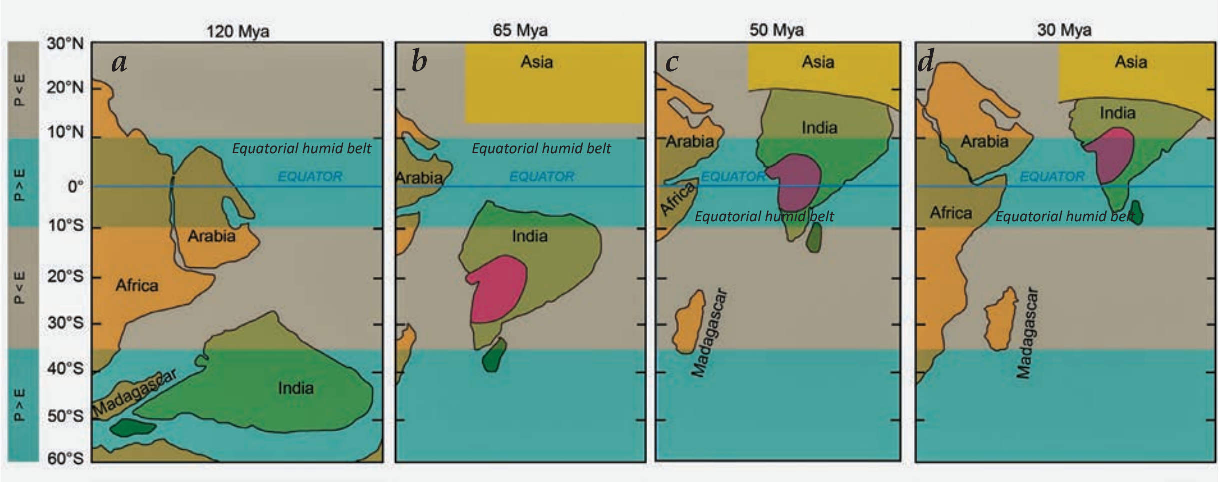

Figure 1.2. Palaeogeographic reconstruction of the approximate position of the India-Sri Lanka plate during its northern transit across the Tethys Sea 120–30 Mya, after Kent & Muttoni (2008). The zonally averaged climatic bands in which precipitation, P, exceeded evaporation, E (*i.e.*, humid zones), or evaporation exceeded precipitation (*i.e.*, arid zones), are also indicated. ***a,*** Early Cretaceous; ***b,*** around the Cretaceous-Tertiary boundary and emplacement of the Deccan Traps; ***c,*** the early Eocene; and ***d,*** the early Oligocene. Note that for much of the period *c–d,* the eastern region of contact between India and Asia lay within the equatorial humid belt (Klaus, 2016; Morley, 2018), allowing exchange of taxa adapted to a perhumid climate. The original extent of the Deccan Trap lava flows on India are indicated in red. The Kohistan-Ladakh Arc and possible contacts between India, Africa, Madagascar and Africa post-90 Mya are not shown.

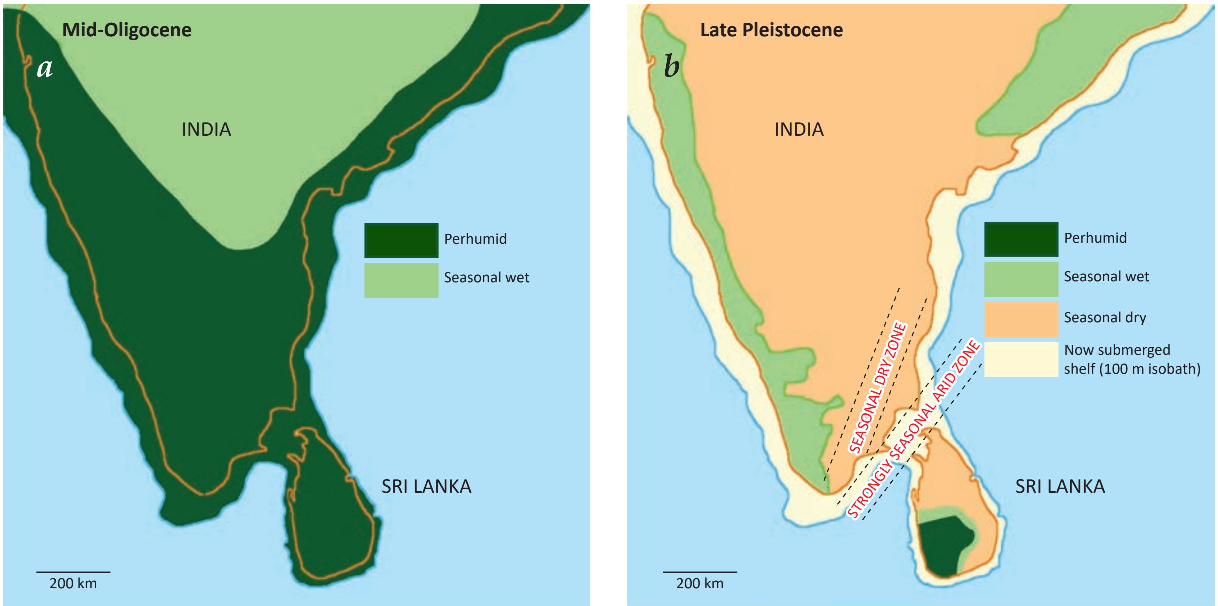

Figure 1.3. Paleoclimate in southern India and Sri Lanka. ***a,*** in the mid-Oligocene, adapted for India from Morley (2018) and inferred for Sri Lanka from Meegaskumbura *et al.* (2019). Meegaskumbura *et al.* (2019) showed that the dispersal to Sri Lanka of the common ancestor of the diversification of some 70 species of *Pseudophilautus* shrub frogs on the island, almost all of which are confined to the rain forests of the southwest, required perhumid conditions on the isthmus connecting Sri Lanka to India. ***b,*** Late Pleistocene, inferred from Ashton & Gunatilleke (1987), Ashton (2014); Gunatilleke *et al.* (2017); and Reuter *et al.* (2021).

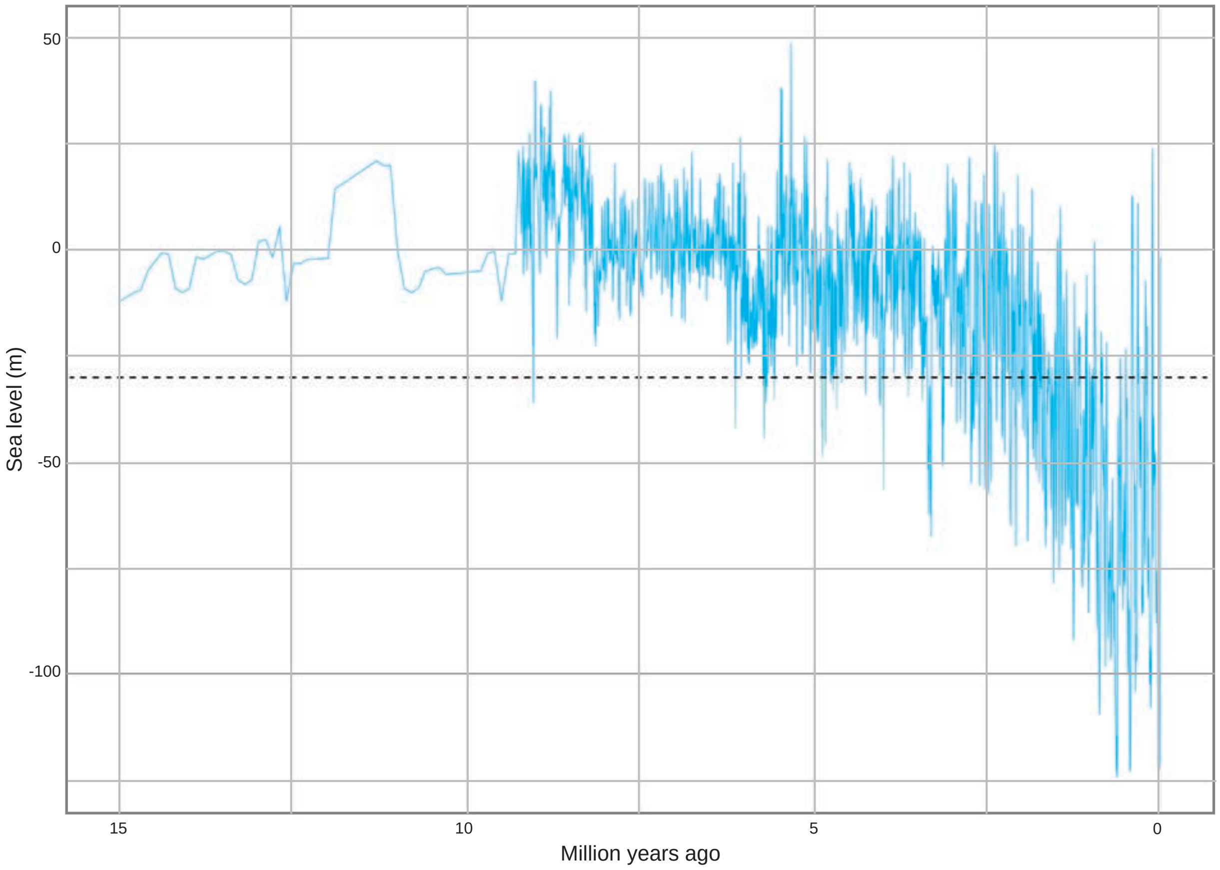

Figure 1.4. Eustatic sea level (*i.e.*, sea level as measured from the centre of the earth to the sea surface) over the past 15 My, showing that sea level has frequently been below that at present (*i.e.*, zero on the Y axis) over the past ~10 My, allowing the Palk Isthmus to emerge. The dashed line indicates sea level 30 m below that at present, during which time the Isthmus was almost certainly emergent, even allowing for subsidence of the sea floor in the region of the Palk Strait. See Figure 3.63 for data sources and detailed plots of Eustatic sea level over the past ~5 My.

lated by the dry zone. Today, the Sri Lankan wet zone combines the highest rainfall and lowest seasonality of any region between tropical Africa and Malesia[*]. This explains the correspondence between the biotas of Sri Lanka's wet zone and of Southeast Asia. After they had dispersed via the Indian subcontinent, aridification led to the extirpation of many of these lineages in India.

Thus it is that the flora of Sri Lanka's lowland rain forests, while related to that of South India, has a striking affinity with that of Malesia. Even the least seasonal parts of the Indian peninsula had, by the Pleistocene, become too seasonal to support rain forests like those of southwest Sri Lanka and Malesia. In support of this idea, we provide examples of disjunct taxa—species, genera and families that occur in Sri Lanka and Malesia or Southeast Asia, but not in between, in India. Additionally, wealth of relict lineages of plants and animals on Sri Lanka demonstrates that its south-western 'wet zone' has for tens of millions of years been a unique reservoir of biodiversity that India's climate is too seasonal to support. But because of the extinctions[†] that occurred prior to the Oligocene, much of its Gondwanan history has been erased.

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[*] Broadly, southern Peninsular Malaysia, together with the Indonesian and Philippine archipelagos.

[†] In the absence of a fossil record, we have no idea how many extinction events there were in Sri Lanka, or when they occurred. The evidence suggests there was at least one event 90–30 Mya. The global K-Pg extinction may have combined with Deccan volcanism to eliminate much of Sri Lanka's Gondwanan biota *ca* 66 Mya. The passage of Sri Lanka through the dry 10–30° S latitudes 60–30 Mya (Figure 1.2) too, may have resulted in extinctions driven by aridification.

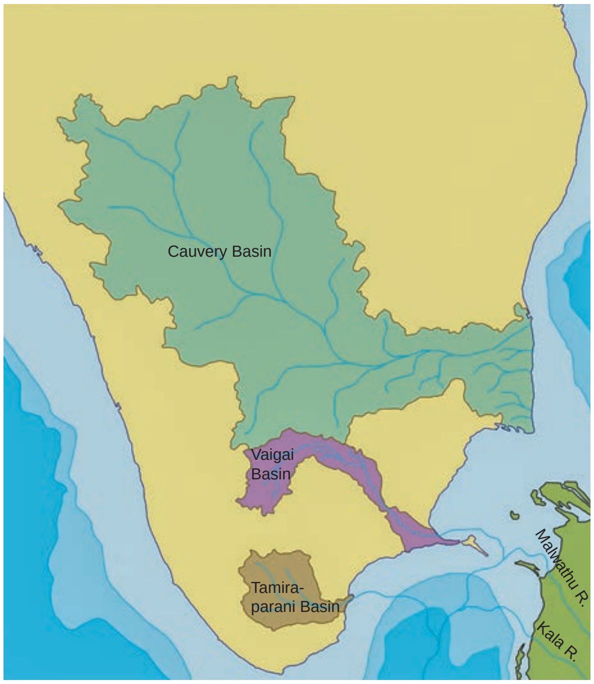

Figure 1.5. During the Pleistocene (and perhaps, even before then), east-flowing rivers in South India, such as the Cauvery, Vaigai, Vaippar and Tamiraparani drained into the Palk Isthmus. Here, they were confluent with the Malwathu and Kala drainages, allowing for the exchange of aquatic organisms between Sri Lanka and the mainland. Note: the tracks of the rivers illustrated in the sea are imaginary, though there is evidence for their existence, for example, in submarine gravel and even tree trunks. Further, the basin boundaries, and the location of deltas, which are shown as they are now, may have been different in former times.

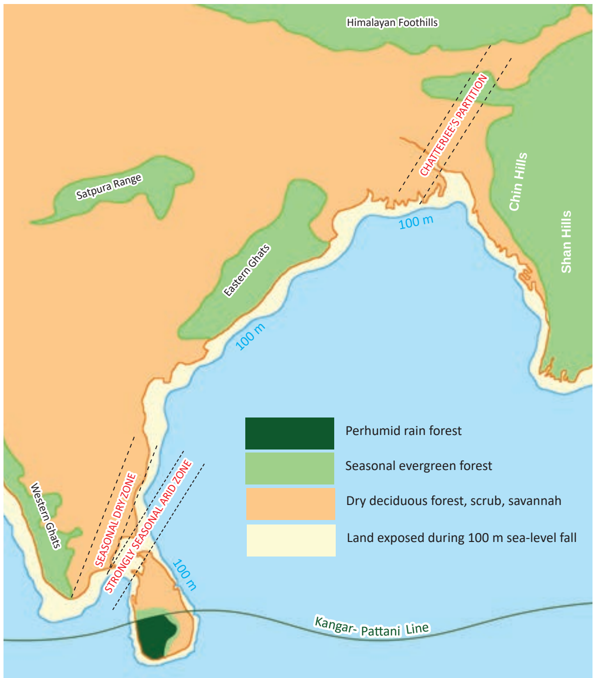

Figure 1.6. The principal barriers to biotic dispersal between Sri Lanka, India, and Southeast Asia in the Plio-Pleistocene. Starting in the early Miocene (*ca* 23 Mya), a corridor with less than four dry months across the Ganges plain, between India and Myanmar, ceased to exist, with the climate becoming increasingly more seasonal until the Pliocene (*ca* 5.3 Mya), establishing Chatterjee's Partition (Chatterjee, 1939; Ashton, 2014). Despite an increasingly seasonal climate, moist dipterocarp forests persisted across the Indian Peninsula until the late Miocene, ~6 Mya (Guleria, 1992; Rust *et al.*, 2010; Shukla *et al.*, 2013). This marks the last exchanges of rainforest-adapted taxa between Sri Lanka and India despite—except during brief intervals—sea levels having remained substantially below the present level since the early Pliocene (see Figure 3.63). Nevetheless, the exposed Palk Isthmus, despite being ~200 km wide, was too arid to facilitate free biotic exchange between even the dry zones of South India and Sri Lanka. Although withdrawing to refugia during spells of increased aridity, such as during Pleistocene glaciations, Sri Lanka's lowland perhumid 'wet' zone, below the westward extension of the Malaysian 'Kangar-Pattani Line' (Whitmore, 1984; see footnote on p. 65), has retained its Mixed Dipterocarp Forest at least since the early Miocene, or perhaps even the Cretaceous (Khan *et al.*, 2020), although the highlands appear to have undergone one or more episodes of intense aridification, perhaps as recently as the Last Glacial Maximum, ~22 kya (Clark *et al.*, 2009; Premathilake, 2012).

Elevated sea levels and subsidence of the seafloor of Palk Bay led to the Palk Isthmus being underwater for most of the period 20 to 15 Mya. Even though the isthmus was emergent on several occasions between 15 and 6 Mya, relatively few plants and animals were able to cross it. This may have been because the soils of the lowland plain that formed the isthmus could not support rain forests, or because the climate was too dry or seasonal. Nevertheless, some lineages associated with rain forest were able to disperse across the isthmus until about 6 Mya.

Though not continuously, for most of the time from about 5 Mya until as recently 10,000 years ago, the isthmus provided a corridor up to 200 km wide between Sri Lanka and the mainland. Perversely, although the isthmus was emergent during most of this interval, its climate was so dry or seasonal that even the dispersal of lineages associated with arid environments was inhibited. The early Pliocene (*ca* 5.3–2.6 Mya) was the last period in which the climate of the isthmus was comparable, if not to today's wet zone, then to the intermediate zone (rainfall 1.8–2.5 m·y^{-1}).

The ancestors of Sri Lanka's diversification of some 50 species of freshwater crabs too, arrived during this last wet phase. The Tamiraparani and Vaigai rivers of southeast India were at that time confluent, on the Palk Isthmus, with Sri Lanka's Malwathu and Kala Rivers, allowing fish to disperse between the mainland and Sri Lanka (Figure 1.5). Thus it is that *Dawkinsia srilankensis,* which is endemic to the Knuckles region, has its closest relative, *D. tambraparniei,* in the Tamiraparani.

After about 6 Mya, however, even though depressed sea level kept the isthmus emergent most of the time, its climate gradually became increasingly more arid and seasonal, similar to the present-day climate of Mannar, in Sri Lanka's northeast littoral. Now, rather than serving as a biodiversity corridor between India and Sri Lanka, the isthmus began acting essentially as a filter. It, together with the dry zones of north-western Sri Lanka and south-eastern India, formed a climatic barrier to the dispersal of plants and animals between the island's biodiversity-rich south-western wet zone and India's Western Ghats (Figure 1.6).

It is for this reason that dozens of vertebrate species that occur in southern India are absent from Sri Lanka. In several cases, we show that even species tolerant of a dry climate could not make it across the isthmus. Among fishes, the last groups that diversified in the island, such as *Rasbora* and *Devario*, are for the most part ones whose ancestors made the crossing during that last wet window in the Pliocene. The fishes that now inhabit the dry zone mostly dispersed to Sri Lanka much later, during the Pleistocene, whenever the arid climate of the isthmus gave rise to ephemeral rivers and streams, as it still does in the dry zone during the October–December rains. Nevertheless, these were fishes adapted to the dry plains of South India and hence, adapted to life in the dry zone. Some of these 'arid adapted' fishes, such as *Systomus sarana, Puntius thermalis, Rasbora microcephala* and *Devario malabaricus* were generalists, equally at home in both the dry zone and the wet zone. Others, such as *Pethia melanomaculata* and *Labeo lankae,* failed to disperse to the wet zone.

Figure 1.7. *Garra ceylonensis,* a species exhibiting adaptations for rheophily that is nevertheless widely distributed in the island.

Then, at some point during the Pleistocene, Sri Lanka's freshwater fishes suffered another extinction[*]. We cannot know what caused this, but it was most likely aridification. Highland streams dried up, even as the smaller ones that drain steeper gradients do even today, during periods of drought.

The whole of the dry zone too, lost most of its fish fauna: the region's present-day fishes comprise species that occur also in the wet zone, or immigrated from South India during the last few hundred thousand years. Such lineages as did survive in Sri Lanka did so in the rainforest refuges that persisted, for example, in moist, protected, lowland valleys. Recent phylogeographic studies of freshwater fishes suggest that the large rivers of the southwestern wet zone (Kelani, Kalu, Gin and Nilwala), headwaters of eastern basins (Gal, Kumbukkan, Menik), and the Knuckles region of the Mahaweli, may have contained such refuges.

The central highlands seem to have borne the brunt of the aridification, as seen also from the studies of pollen cores at Horton Plains. It may be as a result of such an extinction that, while Sri Lanka's lowland forests bear a close affinity to those of Southeast Asia, its highland forests have their closest affinity to those of the southern Western Ghats—the Nilgiri, Anaimalai and Palani hills[†].

When a wet climate finally returned (the present climate of the wet zone may be as wet as it has ever been), and the streams and rivers once

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[*] Again, at least one episode, perhaps several.

[†] See Trimen (1886) quoted on p. 66.

Tharindu Ranasinghe

Figure 1.8. ***a,*** *Channa marulius,* a species that occurs widely across India but in Sri Lanka is confined to the northern dry zone, and ***b,*** *Channa ara*, an endemic which occurs only in the Mahaweli basin (Sudasinghe *et al.*, 2020b).

more began to flow, fishes had opportunities to disperse more widely. Many fishes show genetic signatures of such a history.

1.2 Distributions within Sri Lanka

The distribution of fishes within Sri Lanka has been studied perhaps more than that of any other group of animals. The distribution patterns we report now are broadly consistent with ichthyological surveys conducted in the 1980s, especially with regard to species confined to one or a few adjacent river basins.

Endemism is concentrated in the rain forests of the foothills and lowlands of the south-western wet zone and the Knuckles Range. Recent work by Hiranya Sudasinghe and colleagues, however, has pushed these boundaries outward. Senanayake (1980) and Pethiyagoda (1991) reported high concentrations of endemics principally from the Kelani to the Nilwala river basins, and the Knuckles Hills. The more recent work shows that the Walawe and Ma basins too, have endemic species confined to them (*e.g.*, *Schistura madhavai* and *Devario memorialis*, respectively), while other endemics such as *Pethia reval* and *Ompok argestes* occur as far north as the Deduru basin. Such range expansions have now been discovered even in the case of the fishes endemic to the Knuckles, such as *Dawkinsia srilankensis, Systomus martenstyni,* and *Labeo fisheri*. These were earlier thought to be dependent on fast-flowing tributaries of the Mahaweli draining the Knuckles' foothills. We now know them to be present even in sections of the Amban River as far downstream as Angammedilla.

The recent surveys also revealed endemism within a river basin until recently neglected by ichthyologists: the Gal River, in the island's eastern side. Sudasinghe and colleagues reported a new species, *Laubuka hema*, from streams draining the eastern slopes of the central mountains within the Gal River basin. They also discovered another endemic, *Rasbora adisi*, from the Gal and adjacent rivers draining the eastern slopes of the central hills. These discoveries suggest that new attention needs to be paid to exploring the eastern slopes of the central hills, which have been largely neglected in biodiversity surveys until recently.

The recent works mentioned above also included phylogeographic analyses of some twenty species of freshwater fishes. These studies provide us with a far more nuanced understanding of fish distributions within the island.

Garra ceylonensis (Figure 1.7), for example, is among the most widely distributed freshwa-

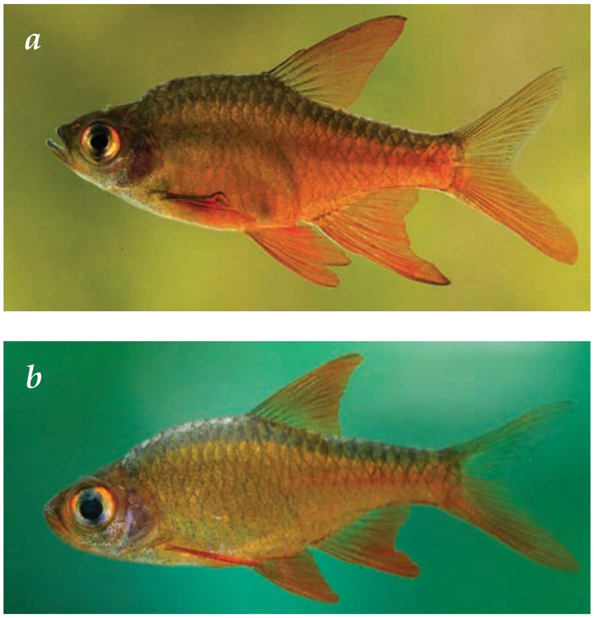

Figure 1.9. ***a,*** *Rasboroides rohani,* which Sudasinghe *et al.* (2018a) showed to derive from a translocated population of ***b,*** *Rasboroides pallidus*.

ter-fish species in Sri Lanka. It occurs in almost every river basin, wherever hard substrates exist, in an elevation range that extends from very nearly sea level to at least 1580 m asl. The ancestor of Sri Lankan *Garra* is estimated to have crossed the Palk Isthmus at around the Pliocene-Pleistocene boundary, ~2.6 Mya. Despite being morphologically conservative, *Garra ceylonensis* represents about five genetically distinct lineages. Although one would expect the population in the Malwathu river to be the basal one (*i.e.,* the one closest to the root of the phylogenetic tree of *G. ceylonensis* populations, given that any fish dispersing to Sri Lanka must necessarily enter via this river), it is in fact the southern population that is basal. This, and other evidence suggests that the species had been extirpated from most of Sri Lanka, but persisted in a refuge in the island's south, probably in the Nilwala basin.

This basin hosts other morphologically conservative species, such as *Systomus pleurotaenia* (see Figures 4.11, 5.22, 5.25), which in the same river have individuals reflecting deep genetic divisions. What then, caused the extirpation of *Garra* in most of Sri Lanka? We think it was most likely aridification. Given that *Garra* now persist even in parts of the dry zone that have a strongly seasonal climate and receive as little as 1.2 m of rain annually, we can infer that Pleistocene aridification event/s must have been much more severe. If so, it could explain many features of Sri Lanka's fish fauna. For example, why the island has so few families, genera and species compared with the Western Ghats—or even Peninsular India in general. It may also explain why the island has so few rheophilic fishes—species adapted to life in fast-flowing waters. Although five freshwater-fish genera in Sri Lanka occur in fast-flowing waters (see Table 5.4), all are abundant also in slow-flowing waters. At least 22 genera of fishes exhibiting rheophilic adaptations inhabit mountain streams in the southern Western Ghats, however (see Table 4.1), and all these are absent from Sri Lanka.

Recent phylogeographic studies have also added to our understanding of the fishes of the dry zone, which occupies more than two-thirds of Sri Lanka's land area. Previous studies had shown the dry zone to host a uniform fish fauna: the same species are found in one basin after another. But we are coming increasingly to appreciate that barriers to dispersal exist between dry zone river basins, although we yet do not know what these barriers are. The giant snakehead (*Channa marulius*) in the northern dry zone, for example, is both genetically and morphologically distinct from that in the Mahaweli (*Channa ara*) (Figure 1.8). Given the dry zone's topographically level landscape, in which the waters of adjacent river basins mingle during the year-end monsoon rains, what has kept such species apart?

Then there are the populations of *Pethia melanomaculata* and *Laubuka lankensis*. These species contain genetically-distinct 'haplogroups' representative of the north-western dry zone (Malwathu and Kala basins), the Mahaweli, and the eastern drainages (Gal, Kumbukkan, Menik basins), which are not shared between the regions. These and other examples demand that we pay new attention to Sri Lanka's topographically and floristically 'uniform' dry zone plains (see Table 2.1 and Figure 2.11 for details of rivers).

Studies by Sudasinghe and colleagues showed that species hitherto considered to be critically endangered narrow-range endemics, such as *Rasboroides rohani*, are no more than undocumented introductions of a widespread species, *R. pallidus*

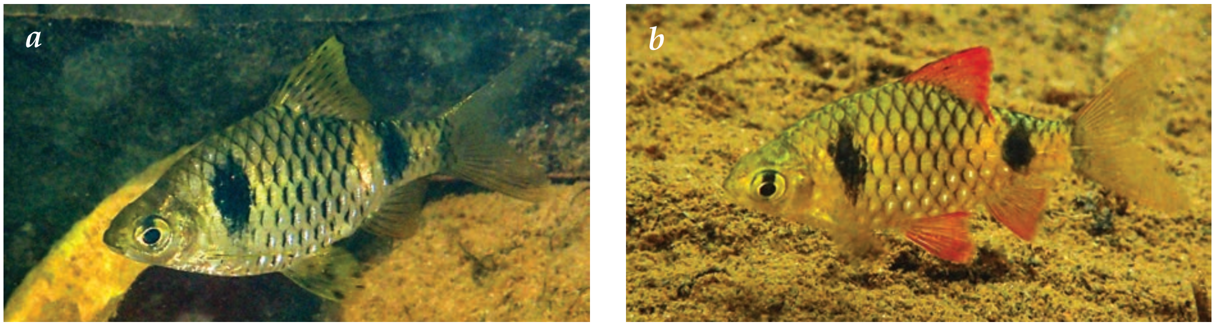

Figure 1.10. ***a,*** *Pethia cumingii,* and ***b,*** *P. reval,* a species-pair that appear to have diverged only recently (see Sudasinghe *et al*., 2021c).

(Figure 1.9). Even in cases where such introductions have been documented, such as the translocation of *R. pallidus* and *P. reval* to Ginigathena in the 1980s, our work has, four decades later, helped identify the origin of the founder populations.

Perhaps the most tantalizing result from these studies was the discovery that the dwarf snakehead, *Channa orientalis*, in fact comprises a pair of genetically distinct but morphologically indistinguishable species. One of these ranges through the wet zone lowlands, from the Kalu to the Nilwala basins, while the other occurs in the Kelani, Attanagalu and Kalu basins and also, unexpectedly, in the upper Mahaweli basin.

Although phylogeographic studies in Sri Lanka are in their infancy, such studies across other taxa clearly offer rich pickings. For example, using fishes as a baseline, future workers could investigate the phylogeographic structure of other organisms,* especially aquatic ones such as paludomid molluscs, parathelphusid crabs and atyid shrimps, which have different life-history patterns. Just as important, this work shines new light not just on species but also on populations, many of which carry unique genetic signatures. These deserve conservation attention in their own right, not only when differences are expressed in morphology, warranting recognition as 'species'.

In a paper published earlier this year (2021), Sudasinghe *et al.* show, for example, that *Pethia reval* and *Pethia cumingii* are genetically quite similar fishes (Figure 1.10). In fact, if not for their dorsal, anal and pelvic fins being conspicuously red and yellow, respectively, and their different geographic ranges, it is unlikely that they would have been considered for recognition as distinct species. Likewise, *Pethia nigrofasciata* and *P. bandula*. While the molecular distance between these two species ranges from 0.8–3.1 percent in the *cytb* gene, that between different populations of *P. nigrofasciata* can be as high as 4.1 percent. Nevertheless, the two species are morphologically distinct. Especially when it comes to conservation, then, we need to pay attention to both species and populations.

This book is a first attempt to draw together the available knowledge on Sri Lanka's biogeography in the context of freshwater fishes, because this is the only group of vertebrate animals for which (albeit partial) data on relationships between Sri Lanka and India, and within Sri Lanka itself, are available. The patterns and processes identified here will probably have wider implications for other faunal and floral groups as they come to be studied, filling the multitude of gaps we have identified in this fascinating story.

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* One such recent study was reported by Wikramanayake *et al*. (2021) who showed the endemic agamid lizard *Ceratophora aspera*, which is confined to the wet zone, to exhibit remarkable phylogeographic structure. There was strong evidence of isolation between even geographically proximal populations, such as those in the southern lowlands, central highlands and Sabaragamuwa Hills, with an estimated divergence between these and the population at Kitulgala prior to ~1 Mya.

SUPPLEMENT 1

Vicariance *vs* Dispersal

The term 'dispersal' is applied in two different ways in the biogeographic literature. In general, all species tend to expand their ranges until constrained by their ecological tolerance: their propagules move away from their parent source to colonize an ever-wider range until limited by an ecological barrier. 'Disperse' is commonly used in reference to this process of range expansion.

When invoked as an alternative to vicariance, however, 'dispersal' involves range expansion through the long-distance movement of propagules across a pre-existing barrier, giving rise to a disjunct distribution (Nathan, 2001; Figure S1.1a,b). Because long-distance dispersal events are stochastic, they tend to be unique and hence rarely amenable to testing. For example, propagules may be carried across marine barriers by rafts of vegetation, the wind, or birds. In this text, for clarity, the latter use is usually qualified as 'long-distance' or 'overseas' dispersal, or used in juxtaposition with 'vicariance'.

Vicariance, by contrast, seeks to explain disjunct distributions by the formation of a new, extrinsic barrier that separates and isolates populations (Figure S1.1c,d). When the Palk Isthmus was emergent and climate was suitable, Sri Lanka's biota was an extension of South India's. However, when the isthmus was submerged or arid, it served as a barrier to the exchange of propagules between India and Sri Lanka, isolating populations on either side. The Palk Isthmus and Strait have thus served as vicariance barriers, and vicariance explains the distribution of lineages shared between Sri Lanka on the one side and India/Asia on the other.

In many cases, especially those involving the fragmentation of Gondwana, the limits of the fossil record and the chronology of tectonic events constrain the accuracy with which phylogenetic divergences can be timed. Therefore, it is not always possible to arrive at a conclusion as to whether present-day disjunctions are the result of vicariance or (long-distance) dispersal (*e.g.*, see Figures S1.2–S1.5, section 4.3.1 for cichlid fishes, 3.3.2 for rhacophorid frogs). In such cases, authors who favour dispersal invoke routes such as land bridges that have since disappeared, while those who favour vicariance wait to be vindicated as plate tectonics and the fossil record improve. Nevertheless, as the rich biodiversity of oceanic island groups such as Hawai'i and the Galápagos testify, dispersal can operate effectively over distances of thousands of kilometres.

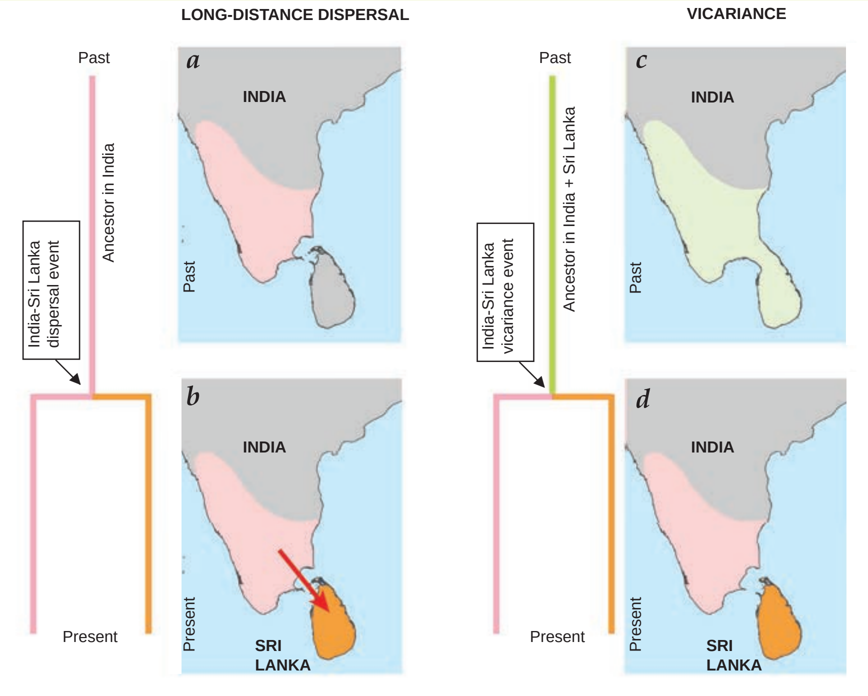

Figure S1.1. Long-distance dispersal *vs* vicariance. ***a,*** A species present in India is absent from Sri Lanka at a time the Palk Isthmus is submerged or too arid for the species to inhabit it. ***b,*** However, a propagule carried to Sri Lanka by a vector such as the wind or a raft of vegetation establishes a population which gradually diverges from the Indian population, from which it remains isolated. ***c,*** A species inhabits both India and Sri Lanka at a time the Palk Isthmus was emergent and habitable. ***d,*** Sea level rises (or the isthmus aridifies), isolating the Indian and insular populations, potentially leading to speciation.

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Figure S1.2. Long-distance dispersal – *Rhipsalis baccifera*, an epiphyte that is the only species of cactus that occurs naturally outside the New World. Though native to tropical America, it occurs in also in Africa, Madagascar, Seychelles, Mauritius and Sri Lanka, all of which are Gondwanan fragments that have been separated by marine barriers since at least the early Paleogene. Though present in Sri Lanka, it is absent from the rest of Asia, including India. The partial overlap of the Indian-Ocean distribution of the species with the East India sailing route since the 16th century suggests that anthropogenic dispersal should not be ruled out. Buxbaum (1980), paraphrased by Cota-Sánchez & Bomfim-Patrício (2010), posited a human-mediated Atlantic crossing, following which "birds may have contributed to further dispersal and the current extensive geographic radiation." The latter authors supported this hypothesis by citing the inability of frugivorous birds to cross the Atlantic Ocean from South America to Southern West Africa. They posited that dispersal of this species into the Old World could be better explained by anthropogenic influence, as a consequence of the East India Route, as proposed by Buxbaum (1980). They allowed, however, that as argued by Renner (2004), marine dispersal may also have played a part in the bizarre distribution of *Rhipsalis baccifera*. The Old-World group, however, comprises three of the six subspecies into which the taxon is divided, together with changes at the chromosomal level (Barthlott & Taylor, 1995: 63; Cota-Sánchez & Bomfim-Patrício, 2010). This suggests dispersal that pre-dates anthropogenic influence. The distribution of this species, therefore, can be explained only within a long-distance dispersal scenario.

Figure S1.3. Vicariance – The burrowing frog *Nasikabatrachus sahyadrensis* (here, in amplexus) belongs to the Nasikabatrachidae, which contains two species endemic to the Western Ghats (Janani *et al.*, 2017). The molecular phylogeny of Biju & Bossuyt (2003) recovered a sister-group relationship between Nasikabatrachidae and Sooglossidae, a family restricted to the Seychelles, with a divergence 131 (95% credibility interval 93–177) Mya. This conflicted with geological evidence that the Seychelles rifted from India ~70 Mya (Chatterjee *et al.*, 2013). The relationships of Sooglossidae had until then been a subject of speculation: while it was known that the Seychelles was a Gondwanan terrane, no Gondwanan anuran lineages showed a close relationship to these frogs. More recently, the phylogenomic study of Hime *et al.* (2021) estimated that Sooglossidae split from Nasikabatrachidae 93–62 Mya, a timing consistent with the Seychelles-India split around the Cretaceous-Paleogene boundary. This suggests that the relationship between the two families is the result of vicariance.

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Figure S1.4. ‘One-sided’ vicariance – ***a,*** The endemic Sri Lankan ‘relict ant’ *Aneuretus simoni,* which is the only surviving member of the formicid subfamily Aneuretinae. ***b,*** A colony of *A. simoni*. The ants nest within twigs on the rainforest floor. Aneuretines are represented in amber from the mid-Cretaceous onwards throughout the Northern Hemisphere. The subfamily diverged from its sister group, the Dolichoderinae, in the mid-Cretaceous (Ward *et al.*, 2010; Lapolla & Barden, 2018). It is today reduced to a single species, *Aneuretus simoni*, known only from scattered mid-elevation rainforest patches in Sri Lanka (Dias & Udayakantha, 2016). The former range of Aneuretinae included Russia and North America, where they are known from Paleocene to Oligocene fossils (Dlussky *et al.*, 2003). They dispersed into the Indian plate when it contacted Asia in the Eocene, dispersed to Sri Lanka, and were extirpated worldwide thereafter, except in Sri Lanka. The only other Asian site from which Aneuretinae have hitherto been recorded is Myanmar, where they are reported from Late Cretaceous amber (Dlussky *et al.*, 2003). The aneuretines then, are unusual in that though they are isolated in Sri Lanka as a result of vicariance caused by the Palk Isthmus/Strait, their endemicity results from extirpation in the remainder of their global range.

Figure S1.5. Multiple long-distance dispersals – *Chamaeleo zeylanicus*, the only Asian member of the Chamaeleonidae. The species is widely distributed throughout the peninsula of India and the dry zone of north-western Sri Lanka, in the region adjacent to the Palk Isthmus. All other members of the family inhabit Madagascar, Africa, Arabia and southern Europe. The sister group of *C. zeylanicus* is comprised of the Arabian chameleons. Although the family has its greatest diversity on Madagascar, to which about half the ~200 extant species are endemic, their phylogeny suggests they rafted there from Africa (Tolley *et al.*, 2013).

Macey *et al.* (2008) posited two alternative scenarios for the transfer of these lizards from Arabia to India. In the first of these, chameleons dispersed from southern Arabia into Laurasia and formed a continuous distribution between Arabia and India-Sri Lanka, followed by extinction in northern Arabia, southern Iran, and western Pakistan.

While the presence of *Chamaeleo* in Yemen adds credibility to this scenario (Tolley & Menegon, 2013: 134), Azevedo *et al.* (2021) caution that Africa-India relationships may be more nuanced. In the case of the, *Plator-Doliomalus-Vectius* clade of flattened spiders (Trochanteriidae), they show that the discovery of a European fossil adds credence to an Asian origin rather than an African one, as previously inferred from phylogencies of extant taxa. While the origin of chameleons is definitively African, such studies highlight the need for caution when making biogeographical inferences regarding disjunct lineages from extant taxa alone.

In the second scenario of Macey *et al.* (2008), India’s northward transit across the Tethys brought it closer to Arabia than previously supposed, with contact or near contact permitting overseas dispersal of chameleons from Arabia to India. They supported this scenario on the basis of overseas dispersal being the only mechanism that explains the exchange of African and Madagascan chameleons (Raxworthy *et al.*, 2002). The discovery of what appears to be a stem-chamaeleonid neonate in ~100 My-old amber in Myanmar by Daza *et al.* (2016), however, hints at a more complex history of the Chamaeleonidae.

The chameleons appear to have arrived in Sri Lanka then, through a complex series of long-distance dispersal events.

2

Ecology

Note. As the ecological literature has grown in the course of the last five decades, the taxonomy of Sri Lanka's freshwater fishes has changed substantially. So that species can be readily identified, we have revised names to reflect the current taxonomy. In some cases, however, it has not been possible definitively to determine the identities of species referred to in earlier texts. The species referred to as *Puntius dorsalis* up to 2008, for example, is now allocated to two species, *P. dorsalis* and *P. kelumi*) (Pethiyagoda *et al.*, 2008a), while the endemic *P. kamalika,* when referenced in the ecological literature, may have been identified as *P. amphibius* or *P. thermalis*. These limitations should be borne in mind when reading this chapter.

2.1 Topography

The topography of Sri Lanka, a 65,610 km^2 'continental island associated with passive margins' in the island classification of Ali (2018), is characterized by three peneplains of erosion (Adams, 1929; Wadia, 1945; Erb, 1984) (Figure 2.1). Centred broadly on the central hills (a fault complex), they occupy the approximate elevation ranges 0–125 m, 125–750 m and 750–2500 m, though a few peaks and valleys within each peneplain may transgress these limits (*e.g.*, Ritigala, 766 m, in the first peneplain, and Pidurutalagala, at 2524 m asl the island's highest peak, in the third).

Several theories have been offered for orogeny in Sri Lanka (Adams, 1929; Wadia, 1945; Vitanage, 1972). In the most widely mentioned scenario (Wadia, 1941; Vitanage, 1972), the peneplains were formed by block uplift[*], the highest being also the youngest, having arisen supposedly as recently as the Pliocene. Wadia pointed to the flat-topped hills, ridges and buttes (isolated hills with steep sides and a relatively level top), especially in Sri Lanka's hill country (Figures 2.2a, 2.3), which suggest a previously elevated topography subjected to subsequent erosion. The streams that drain the third peneplain are characterized by high gradients and granitic substrates, descending to the second peneplain usually via waterfalls or cascades (Figure 2.2). Both Adams (1929) and Wadia (1943) agreed that the alluvia which compose the soils of the first peneplain are the erosional product of the second and third peneplains.

Senanayake (1993) inferred from the absence of marine deposits except in the lower littoral of the first peneplain, that the island has remained substantially above sea level since it, together with the Indian plate, rifted from Madagascar ~90 Mya. This is supported also by the Jurassic fluvial fossils occurring at Tabbowa and Andigama in the island's north-eastern lowlands, which suggest that part of the island to have been close to sea level even then[†] (see 3.9.1).

The orogeny of Sri Lanka's central hills, however, remained poorly understood until relatively recently. Cooray (1984), in his otherwise com-

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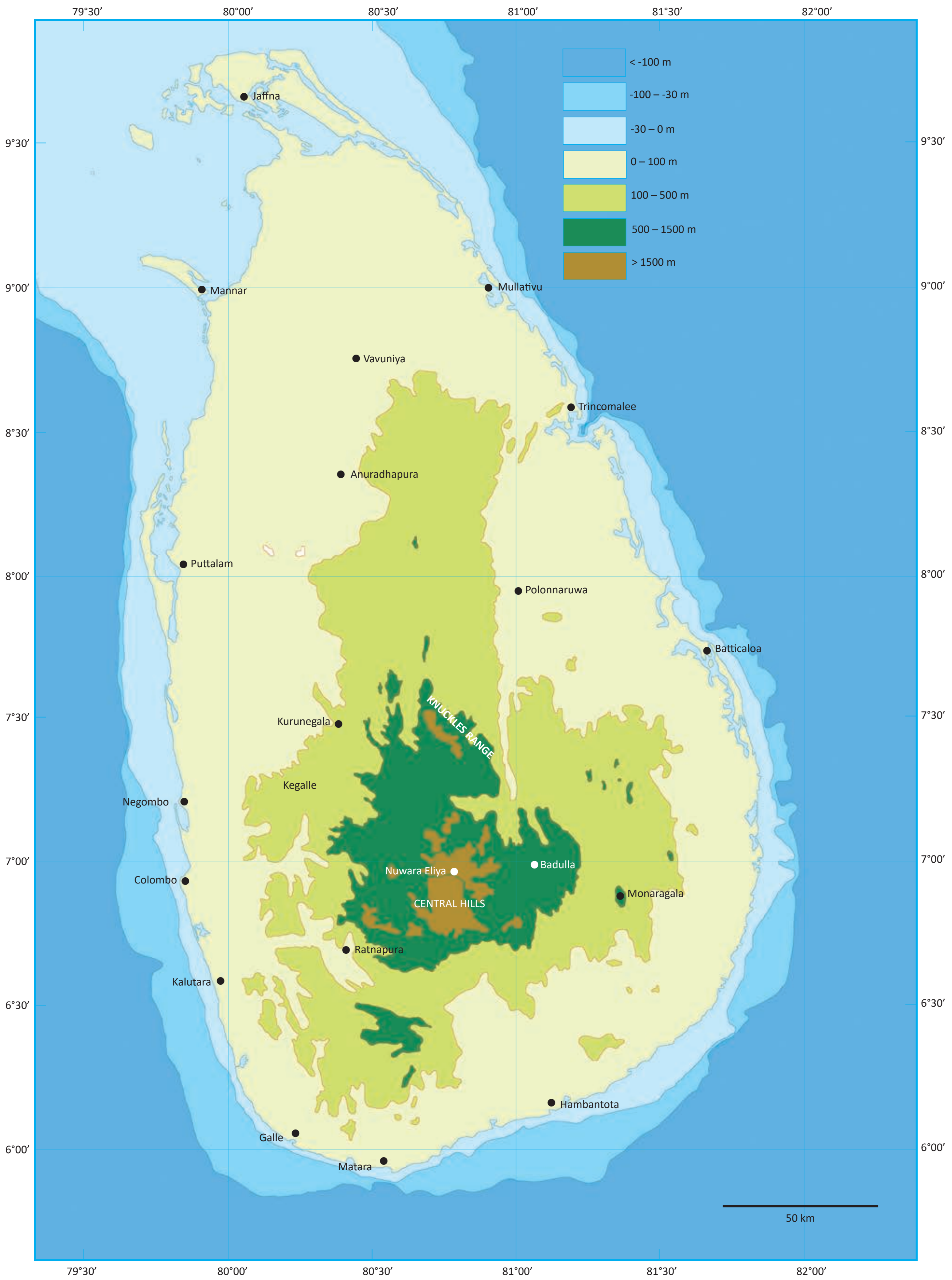
[*] This demands, however, that we treat as coincidence the very similar elevations of the Sri Lankan hills, which rise to 2524 m at Pidurutalagala, and those of the southern Western Ghats: the highest peak of the Nilgiris (Doddabetta) reaches 2637 m, while that of the Anaimalai's (Anamudi) reaches 2695 m and that of the Palanis (Vandaravu) reaches 2533 m, all within a standard deviation of 2.8 percent of the mean elevation of 2597 m. Besides, the southern Indian and Sri Lankan mountains all experience approximately the same rate of denudation (see table 5 of von Blanckenburg *et al.*, 2004).

[†] Eustatic sea level amplitude has, since the Jurassic, varied by more than ±150 m (Miller *et al.*, 2005).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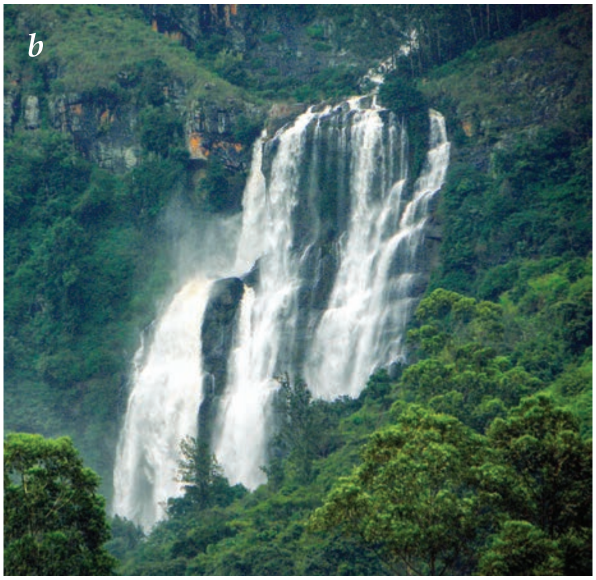
-30 – 0 m
0 – 100 m
100 – 500 m
500 – 1500 m
> 1500 m
Jaffna
Mannar
Mullativu
Vavuniya
Trincomalee
Anuradhapura
Puttalam
Polonnaruwa
Batticaloa
KNUCKLES RANGE
Kurunegala
Kegalle
Negombo
Nuwara Eliya
Badulla
Colombo
Monaragala
CENTRAL HILLS
Ratnapura
Kalutara
Hambantota
Galle
Matara
50 km

Dominic Sansoni

Figure 2.2. The ring of waterfalls around the third peneplain illustrate its sharp ascent from the second peneplain. ***a,*** Laxapana Falls (foreground), Kelani basin, and the Seven Virgins ridge (background; rising to ~1550 m asl, from ~700 m at the foot of the waterfall) ; ***b,*** Bomburu Falls, Mahaweli basin; ***c,*** St Clair Falls, Mahaweli basin; and ***d,*** Galboda Falls, Mahaweli basin.



Buddhika Mawella CC BY 3.0

◄ **Figure 2.1.** Physical map of Sri Lanka, with principal place names mentioned in the text. The 30 m and 100 m isobaths allow inference of the approximate subaerial terrestrial extent during periods of sea-level depression (see Figure 3.63). The 1500 m isohypse indicates the approximate maximum elevation at which native freshwater fishes occur.

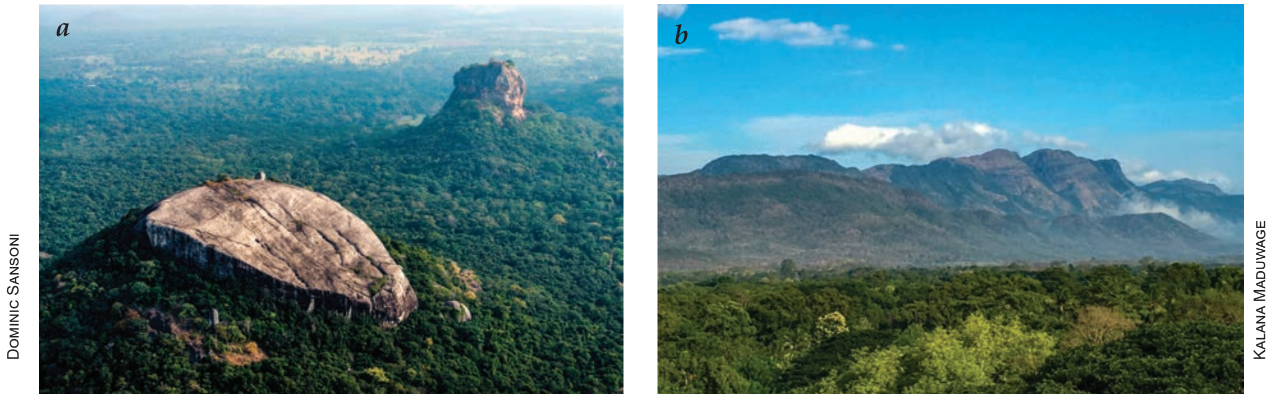


Figure 2.3. ► ***a,*** Pidurangala (foreground), and Sigiriya (background), among the bornhardts or inselbergs that punctuate the mostly flat terrain of the first peneplain. Von Blanckenburg *et al.* (2004) showed the rates of denudation (erosion) of these granitic structures to be exceedingly slow: approximately 5 m per million years. ***b,*** the eastern slopes of the central massif, seen from Loggal Oya: note the flat-topped hills and ridges.

prehensive geology of the island, was indifferent to the genesis of the island's topography: 'These theories of origin do not concern us here.' His dismissiveness is perhaps justified given that in the decades since, little further light has been shed on this problem. Even the orogeny of the Western Ghats, which has been subjected to much closer study, is poorly understood (see Subrahmanya, 2001). These mountains were formed evidently by a regional upwarp of the western margin of the Indian Peninsula, followed by the formation of its western scarp as a sea cliff in the Pliocene, as evidenced by the deposition of coastal sediments (Radhakrishna 2001b; Widdowson, 1997). The origin of the Ghats, however, has been placed in the Late Cretaceous, coincident with the breakup of Madagascar and India (Subrahmanya, 2001), and in the Eocene (Radhakrishna, 2001a), both in the same volume, though Radhakrishna *et al.* (2019) date the mountain chain to the end-Cretaceous.

Sri Lanka is composed of four distinct geochronologically contrasted Proterozoic rock belts which do not share a common premetamorphic history: the Highland, Wanni, Kadugannawa and Vijayan Complexes, fringed to the northeast by extensive Miocene limestone deposits (Milisenda *et al.*, 1994; Mathavan *et al.*, 1999). The upthrust of the Highland Complex is starkest along its southern boundary, manifested in steep ~800 m escarpments such as at Haputale and 'Worlds End' on Horton Plains (Figure 2.4). The boundary between the Highland Complex to the southeast, and the Wanni and Kadugannawa Complexes northwest of it, is not as dramatic except perhaps along the ~30 km long shear zone in the vicinity of Digana, through which the Mahaweli River drains.

Although Wadia's model of recent uplift continues to be cited even now, there is scant evidence to support it. Sri Lanka is now generally accepted as being 'one of the highest stable shield regions in the world' (Emmel *et al.*, 2012), at least during the course of its post-Gondwanan history. The evidence presently available suggests that in the ~130 My since Sri Lanka-India rifted from Antarctica, the island's landscape has been shaped by escarpment retreat and rapid downwearing (von Blanckenburg *et al.*, 2004), rather than uplift or faulting. As these authors point out, no faults have been traced along the base of the Central Highlands or along its scarp zone. Neither is there evidence that the island's north-western limestone region has been uplifted significantly since its deposition during the early-mid Miocene.

Thus, the high relief in Sri Lanka appears to represent 'the remnant of a geomorphic block that was uplifted during rifting at 130 [Mya] or even earlier and that was reduced to the interior of the island by rapid receding of escarpments after continental breakup' (von Blanckenburg *et al.*, 2004). Further, their results suggest a scarp retreat in the central mountains of 125 km in the course of the past 130 My, consistent with the 300 km distance that now separates this region from the Western Ghats.

Figure 2.4. The ~800 m high World's End escarpment on Horton Plains is perhaps the most dramatic example of the steep descents from the Third to the Second Peneplain. The top of the cliff is about 2100 m asl.

2.2 Climate

Sri Lanka's climate is modulated by the South Asian monsoon system, with south-westerly winds from May to September, and north-easterly winds from December to February. In the periods between these dominant seasons, the monsoonal winds converge, resulting in strong convective activity that results in heavy rainfall during the intermonsoons (the first in March-April, and the second in October-November). Cyclonic storms occur over the island in November-December every two or three years. Though explained largely by the north-south drift of the Intertropical Convergence Zone during the northern summer (Figure 2.5), rainfall over the island is mediated also by the Southern Oscillation and the Indian Ocean Dipole. The spatial distribution of rainfall is affected also by distance from the sea and local topography.

Although the island receives a total rainfall of ~12×10^{10} m^3y^{-1}, averaging 1850 $mm\cdot y^{-1}$, there is substantial temporal and spatial variation between regions. The most arid regions, with annual rainfall less than 1.5 $m\cdot y^{-1}$, declining to below 1.0 $m\cdot y^{-1}$ in coastal areas, are in the northwest and southeast (see Figure 2.6). These 'arid zones', are also the most strongly seasonal, receiving almost half their annual rainfall during the second intermonsoon. By contrast, the western slopes of the central hills receive the highest and least seasonal rainfall, more than 5.0 $m\cdot y^{-1}$ in places. In addition to an average rainfall of 2.5–6.0 $m\cdot y^{-1}$, they experience almost no dry season, with even the driest months (January-February) recording more than 100 mm of rainfall[*] (Figure 2.6b). The perhumid 'wet zone'

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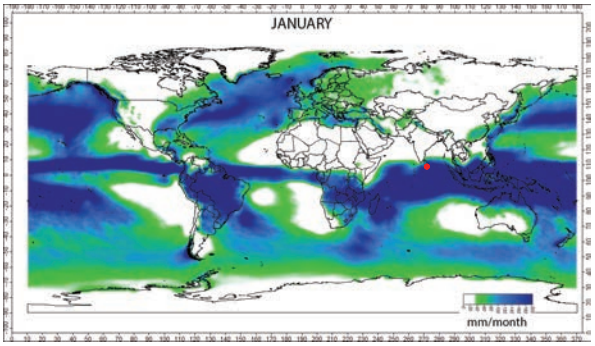
[*] We treat as 'perhumid' a climate in which average monthly rainfall remains above 100 mm during the dry season, which lasts three or fewer months, averting water stress (see also Ashton, 2014; Gunatilleke *et al.*, 2017). This coincides approximately with the region that receives more than 3.0 $m\cdot y^{-1}$ rainfall, indicated in Figure 2.6a.

In the southern Western Ghats too, the highest rainfall is experienced on the western slopes, which harbour evergreen forest, with the forest type becoming progressively more deciduous further eastwards (Kumar 1994; Barboni & Bonnefille 2001). Although the climate of the western slopes is more


JANUARY
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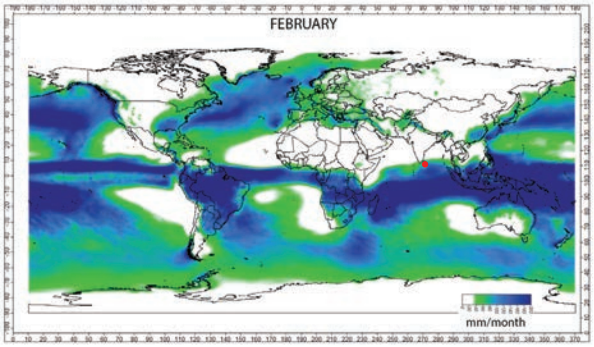
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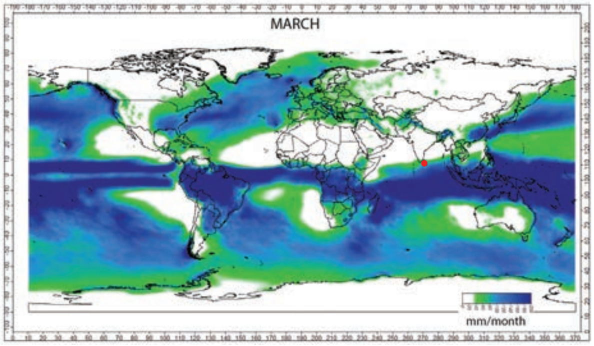
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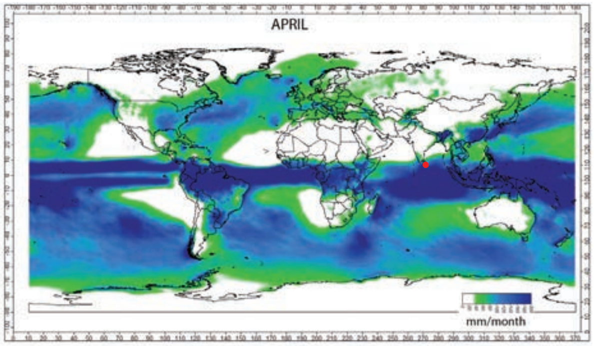
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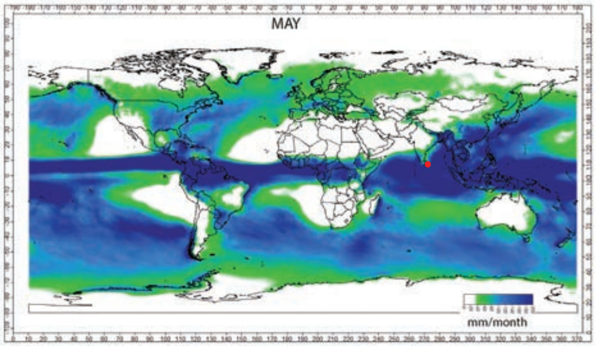
MAY
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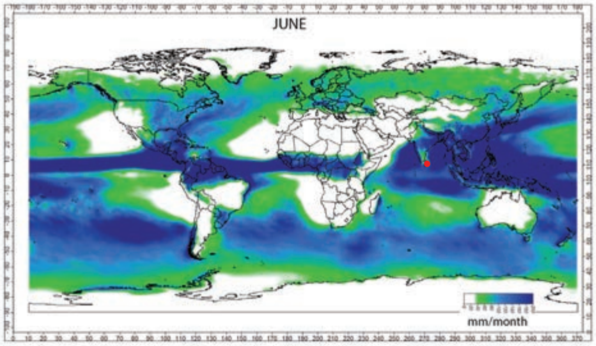
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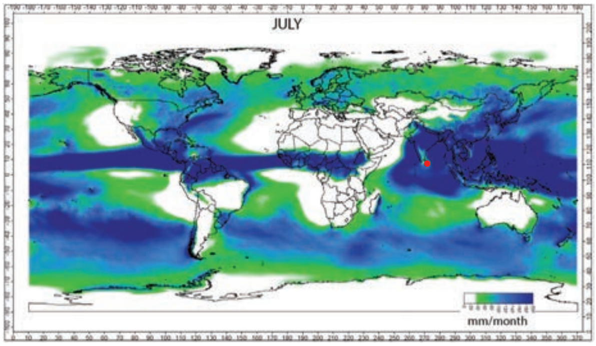
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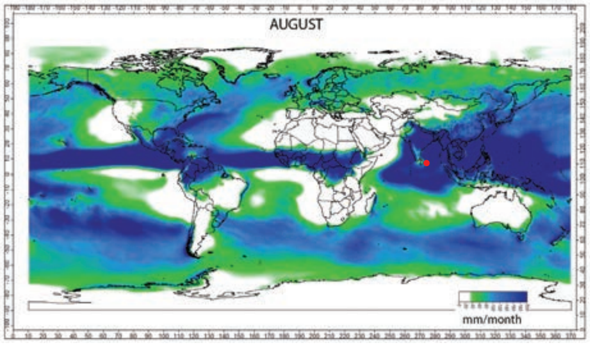
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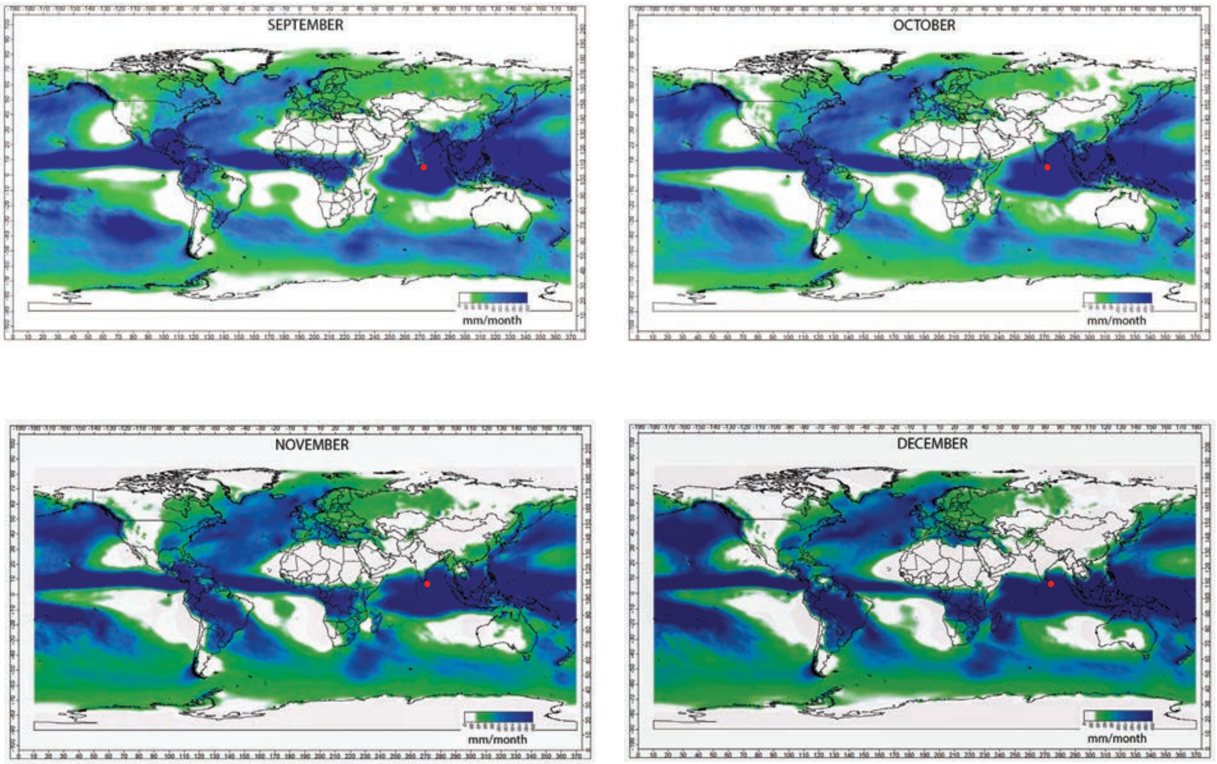

Figure 2.5. Global spatial distribution of rainfall by month. Rainfall over Sri Lanka is correlated with the inter-tropical convergence zone (perhaps more accurately, the annual latitudinal migration of the Hadley cells), the El Niño-Southern Oscillation, the Indian Ocean Dipole, and the island's topography. The red dot indicates Sri Lanka.

of the island's southwest quadrant (rainfall > 2.5 $m \cdot y^{-1}$, Figure 2.6a), which exhibits the least seasonality of any region of South Asia (Ashton, 2014), is characterized by Mixed Dipterocarp Forests*. This is the region described by Gunatilleke *et al.* (2017) as 'an unique phylogeographic oasis in an otherwise seasonal region in South Asia' (*i.e.*, the Indian Subcontinent). By contrast, even the least seasonal part of the Western Ghats, that south of the Palghat Gap, has a dry season lasting 2–3 months (Ramesh & Pascal, 1991).

Additionally, as observed by Somasekaram *et al.* (1988), the southwestern wet zone, and the Namunukula and Rakwana hills, receive roughly equal proportions of their annual rainfall in the four 'seasons': the two monsoons and the two intermonsoons. Similarly, many parts of the higher hills, such as Nuwara Eliya and Horton Plains, receive less than 2000 mm of rainfall annually, but the absence of a prolonged dry season enables them to harbour montane forests ('tropical montane cloud forests': Pethiyagoda, 2012a). This aseasonality is reflected in the remarkably high biodiversity of this region which, together with the south-western lowlands, harbours the preponderance of endemic species, both plant and animal. By contrast, the dry zone contains relatively few endemics though, as Wijesundara *et al.*(2020) point out, it does contain important pockets of angiosperm endemics, including narrow-range endemics. However, only two of 80 freshwater fishes, two of 120

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seasonal than Sri Lanka's wet zone (the dry season lasts up to four months, as against up to three months in Sri Lanka), locations such as Agumbe (13–14°N), may receive as much as 7.6 m of rainfall annually, more than anywhere in Sri Lanka (Dahanukar *et al.*, 2004; Srivastava *et al.*, 2016; Bose *et al.*, 2016; Somasekaram *et al.*, 1988). As in Sri Lanka, in the Western Ghats too, rainfall and aseasonality correlate positively with vegetation-community type and tree-species richness (Pascal, 1982; Barboni & Bonnefille, 2001; Barboni *et al.*, 2003; Joseph *et al.*, 2012).

* Characterized by Dipterocarpaceae and Clusiaceae, these forests occur across perhumid south-western Sri Lanka (Ashton, 2014; Gunatilleke *et al.*, 2006). Elsewhere in South Asia, they occur only on the western slopes of the southernmost region of the Western Ghats.

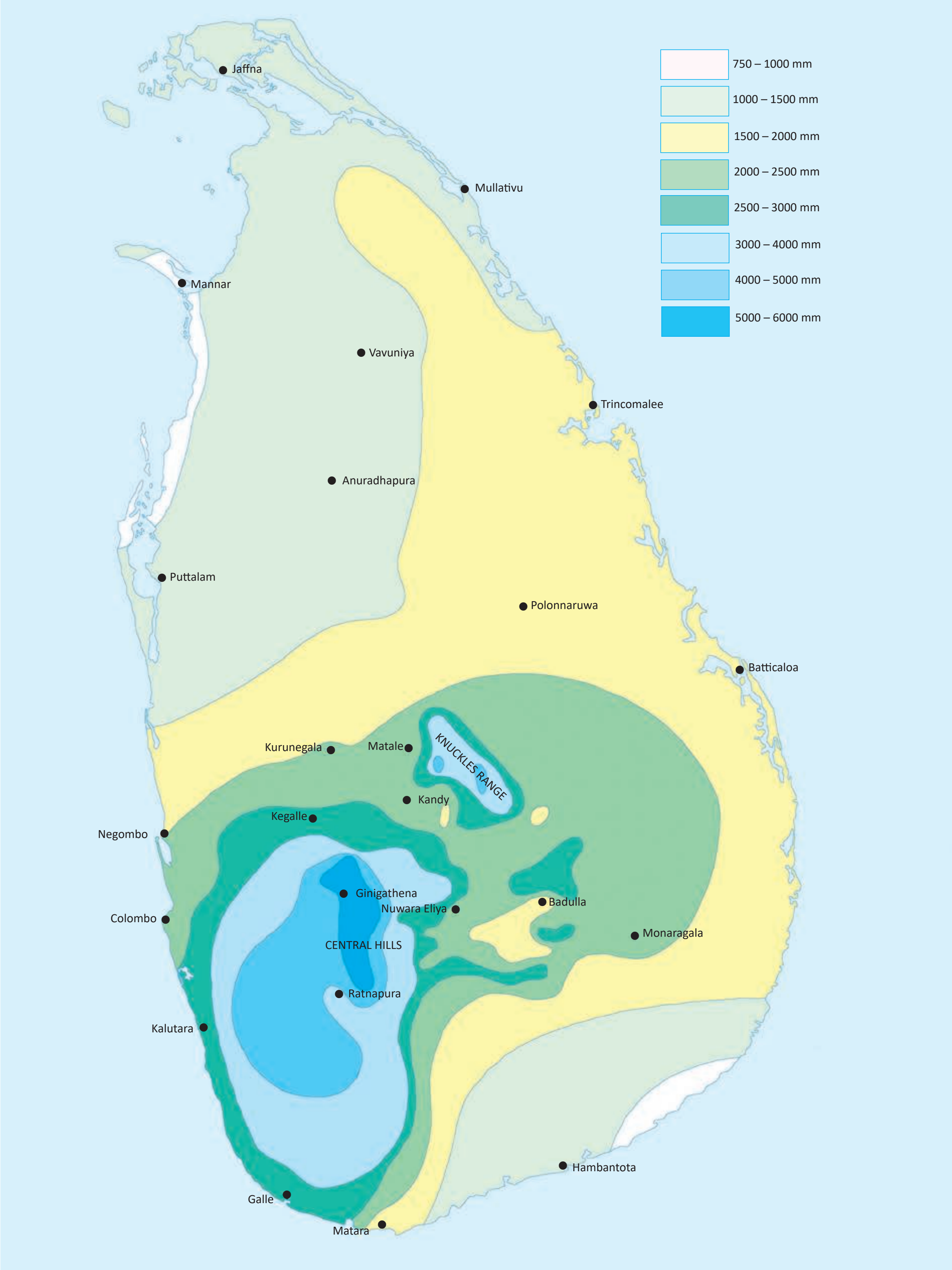
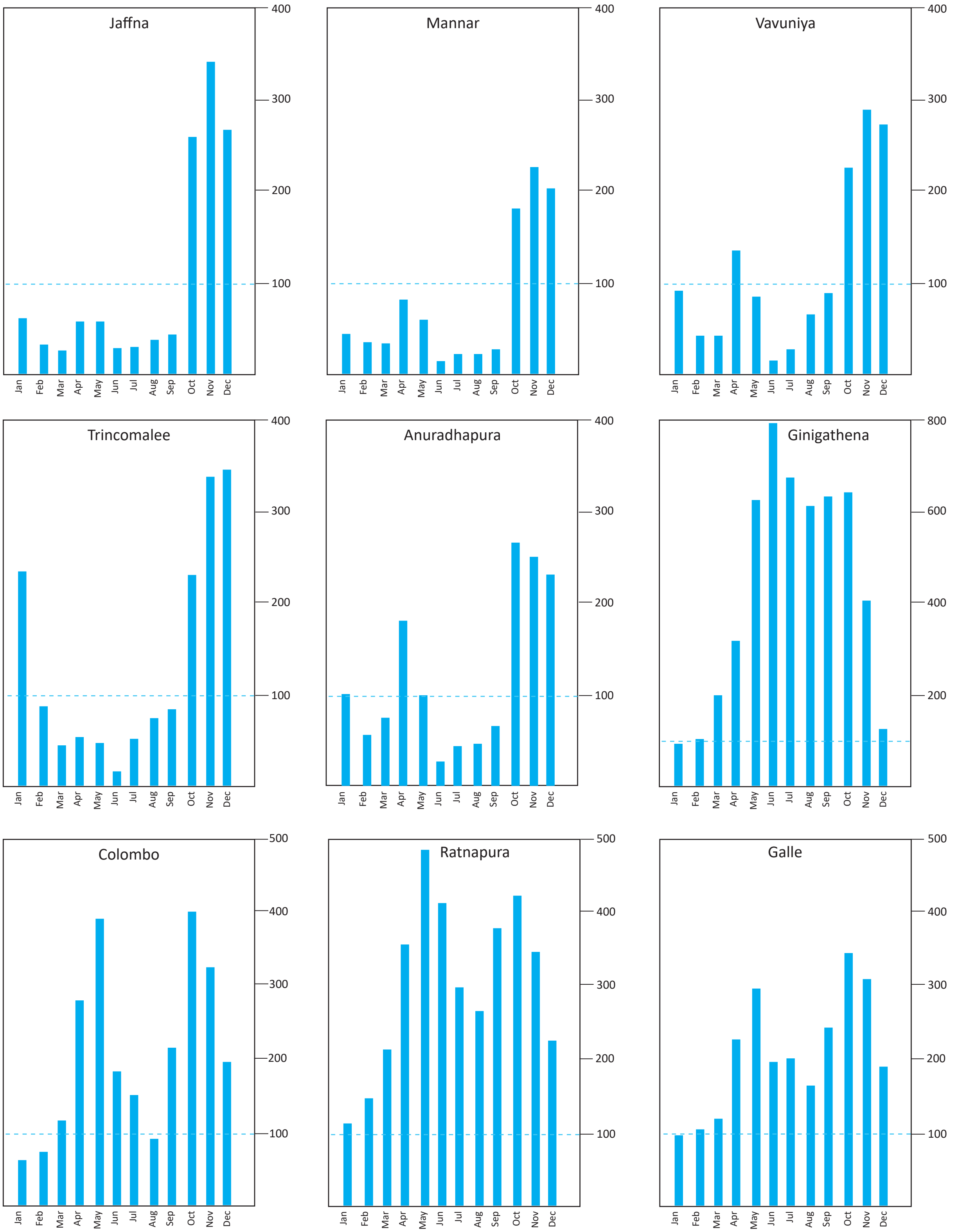


Figure 2.6. ***a*****,** Spatial distribution of rainfall in Sri Lanka. Though the 'wet zone' is usually characterized by the 2000 mm or 2500 mm isohyets, the temporal distribution of rainfall (***b***) is as relevant to the structure of plant and animal assemblages (continued opposite ►).



(◀ Continued from opposite page.) **Figure 2.6 *b*,** Temporal distribution of rainfall: mean monthly rainfall (in mm) at selected locations in Sri Lanka, based on Somasekaram *et al.* (1988). The dotted line indicates the 100 mm level of monthly rainfall; areas that have two or more consecutive months below this limit usually do not support Mixed Dipterocarp Forest.

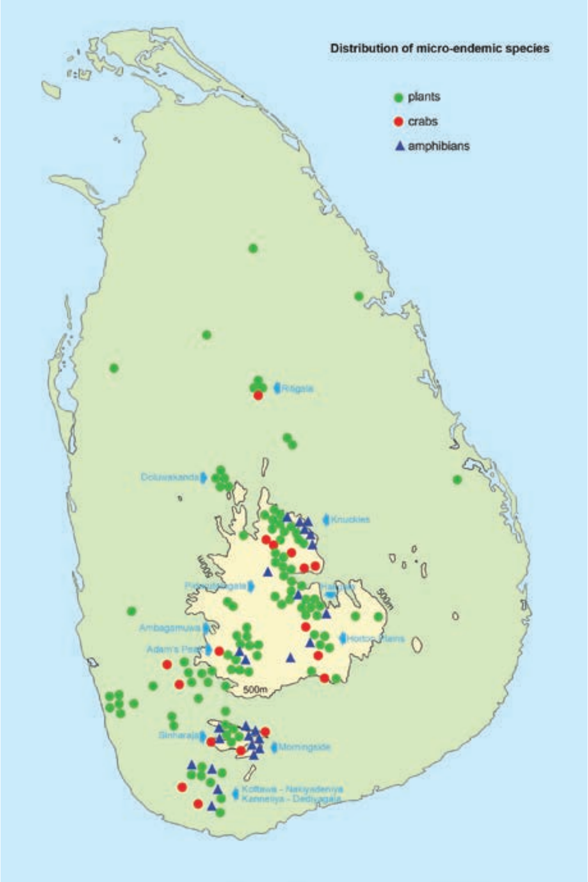


Figure 2.7. Distribution of local endemics among flowering plants, amphibians and freshwater crabs, from Pethiyagoda & Sudasinghe (2017), based on data for plants from Dassanayake & Fosberg (1980–2006) and for amphibians and freshwater crabs from the respective collections in the National Museum of Sri Lanka. As observed by Trimen (1886), at least some local endemics earn this status not because they are naturally restricted to a single locality but because the remainder of their habitat has been lost. In many cases, it is possible also that apparent local endemism is a result of limited or biased sampling.

amphibians, one of 51 freshwater crabs, and one of 61 odonates are confined to the dry zone (see also Figure 2.7). What is more, no endemic mammals, birds or butterflies are restricted to this zone (Warakagoda *et al*., 2012; Yapa & Ratnavira, 2013; Bedjanič *et al*., 2014; van der Poorten & van der Poorten, 2016). As Dias *et al*. (2020) show, though possibly subject to sampling bias, 231 of the island's inventory of 341 ant species (82 of which are endemic), occur in the wet zone.

Mean annual temperature is highest in the island's northern coastal belt, from Kalpitiya to Batticaloa. The diel variation of temperature in the wet zone is around 10° C, falling to about 7° C in the dry zone, while maximum daily temperature in the wet zone lowlands remains mostly in the range 28–33° C. Temperatures in the hill country are lower, consistent with the lapse rate of ~0.65° C per 100 m rise in elevation typical of the tropics (McGregor & Nieuwolt, 1998). Relative humidity remains high everywhere in the island, usually ranging from 70–90 percent.

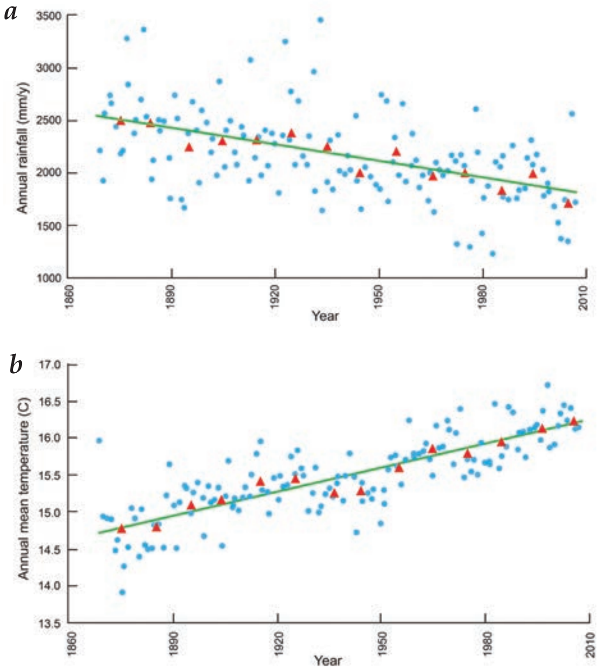


Figure 2.8. ***a***, Annual mean rainfall, and ***b***, annual mean temperature at Nuwara Eliya (1800 m asl) for the period 1870 to 2008, adapted from De Costa (2008). The red triangles represent 10-year averages.

2.2.1 Climate change. Climate change in Sri Lanka has involved starker warming and drying trends at higher elevations than in the low country. At Nuwara Eliya, elevation 1800 m, for example, annual rainfall has declined from about 2.5 m a century ago, to about 1.9 m (Figure 2.8; De Costa, 2008; De Silva & Sonnadara, 2016). The decline in rainfall, of about 5 mm per year (De Costa, 2008), is experienced mainly during the first intermonsoon, which ends the December–February dry period, hence making the climate more strongly seasonal. What is more, the percentage of wet days during the southwest monsoon that follows, has declined from 59 to 47 percent over the past century (Thevakaran *et al.*, 2019). On the western and southern slopes of the highlands, an important region for endemic fishes, while the average rainfall on a rainy day remained steady at around 12 mm during the 20th century, the length of wet spells (consecutive rainy days) has declined from more than 4 days to less than 3 days.

At lower elevations in the southwestern lowlands (*e.g.*, between Ratnapura and Galle), where endemism is highest, however, there does not appear to be a negative trend in total annual rainfall. Here, the southwest monsoon's rainy period (May–July) is gradually becoming longer, while the first intermonsoon (March–April) is yielding less rain, delaying the onset of the rains that follow the December–February dry season (Ahmed & Strepp, 2016).

Meanwhile, average temperatures in Sri Lanka show a rising trend. Annual average temperatures have risen by about 0.8° C over the past century, with temperature in the highlands up by about 1.1° C (De Costa, 2008). The cited studies leave little room for doubt that increasing temperatures across Sri Lanka are correlated with increasing rainfall seasonality, with clear consequences for the island's aquatic habitats.

2.3 Vegetation

For an island of its size, Sri Lanka contains a remarkably diverse and highly endemic flora. Some 3087 angiosperm species (863 of them endemic) and 18 endemic genera[*], in addition to two gymnosperms (one endemic) and 392 pteridophytes (42 endemic) are reported from the island (Wijesundera *et al.*, 2020; Ranil *et al.*, 2020)[†]. The preponderance of species and endemics is restricted to the island's south-western 'wet zone' (rainfall > 2.5 m·y^{-1}), a distribution attributed to species' water economy, edaphic factors and landscape (Gunatilleke *et al.*, 2017).

2.3.1 Wet zone. The wet-zone (rainfall > 2.5 m·y^{-1}) lowlands of the first and second peneplains contain a highly-fragmented matrix of around 1240 km^2 of tropical lowland wet evergreen forests (hereafter 'lowland rain forests'), with ~660 km^2 of tropical submontane forests in the upper regions of the second peneplain (Gunatilleke *et al.*, 2008; see Figure 3.3). The protection of riparian vegetation has led to ~225 km^2 of riverine forest being conserved. The remainder of the island, principally its dry and intermediate zones, contains ~10,000 km^2 of tropical moist evergreen forests and 4500 km^2 of tropical dry mixed evergreen forest (Gunatilleke *et al.*, 2008). In all, natural—even if only secondary or forestry—vegetation occurs on around 19,400 km^2 (~29 %) of the island's terrestrial extent, about half of this being dry monsoon forest.

Ashton & Gunatilleke (1987) recognized 15 floristic regions in Sri Lanka, each with a characteristic flora (see Figure 3.2). Mixed Dipterocarp Forests, their canopy reaching 30–45 m above ground, occur in the least seasonal parts of the southwest quadrant, up to elevations of around 900 m. These lowland rain forests are dominated by the families Dipterocarpaceae, Clusiaceae, Sapotaceae, Bombacaeae and Myrtaceae. *Dipterocarpus zeylanicus* and *D. hispidus* dominate in the lowest (<100 m asl) of these forests, replaced by *Mesua ferrea* and *Shorea trapezifolia* higher up. The subcanopy of these forests is dense, vegetated by species such as *Durio rosayroanus*, *D. zeylanicus* and *Myristica dactyloides*, with *Xylopia championii* and *Garcinia hermonii* dominating the understorey. Large leaves, drip tips on leaves, trees with buttress roots, cauliflory (flowering and fruiting from woody trunks) and high endemicity (>60 % of woody species) characterize this vegetation, in which lianas and epiphytes occur only sparsely (Gunatilleke *et al.*, 2008).

The shallow, heavily shaded streams that flow through these forests, their substrates composed of decaying leaves and detritus, contain most of the island's endemic fishes, and especially the lineages that appear to possess relictual status, such as *Rasboroides*, *Malpulutta* and *Belontia*. The former

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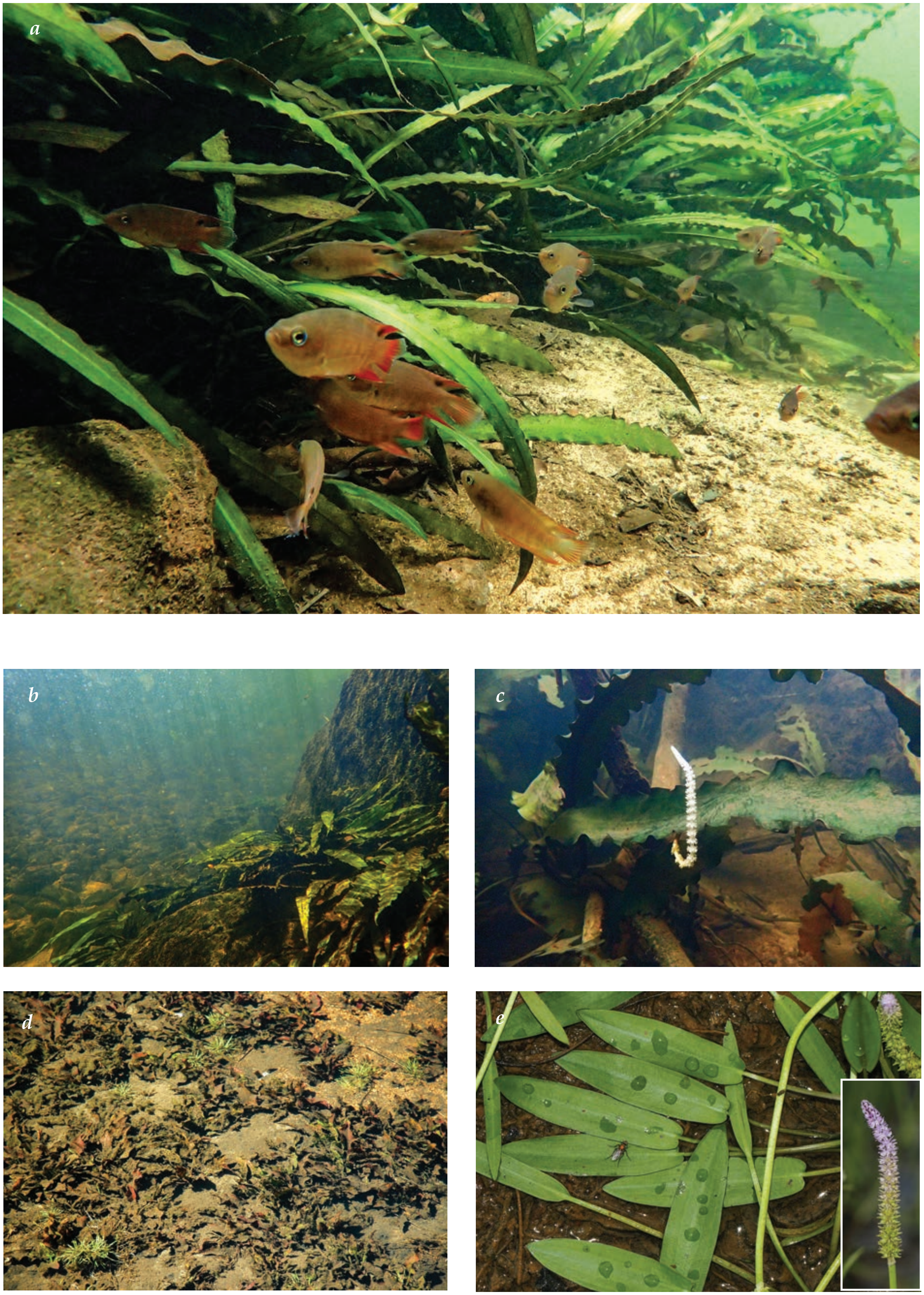
[*] *Adrorhizon* (Orchidaceae), *Championia* (Gesneriaceae), *Chlorocarpa* (Achariaceae), *Davidsea* (Poaceae), *Dicellostyles* (Malvaceae), *Diyaminauclea* (Rubiaceae), *Farmeria* (Podostemaceae), *Hortonia* Monimiaceae), *Kokoona* (Celestraceae), *Leucocodon* (Rubiaceae), *Loxococcus* (Arecaceae), *Nargedia* (Rubiaceae), *Phoenicanthus* (Annonaceae), *Schumacheria* (Dilleniaceae), *Scyphostachys* (Rubiaceae), and *Stemonoporus* (Dipterocarpaceae).

[†] The entire peninsula of India, by comparison, has 56, of which 45 are monotypic (Nayar, 1980).



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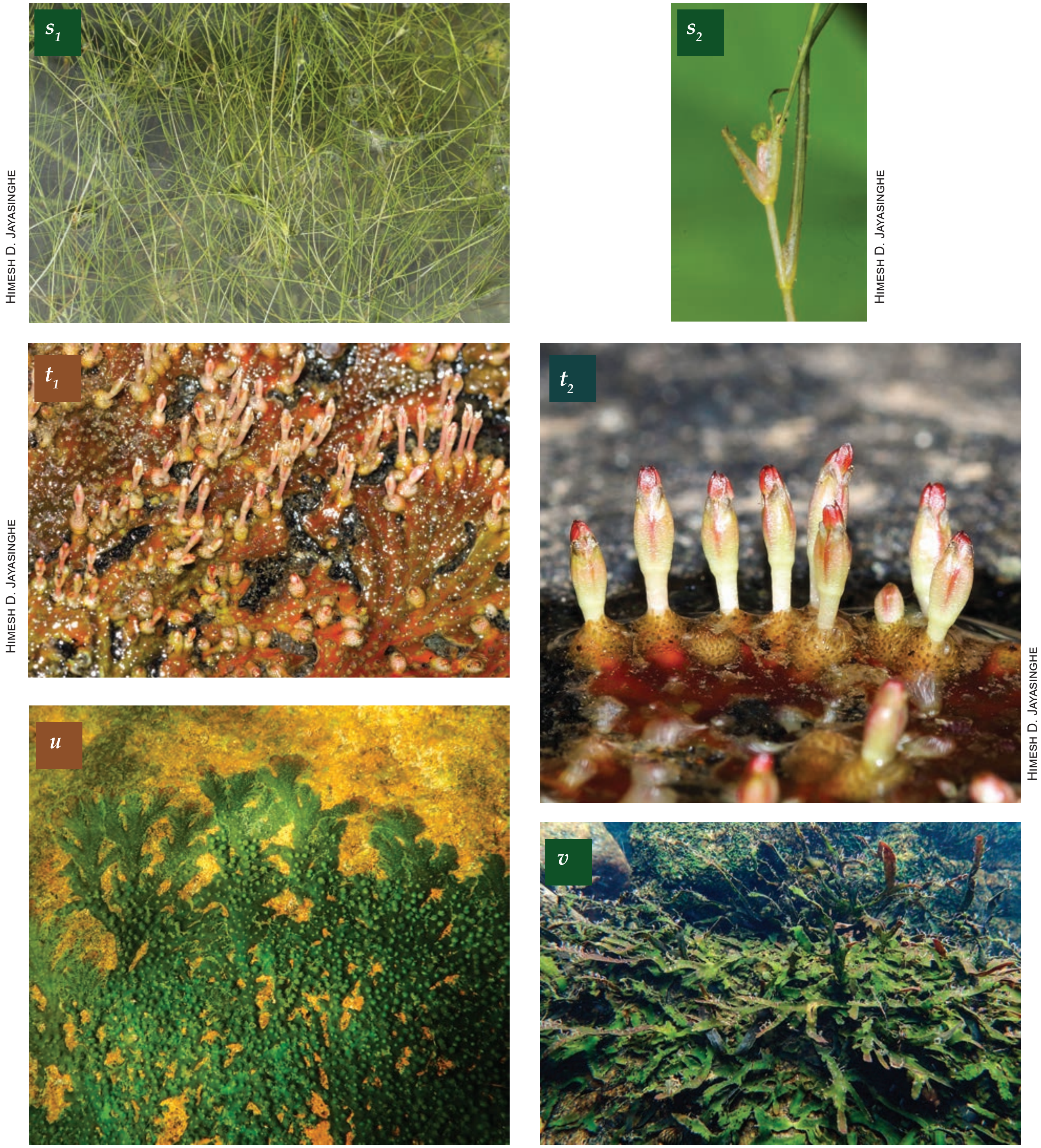

Figure 2.9. A selection of water plants occurring in Sri Lanka. ***a,*** A school of *Belontia signata* patrol a marginal stand of *Aponogeton* sp. (Aponogetonaceae) at Atweltota; ***b,*** *Aponogeton* species at Pahiyangala; ***c,*** *Aponogeton kannangarae*, at Morningside, Eastern Sinharaja: ***d,*** *Aponogeton jacobsenii* at Horton Plains, with light-green clumps of *Isolepis fluitans* (Cyperaceae); ***e,*** *Aponogeton natans*; ***f,*** *Cryptocoryne thwaitesi*; ***g,*** *Cryptocoryne* cf. *undulata*; ***h,*** *Lagenandra praetermissa* (Araceae), perhaps the most conspicuous of the emergent water plants in Sri Lanka's lowland and mid-hill streams; ***i,*** *Blyxa* sp. (Hydrocharitaceae) at Yagirala; ***j,*** *Ceratophyllum demersum* (Ceratophyllaceae); ***k,*** *Nymphoides hydrophilla* (Menyanthaceae); ***l,*** *Limnophila heterophylla* (Plantaginaceae); ***m,*** *Nymphaea nouchali* (Nymphaeaceae); ***n,*** *Blyxa octandra*; ***o,*** *Nelumbo nucifera* (Nelumbonaceae); ***p,*** *Pontederia vaginalis* (Pontederiaceae); ***q,*** *Potamogeton nodosus* (Potamogetonaceae); ***r,*** *Utricularia aurea* (Lentibulariaceae); ***s,*** *Ruppia maritima* (Ruppiaceae); ***t,*** *Dalzellia ceylanica* (Podostemaceae); ***u,*** Podostemaceae cf. *D. ceylanica* at Sulugunė; ***v,*** Podostemaceae sp. at Aranayake.

two appear to be adapted (Helfman, 1981) primarily to such shaded habitats. The aquatic vegetation of these streams too, is characterized by endemism, especially in genera such as *Aponogeton* (six species, four endemic) and *Cryptocoryne* (ten species, all endemic): Dissanayake *et al.* (2007), De Silva *et al.* (2016), Manawaduge *et al.* (2016); Figure 2.9.

Lower-montane forests vegetate the upper region of the second peneplain (900–1500 m). Although still dominated by Dipterocarpaceae (especially localized stands of *Stemonoporus*), Clusiaceae and Myrtaceae, these forests are less lofty (20–25 m) than lowland rain forests. Streams traversing these forests tend to have much higher gradients, however, and may desiccate during the January-February dry season that precedes the rains of the first intermonsoon, especially given the attrition of deforestation. The fish fauna of these streams is reduced to a small subset of common lowland 'open-habitat' cyprinids such as *Devario malabaricus, Garra ceylonensis, Puntius bimaculatus* and *Rasbora dandia*, as well as nemacheiline *Schistura* loaches.

Above elevations of ~1500 m, lower-montane forest transitions to montane forest. The highest hills and ridges contain some 350 km^2 of residual tropical montane cloud forest, some 2000 km^2 of the highlands having been cleared for the cultivation of tea during the colonial era, and European vegetables in post-colonial times (Pethiyagoda, 2007). This is also about the altitudinal limit for indigenous fishes.

2.3.2 Intermediate zone (rainfall 1.8–2.5 m·y^{-1}). Tropical moist evergreen forest with a 25–30 m tall canopy occurs in the transition between the aseasonal rain forests of the wet zone and the tropical dry mixed evergreen forests of the dry zone. Very little of this forest type survives, however, in isolated patches, most notably around the reservoirs of Randenigala and Samanalawewa. The endemicity of the tree flora (17 %) too, is much lower than in the wet zone, though the common trees—*Filicium decipiens, Dimocarpus longan, Nothopegia beddomei* and *Gironniera parvifolia*—include the endemics *Mangifera zeylanica* and *Canarium zeylanicum* (Gunatilleke *et al*., 2008).

2.3.3 Dry zone (rainfall < 1.8 m·y^{-1}). The dry zone accounts for around two-thirds of Sri Lanka's terrestrial area and contains three-quarters of the island's forest extent (Ranagalage *et al.,* 2020). The tropical dry mixed evergreen forests of this zone account for just over half of Sri Lanka's remaining forest over (~16 % of the island's land area). With a canopy that often reaches 25 m above ground, these forests are characterized by trees such as *Manilkara hexandra, Chloroxylon swietenia, Schleichera oleosa*, and *Pleurostylia opposita*, with endemic species occurring only rarely. Many of the canopy trees in these forests shed their leaves in the summer (June-August), allowing more light to reach the forest floor and, in turn, grass and herbaceous species to flourish at the onset of the rainy season, before new foliage emerges. Unlike in rain forests, the leaves are generally small, lacking drip tips; the trees branch lower down and possess no buttresses, and epiphytes and lianas are sparse (Gunatilleke *et al*., 2008).

The more arid parts of the dry zone, such as around Mannar and Yala in the northwest and southeast, respectively (Figure 2.6a), contain thorn scrub forests. Thorny shrubs abound, reaching to a height of ~5 m, with the flora shared almost in its entirety with the arid south-eastern plain of India: with rare exceptions such as *Murdannia dimorphoides* (Commelinaceae), almost no endemic plant species occur here.

2.4 Population and land use

Sri Lanka's population as at 2012 was 21.2 million, *i.e.*, a population density of 323 km^{-2}, which is by far the highest among the Global Biodiversity Hotspots (Cincotta *et al.* 2000; DCS, 2015). The annual rate of population growth, while declining, presently stands at 1 percent. Population density in the biodiversity rich south-western 'wet zone' (~15,000 km^2) is about double the national average, exerting substantial pressure on land and other natural resources.

While several thousand reservoirs ('tanks') have sustained rice cultivation in the dry zone for more than two millennia (de Silva, 1981), the region's population subsisted historically mostly on shifting 'slash and burn'—or swidden—agriculture. The human population density in the dense rain

Figure 2.10. Endemic fishes persist even in such heavily degraded habitats as rubber (***a,*** Waga, Kelani basin: *Puntius titteya, Channa orientalis, Aplocheilus dayi*) and oil palm (***b,*** Nakiyadeniya, Gin basin: *Belontia signata, Aplocheilus werneri*) plantations, and streams in agricultural landscapes (***c,*** Habarakada, Kelani basin: *Channa orientalis, Puntius titteya*) in the wet zone of Sri Lanka.

forests of the wet zone was, by comparison, far lower until the widespread clearing of forest commenced in the mid-19th century, when the colonial administration vested all non-agricultural land with the crown and proceeded to market it to European investors for the cultivation first of cinchona, and later coffee, tea and rubber (Meyer, 1998). Meanwhile, native entrepreneurs had begun deforesting the wet zone's coastal floodplain for the cultivation of coconut and cinnamon. This resulted in the severe fragmentation of the region's forest cover, a predicament exacerbated by a spiraling demand for arable land resulting from the rapid growth of the human population in the post-colonial era. Indeed, even as early as 1880, Sri Lanka's colonial governor, Sir James Longdon, had noted: 'It may without an exaggeration be said that there are no forests left of such value as to require or justify the creation of an expensive Forest [Conservation] Department,' (Meyer, 1998).

Although closed natural forest covered 24 percent of the island's land area until the 1990s (Legg & Jewell, 1995), only an estimated 3.6–4.7 percent of the wet zone was forested even then (Perera, 2001; Forestry Planning Unit, 1995), and this fraction is almost certainly substantially lower now. Of the wet zone's ~16,000 km^2, primary or old-secondary forest accounts for only ~800 km^2 (Forestry Planning Unit, 1995). Even this modest extent of forest exists as several fragments, the largest of which are Peak Wilderness Sanctuary (224 km^2), the Knuckles Reserve (175 km^2) and the Sinharaja World Heritage Site (112 km^2) (see Figure 3.3). The remainder is mostly in the form of some 60 fragments, each of extent less than 500 ha, most of them threatened by encroachment by a land-hungry population. In addition to this 800 km^2 extent of forest, the wet zone contains some 1180 km^2 of secondary and partly harvested forest, mostly at lower elevations (Perera, 2001).

The comparative biodiversity of the two climatic zones is exemplified by the density of endemic flowering-plant species, which in the wet zone is 5.7 per 100 km^2, ~50 times that of the dry zone's 0.11 per 100 km^2 (Gunatilleke *et al*., 2008).

An analysis of gross land use in the island shows 20 percent of the terrestrial extent in sparsely used croplands, 12 percent in homesteads, 16 percent with sparse vegetation (*e.g.,* grassland, scrubland, wetlands) and 27 percent in forest. While 25 percent of the island as a whole is used for permanent agriculture, this is heavily skewed against the wet zone, of which 67 percent is devoted to this land use. The most intensive agricultural use of land is for the cultivation of rice, to which ~6000 km^2 is dedicated. Coconut (4000 km^2), tea (2200 km^2) and rubber (1900 km^2) have the next highest demand for agricultural land, the latter two being entirely

Table 2.1. The 103 river basins of Sri Lanka (see Figure 2.11), with catchment area, gross rainfall and average rainfall within the area of the catchment (based on Somasekaram *et al.*, 1988). Note: the epithets ara, aru, ela, ganga and oya are local-language words for various kinds of waterways.

River	catchment area (km^2)	rainfall volume (10^6 m^3)	average rainfall (m·y^{-1})
1. Kelani Ganga	2278	8692	3.82
2. Bolgoda Lake	374	1080	2.89
3. Kalu Ganga	2688	10122	3.77
4. Bentara Ganga	622	2213	3.56
5. Madu Ganga	59	214	3.63
6. Madampe Lake	90	259	2.88
7. Telwatta Ganga	51	148	2.90
8. Ratgama Lake	10	30	3.00
9. Gin Ganga	922	3039	3.30
10. Koggala Lake	64	127	1.98
11. Polwatta Ganga	233	768	3.30
12. Nilwala Ganga	960	2775	2.89
13. Sinimodera Oya	38	62	1.63
14. Kirama Oya	223	357	1.60
15. Rekawa Oya	755	121	0.16
16. Urubokka Oya	348	738	2.12
17. Kachigal Ara	220	255	1.16
18. Walawe Ganga	2442	9843	4.03
19. Karagan Oya	58	67	1.16
20. Malala Oya	399	434	1.09
21. Embilikala Oya	59	62	1.05
22. Kirindi Oya	1165	1606	1.38
23. Bambawe Ara	79	84	1.06
24. Mahasilawa Oya	13	15	1.15
25. Butawa Oya	38	44	1.16
26. Menik Ganga	1272	1472	1.16
27. Katupila Ara	86	100	1.16
28. Kurunde Ara	131	151	1.15
29. Namadagas Ara	108	124	1.15
30. Karambe Ara	46	53	1.15
31. Kumbukkan Oya	1218	2140	1.76
32. Bagura Oya	92	106	1.15
33. Girikula Ara	15	18	1.20
34. Helawe Ara	51	82	1.61
35. Wila Oya	484	653	1.35
36. Heda Oya	604	967	1.60
37. Karanda Oya	422	676	1.60
38. Saymena Aar	51	82	1.61
39.Tandiadi Aar	22	50	2.27
40. Kangikadichi Aar	56	127	2.27
41. Rufus Kulam Aru	35	77	2.20
42. Pannela Oya	184	415	2.26
43. Ambalam Oya	115	259	2.25
44. Gal Oya	1792	4031	2.25
45. Andella Oya	522	869	1.66
46. Thumpankeni Tank	9	20	2.22
47. Namakada Aru	12	26	2.17
48. Mandipattu Aru	100	223	2.23
49. Pathanthe Aru	100	225	2.25
50. Vett Aru	26	58	2.23
51. Magalavatavan Aru	346	605	1.75
52. Mundeni Aru	1280	2236	1.75
53. Miyangolle Ela	225	362	1.61
54. Maduru Oya	1541	2476	1.61
55. Pulliyanpota Aru	52	84	1.62
56. Kirimechchi Odai	77	123	1.60
57. Bodigoda Aru	164	303	1.85
58. Mandan Aru	13	21	1.62
59. Makarachchi Aru	37	60	1.62
60. Mahaweli Ganga	10327	26804	2.60
61. Kantale basin	445	703	1.58
62. Palampotta Ara	69	111	1.61
63. Pan Oya	143	230	1.61
64. Pankulam Aru	382	594	1.55
65. Kunchikumban Aru	205	329	1.60
66. Pulakutti Aru	20	33	1.65
67. Yan Oya	1520	2269	1.49
68. Mee Oya	90	144	1.60
69. Ma Oya	1024	1510	1.47
70. Churiyan Aru	74	119	1.61
71. Chavar Aru	31	49	1.58
72. Paladi Aru	61	98	1.61
73. Nai Aru	187	300	1.60
74. Kodalikkllu Aru	74	119	1.61
75. Per Aru	374	547	1.46
76. Pali Aru	84	136	1.62
77. Maruthapilly Aru	41	66	1.61
78. Toravil Aru	90	144	1.60
79. Piramenthal Aru	82	132	1.61
80. Netheli Aru	120	164	1.37
81. Kanakarayan Aru	896	1264	1.41
82. Kalavalappu Aru	56	84	1.50
83. Akkarayan Aru	192	261	1.36
84. Mandekal Aru	297	404	1.36
85. Pallavarayankaddu Aru	159	255	1.60
86. Pali Aru	451	637	1.41
87. Chippi Aru	66	107	1.62
88. Parangi Aru	832	1234	1.48
89. Nay Aru	560	630	1.13
90. Malwathu / Aruvi Aru	3246	4592	1.41
91. Kal Aru	210	290	1.38
92. Modaragam Aru	932	1288	1.38
93. Kala Oya	2772	4424	1.60
94. Moongil Ara	44	60	1.36
95. Mi Oya	1516	2175	1.43
96. Madurankuli Aru	62	100	1.61
97. Kalagamu Oya	151	209	1.38
98. Rathambala Oya	215	297	1.38
99. Deduru Oya	2616	4794	1.83
100. Karambalan Oya	589	1095	1.86
101. Ratmal Oya	215	297	1.38
102. Maha Oya	1510	4132	2.74
103. Attanagalu Oya	727	2483	3.42

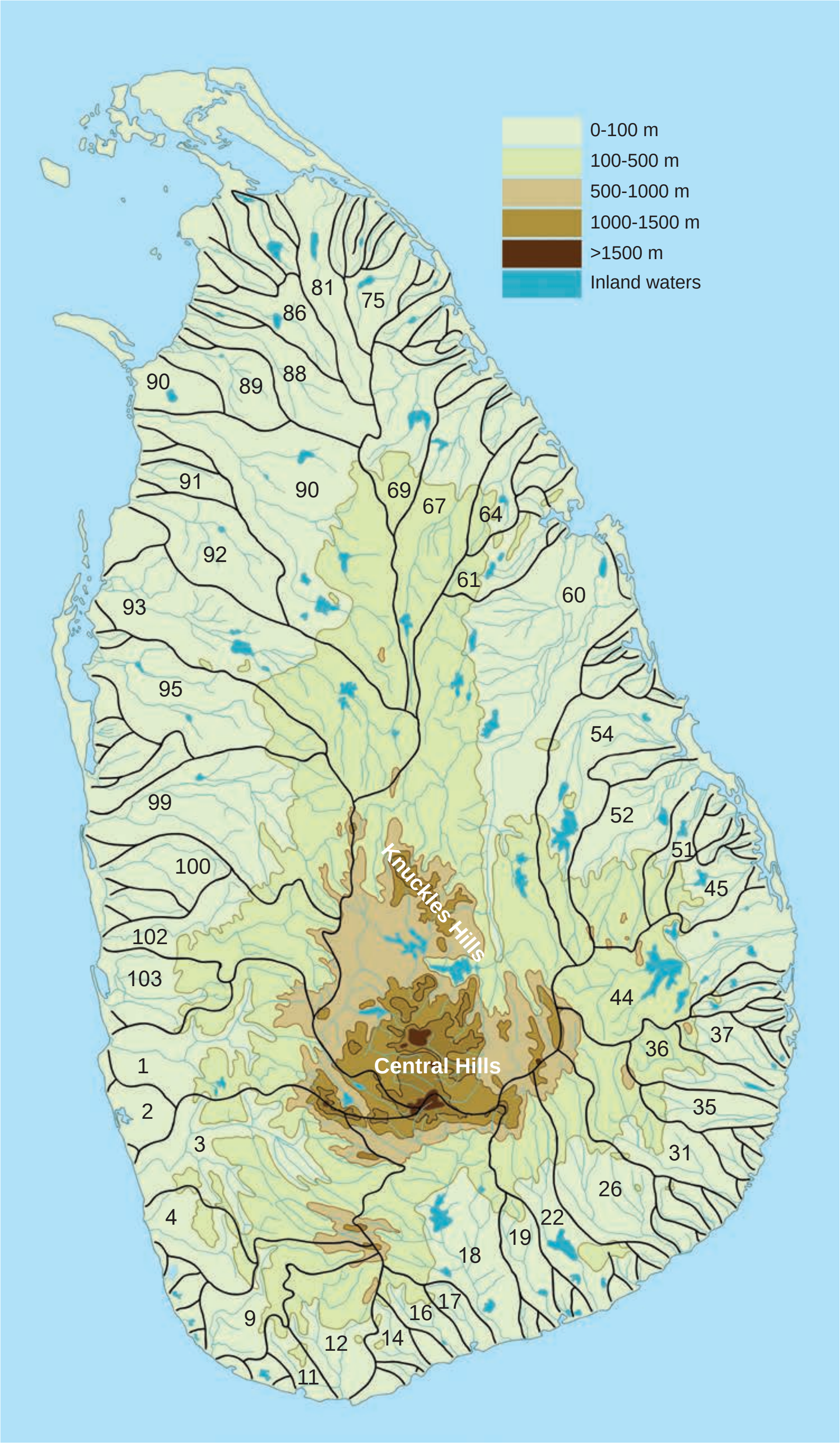

Figure 2.11. The principal river basins of Sri Lanka (see Table 2.1 for list). Black lines demarcate basins.

within the wet zone. Natural (including secondary) forest accounts for 17,300 km², with plantation forests (eucalypts, pines, mahogany and teak) accounting for a further 1000 km². Inland waters potentially inundate some 1160 km² (Ganashan *et al.*, 1996; Mapa *et al.*, 2002; FAO, 2009).

Notwithstanding this, endemic fishes persist—and new ones continue to be discovered—in these severely modified habitats (Figure 2.10).

2.5 Biodiversity

For a shelf island of its size, Sri Lanka hosts remarkable biodiversity (Gunawardene *et al.* 2007). Its floral diversity includes 4086 vascular plant species, 986 of them endemic (Dassanayake & Fosberg, 1980–2006). Diversity and endemism in many groups of terrestrial animals too, is high: 146 of the island's 233 species of reptiles are endemic (Gibson *et al.*, 2020); 51 of 78 freshwater fishes (Tables 5.1, 5.2); 205 of 253 land snails (Naggs & Raheem, 2000); and all 51 species of freshwater crabs (Bahir *et al*., 2005). Endemicity within the more vagile groups, and those able to make short marine transits, in which exchange with the Indian mainland would be expected to have been more frequent, is lower: only 24 of 97 mammal species (Yapa & Ratnavira, 2013); 33 of 482 bird species (MOE, 2012); and 31 of 247 butterfly species (van der Poorten & van der Poorten, 2016), are endemic.

The evergreen forests of the wet-zone lowlands harbour the greatest proportion of endemic plants and animals. For example, while 219 flowering-plant species are confined to the wet-zone lowlands, 104 to the lower montane region and 111 to the montane zone, only 12 and 18 species are restricted to the intermediate and dry zones, respectively (Dassanayake & Fosberg, 1980-2006). There is a high incidence of local-endemism (*i.e.*, taxa recorded from only a single restricted locality), even within these zones, including 115 angiosperm species (Figure 2.7).

Ali & Geiger (2019) compared 'evolutionary maturity' on different islands by means of an 'assemblage lineage-taxonomy spectrum' of taxonomic distinctiveness and diversity of individual lineages, declared as a series of six endemicity metrics. These make it possible for the spectra of similar islands to be compared. See Table 2.2 (p. 41) for application to the squamates of Sri Lanka, Taiwan and Hainan, all of which are continental islands associated with passive margins (Ali, 2018). Colonization of these islands from the adjacent mainland is different in each case, but Sri Lanka clearly has a higher proportion of middle- and high-end lineages in its assemblage spectrum. Concurring with Bossuyt *et al*. (2004), Ali & Geiger (2019) concluded that the reason for this was 'a strong environmental filter impeding transfers between the island and the main subcontinent during the late Cenozoic.'

2.6 The Aquatic Environment

2.6.1 Rivers. Sri Lanka contains 103 river basins, its principal rivers having a combined length of about 4500 km (Figure 2.11; Table 2.1; Arumugam, 1969; Somasekaram, *et al.,* 1988). These discharge some 5×10^{10} m³ (50 km³) of water into the sea annually. Most major rivers that originate in the central hills or the wet zone are perennial. However, most rivers originating in the dry zone—the region served by mainly the north-east monsoon—flow only during the rainy season or, if perennial, are

Figure 2.12. The Belihul River, a headwater tributary of the Walawe River, at Horton Plains. The introduction of rainbow trout to this stream *ca* 1890 perhaps explains the absence of indigenous fishes there.

Figure 2.13. Most endemic freshwater-fish species in Sri Lanka are associated with shaded streams traversing the rain forests of the south-western wet zone: ***a,*** Eratne; ***b,*** Athweltota; ***c,*** Kottawa.

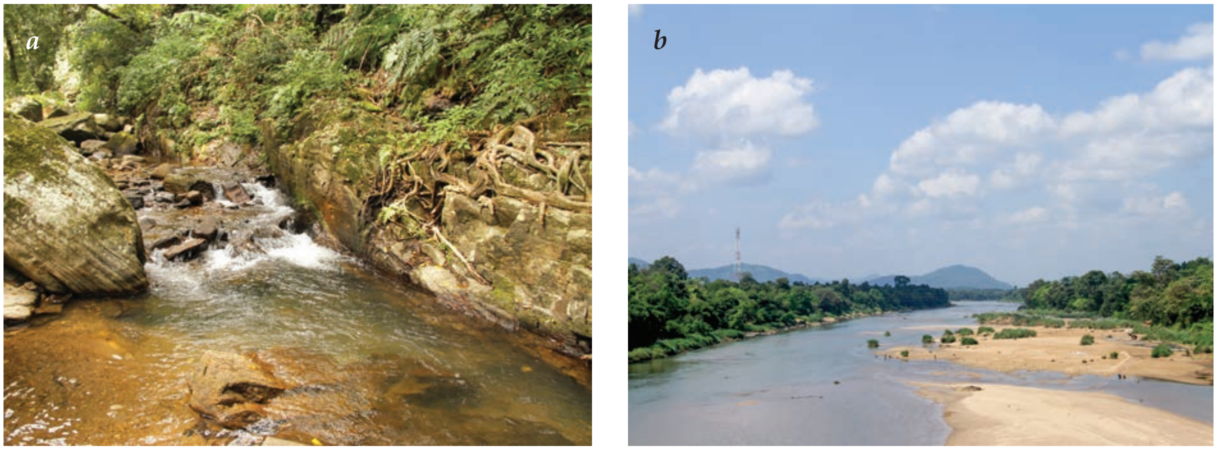

Figure 2.14. ***a,*** The Knuckles Range, separated from the central hills by the ~500 m asl Mahaweli Valley, contains several endemic fish species. Benefitting from orographic rainfall, the Knuckles represents an 'island wet zone' of its own, with a distinctive and highly endemic flora, though the climate is nevertheless more seasonal than that of the island's southwest. Many fishes considered to be confined to the Mahaweli Basin are in fact inhabitants of streams draining the Knuckles. ***b,*** The Mahaweli River, Sri Lanka's largest, traversing the dry zone lowlands near Mahiyangana. The headwaters of the basin derive separately from the central highlands and the Knuckles hills, with the latter, in particular, harbouring several endemic fishes. The mainstream of the river, however, contains almost exclusively the generalized fish fauna of the dry zone plains, together with a few endemics such as *Channa ara*.

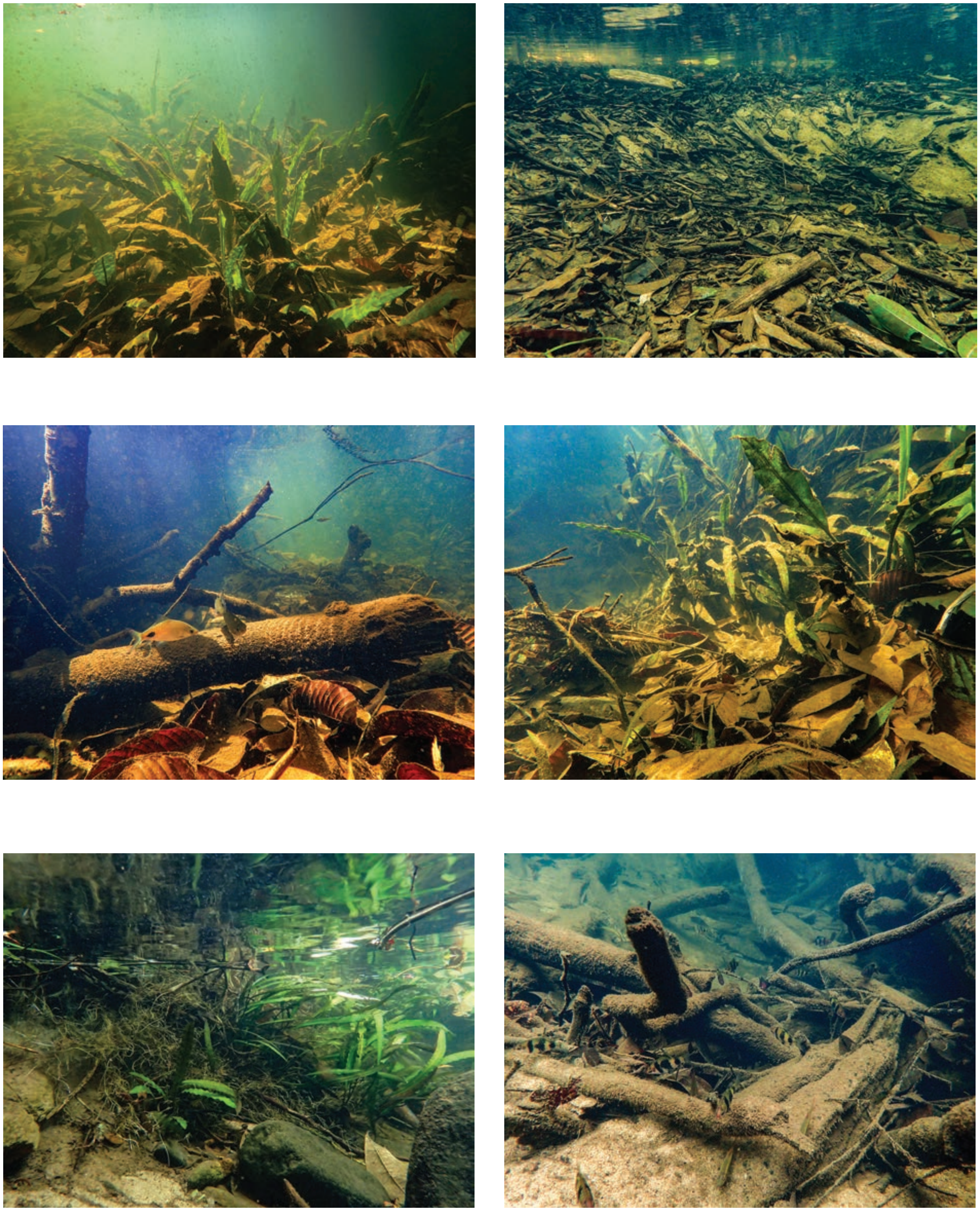

Figure 2.15. The lotic subaquatic environment: shaded or partially shaded streams with slow to moderate flow and a silt substrate, with a mix of leaf debris, submerged roots, aquatic plants such as *Lagenandra* spp. *Aplocheilus dayi, A. werneri,* and *Rasbora dandia* usually occur at the top of the water column, towards the margin, with *Belontia signata* in the midwater region. *Pethia nigrofasciata, Pethia cumingii, Pethia reval, Puntius titteya*, juveniles of *Dawkinsia filamentosa* and *Puntius kelumi* usually remain close to the bottom, while *Mystus nanus, M. ankutta, Ompok argestes, Clarias brachysoma, Channa kelaartii,* and *C. orientalis* are associated with the benthic zone.

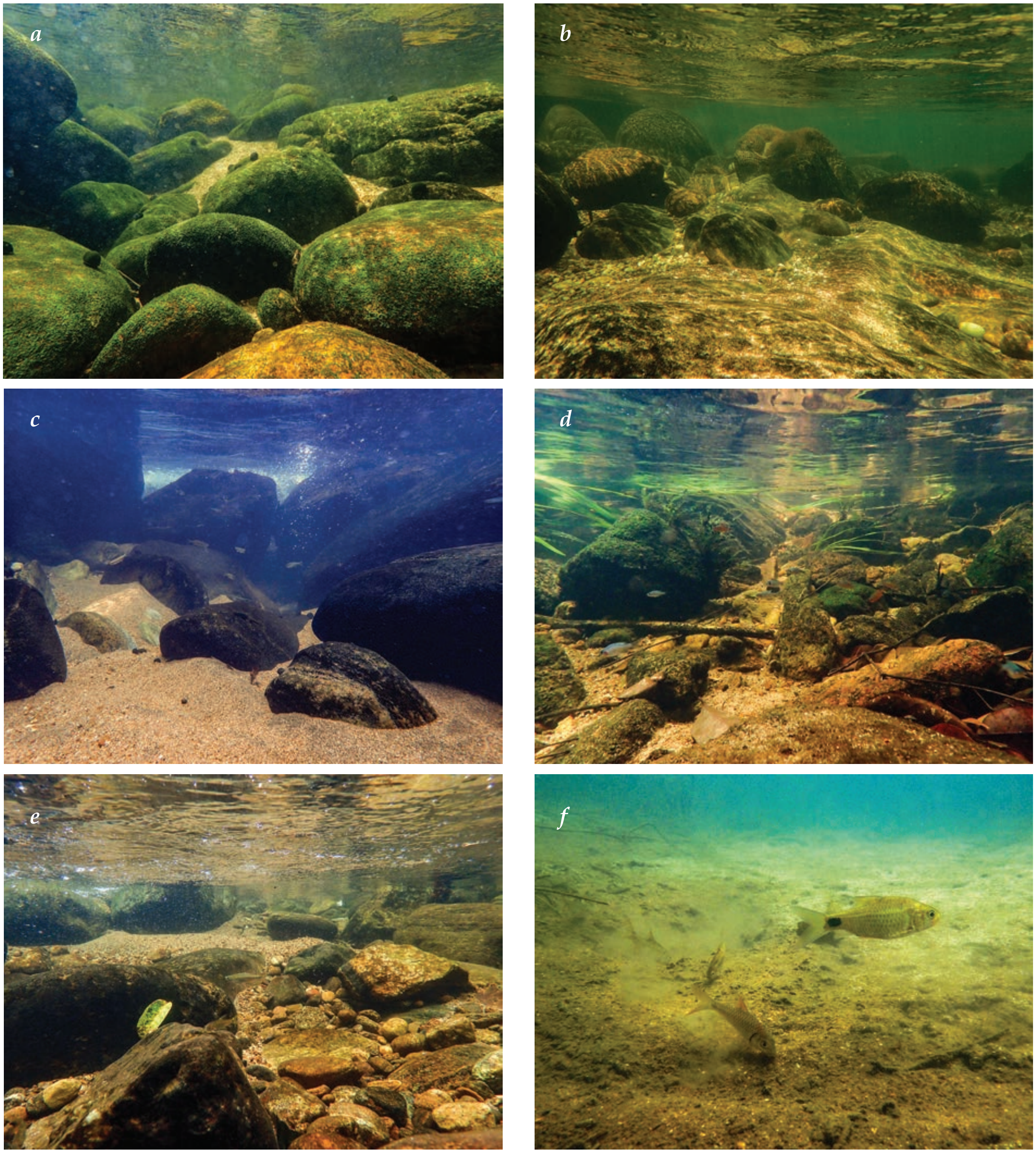

Figure 2.16. The lotic subaquatic environment: ***a–c,*** clear, unshaded or partially shaded, fast-flowing, highly aerated, deep water with a substrate of small to large boulders—both rivers and streams; usually associated fishes include *Devario* spp., *Dawkinsia srilankensis* (Mahaweli), *Garra ceylonensis, Systomus pleurotaenia, Systomus martenstyni* (Mahaweli), *Tor khudree*, and *Mastacembelus armatus*. In the south-western wet zone, sicyidine gobies such as *Sicyopus jonklaasi* and *Sicyopterus* spp. are also encountered in such habitats. ***d,e,*** Clear, unshaded, fast-flowing, shallow water, with a substrate of small to large boulders—usually relatively small streams, associated with *Schistura* spp. and *Devario* spp. ***f,*** Unshaded streams with deep water, slow to moderate flow, turbid, with the substrate being a mix of silt, mud and leaf debris, and with aquatic vegetation along the margins. Species commonly encountered include generalists such as *Devario malabaricus, Esomus thermoicos, Rasbora dandia, R. microcephala* and *Channa striata* (usually at the top of the water-column), *Dawkinsia filamentosa, Puntius dorsalis* and *Systomus sarana* (usually close to the substrate, towards the centre), and *P. thermalis, C. punctata* and *Mystus nanus* (usually close to the substrate, towards the margins).

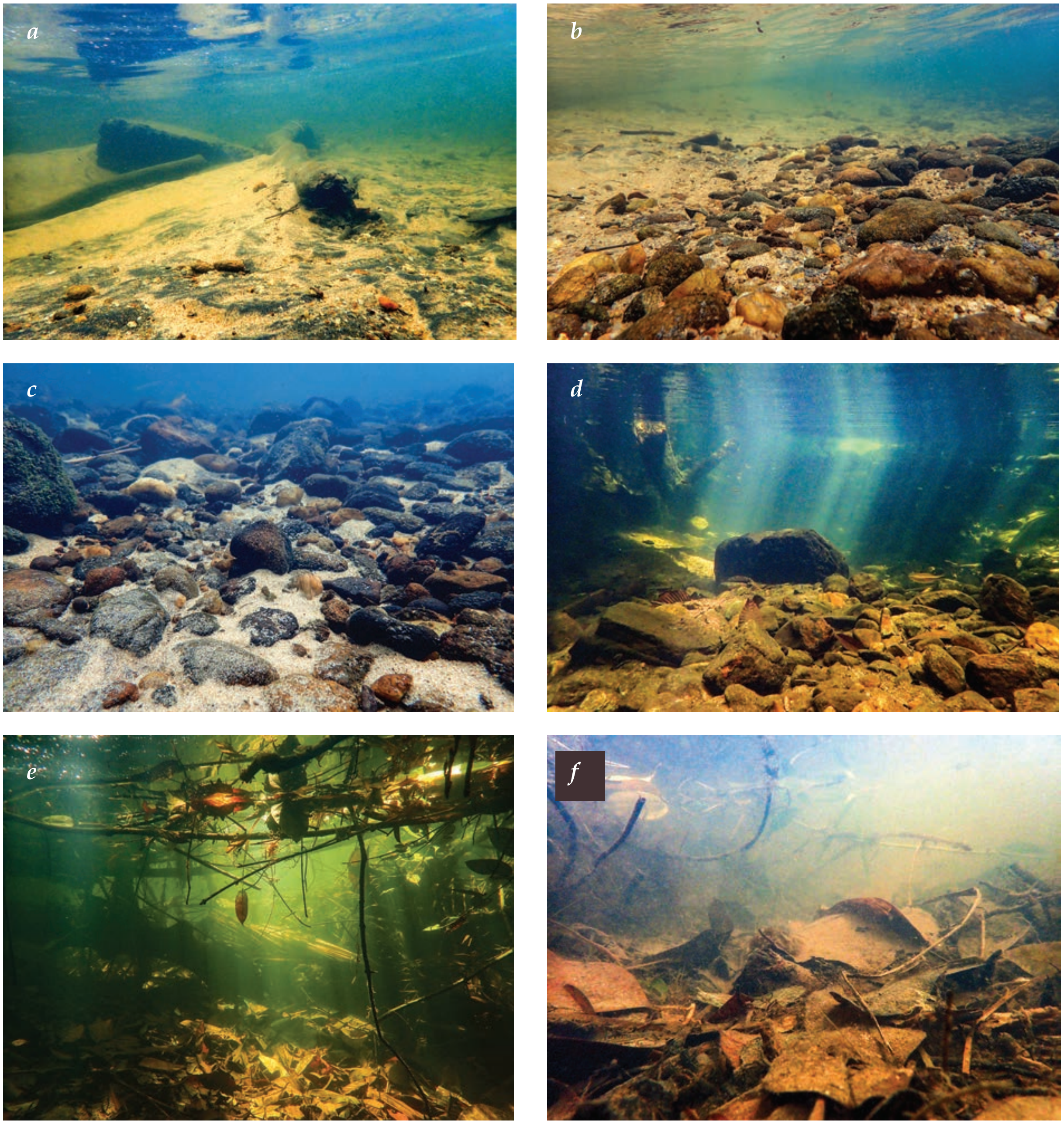

Figure 2.17. The lotic subaquatic environment: ***a–c,*** clearwater, unshaded rivers and streams with moderate flow and a substrate of sand and gravel, associated with *Awaous* spp. and, in the south-western wet zone, less commonly, *Schismatogobius deraniyagalai*. ***d,*** Clearwater, shaded or partially shaded rivers and streams with slow to moderate flow, and a substrate mix of small to large boulders, gravel and leaf debris, frequently encountered in the wet zone. Species commonly encountered include *Devario malabaricus* / *D. micronema* (usually at the top of the water-column, towards the stream centre); *Rasbora dandia, Xenentodon cancila* (usually at top of column, towards the margin); *Dawkinsia filamentosa, Systomus sarana* (usually middle of column, towards stream centre); *Pethia nigrofasciata, Puntius kelumi* (close to the substrate). ***e,*** Slow-flowing, shaded wet-zone rivers and streams with floating vegetation, carpeted with leaf debris on the substrate, a typical habitat of *Rasboroides* spp., towards the margins. ***f,*** Unshaded streams with shallow water, slow to moderate flow, turbid, with the substrate being a mix of silt, mud and leaf debris, and with aquatic vegetation along the margins. In habitats such as this, species commonly encountered include generalists such as *Devario malabaricus, Esomus thermoicos, Rasbora dandia* and *R. microcephala* (usually at the top of the water-column), and *Puntius bimaculatus, P. vittatus, Lepidocephalichthys thermalis, Channa kelaartii, C. punctata* and *Pseudosphromenus cupanus* (usually close to the substrate, towards the margins).

so heavily drained for agriculture that very little freshwater reaches the coastal plain, much less the sea, during the dry season. A curious condition therefore exists in that the dry zone rivers attribute almost 85 percent of their runoff to rainfall in the wet zone. Thus, although the central hills lie within the wet zone, they constitute an important catchment for the dry zone and contribute significantly to its hydrography. Although the dry zone accounts for 70 percent of the island's terrestrial extent, the catchments of the wet zone account for about 65 percent of the island's fluviatile discharge (Arumugam, 1969: Appendix 1).

Several irrigation schemes, some involving trans-basin diversions of water, serve to distribute more evenly—both spatially and temporally—the runoff of the dry zone's rivers. Additionally, many rivers and streams have been dammed to form hydropower and/or irrigation reservoirs. The Mahaweli, at 335 km the island's longest river, for example, has been impounded at seven locations, resulting in reservoirs with a combined surface area of more than 170 km^2 and capacity of 3×10^9 m^3. Rivers and streams representative of the climatic zones and elevations of Sri Lanka are illustrated in Figures 2.12–2.14, and the subaquatic environment in Figures 2.15–2.17.

2.6.2 Flood lakes. Intense and prolonged rainfall often causes rivers to overflow and gives rise to large, temporary flood lakes (Figure 2.19a). These tend to dry up after the rains but are an import-

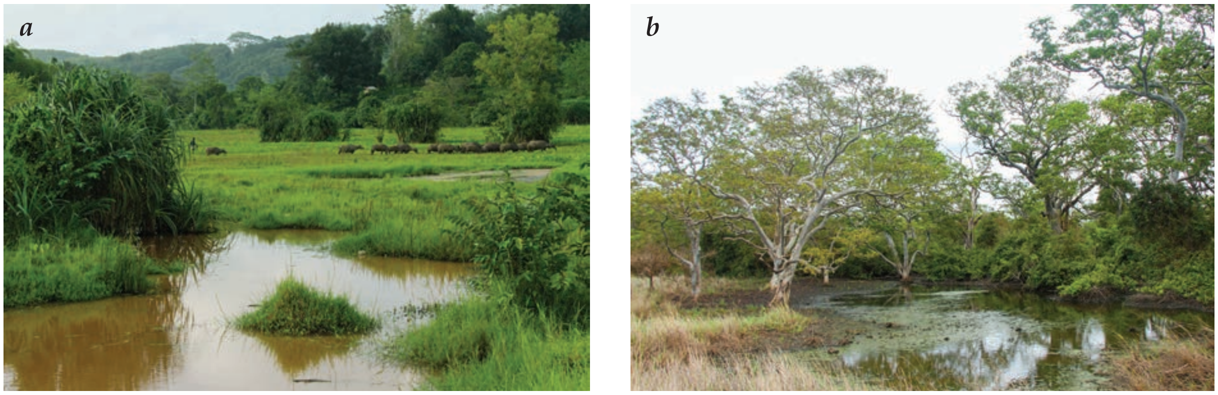

Figure 2.18. Although floodplain pools such as these, at ***a,*** Matugama in the wet zone, and ***b***, Wilpattu in the dry zone may desiccate completely during periods of drought, they nevertheless host a rich fauna of small cyprinids as well as aplocheilids, anabantids, channids, and bagrid and stinging catfishes.

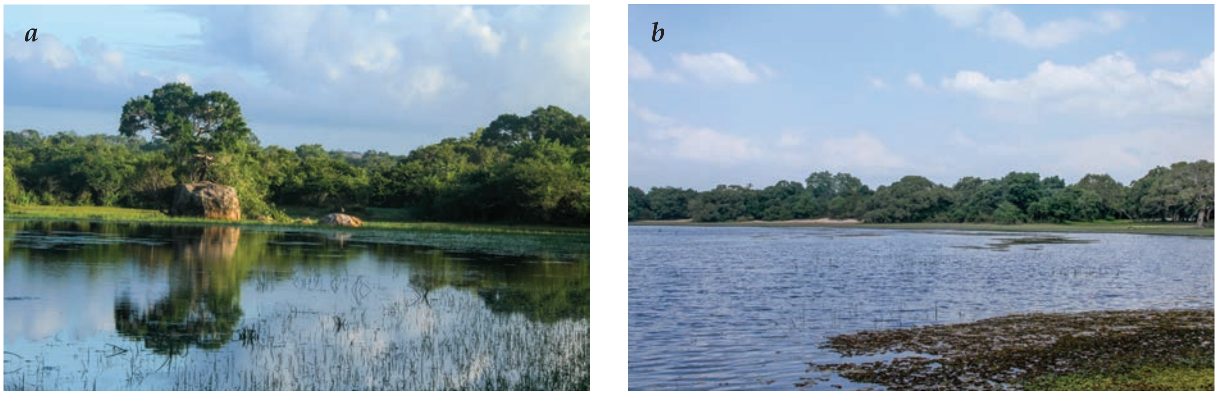

Figure 2.19. ***a,*** Seasonal flood lakes occur in the flat lowlands of the island, now principally in the dry zone (in the wet zone, rice is cultivated in almost all such lowlands). Irrigated by floodwaters from adjacent rivers, these shallow, ephemeral water bodies represent an important breeding habitat for lowland fishes. Such 'open' habitats also provide connectivity between river basins draining to the sea across the coastal lowlands during periods of heavy rainfall. ***b,*** A 'villu' in Wilpattu National Park (1317 km^2), which is served by only a single perennial river. The park's villus therefore constitute an important source of water for its wildlife.

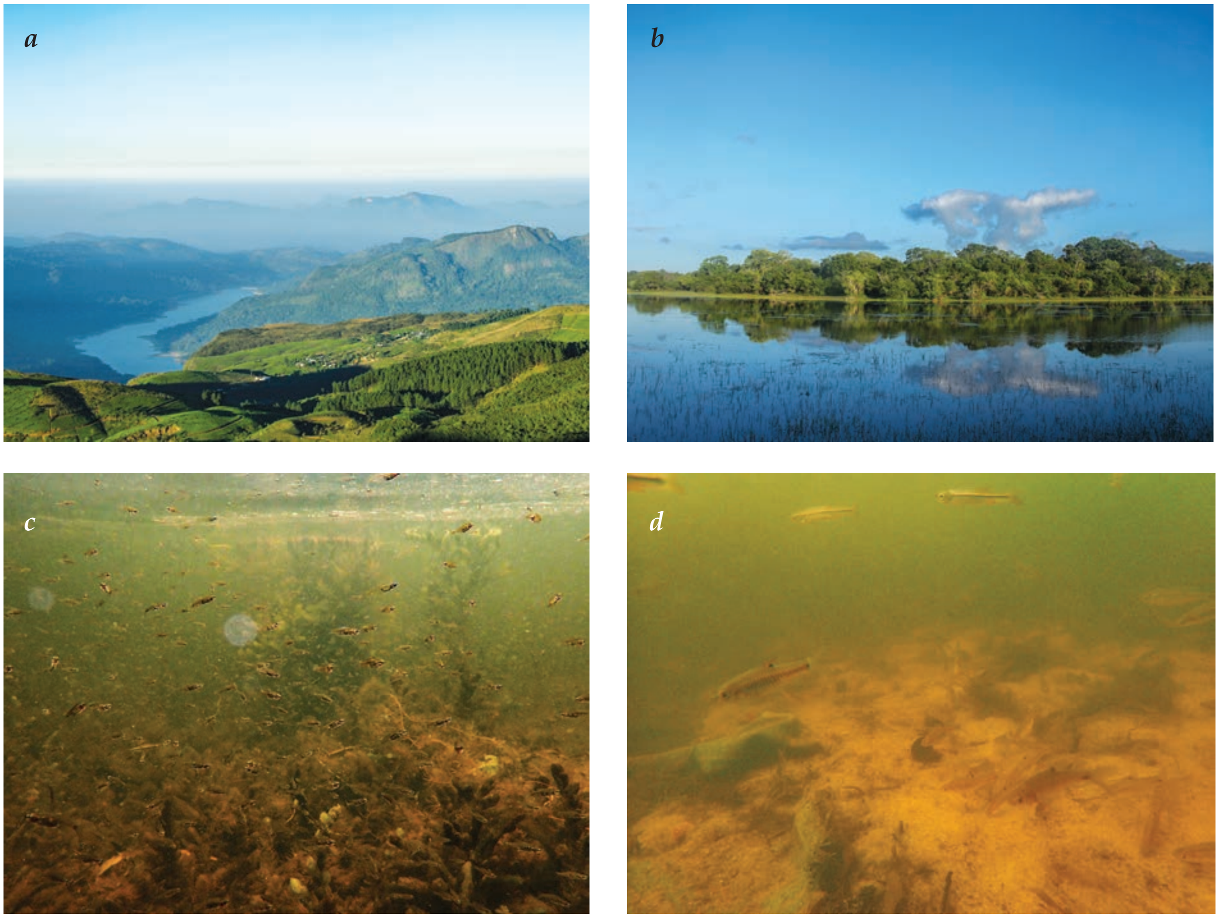

Figure 2.20. ***a,*** The Kotmale Reservoir, one of the many impoundments in the Mahaweli Basin. ***b,*** Some 3000 rainfed reservoirs ('tanks') are scattered across Sri Lanka, especially in the dry zone, supplying water for agricultural and domestic use and helping to tide over the dry months of the southwest monsoon. They are also a key resource for wildlife, ranging from fish to elephants, as is this one, in Kumana National Park. ***c, d*** The lentic subaquatic environment: unshaded, slow-flowing to stagnant, turbid, with the substrate being a mix of silt, mud and leaf debris, and with aquatic vegetation along the margins. In habitats such as this, species commonly encountered include generalists such as *Aplocheilus parvus, Amblypharyngodon grandisquamis, Esomus thermoicos, Horadandia atukorali, Rasbora dandia, R. microcephala* (usually at the top of the water-column), *Dawkinsia filamentosa, Puntius bimaculatus, P. dorsalis, P. thermalis, P. vittatus, Systomus sarana, Lepidocephalichthys thermalis, Anabas testudineus, Channa punctata, Mystus nanus,* and *Pseudosphromenus cupanus* (usually close to the substrate, towards margins).

ant medium for the migration of fishes from rivers to floodwater pools, and the dispersal of fishes between rivers traversing the first peneplain (see also Thayaparan, 1982).

Rice (paddy) fields, which are flooded seasonally with about 30 cm of water, occupy an extent of some ~6000 km^2 in Sri Lanka and serve an ecological role similar to that of flood lakes. Rice is a seasonal crop, a period of about five months elapsing between planting and harvesting (by which time the fields have been allowed to dry down). Fernando (1956b) showed that rice fields regularly host some 24 species of freshwater fishes*.

While these ephemeral water bodies form an important ichthyofaunal habitat, the seasonal nature of the water necessitates fresh stocking each season, usually by the natural process of fish being washed into the fields with irrigation water. The practice of stocking rice fields with commercial varieties of fish, whether for food or ornamental purposes, has not yet found acceptance in Sri

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* The claim by Weeraratna & Fernando (1984) that 'The fish species inhabiting rice fields include almost all the species found in Sri Lanka' is, of course, incorrect.

Table 2.2. Assemblage lineage-taxonomy spectrum of taxonomic distinctiveness and diversity of individual lineages of squamates in three Asian shallow-shelf continental islands: Sri Lanka, Taiwan and Hainan, from Ali & Vences (2019). **LT1**: island lineage comprises a non-endemic species present also on the mainland (such lineages are usually recent and little differentiated from mainland conspecifics) — *e.g., Hypnale hypnale*; **LT2**, island lineage comprises a single endemic species (differentiation could be the result of anagenesis or anacladogenesis *sensu* Stuessy *et al.*, 1990, or the extinction of an insular sister species) — *e.g., Craspedocephalus) trigonocephalus*; **LT3**, island lineage comprises multiple endemic species resulting from *in situ* cladogenesis — *e.g., Cnemaspis*; **LT4**, island lineage comprises an endemic genus represented by only a single species — *e.g., Haplocercus*; **LT5**, island lineage comprises an endemic genus that has diversified into multiple species — *e.g., Aspidura;* and **LT6,** island lineage comprises multiple genera that originated *in situ — e.g., Ceratophora, Cophotis, Lyriocephalus.*

	Sri Lanka	Taiwan	Hainan
Extent (× 1000 km^2)	65	36	33
Depth of isthmus (m)	10	70	40
Distance to mainland (km)	30	130	20
LT1	49	78	88
LT2	16	16	6
LT3	20	5	6
LT4	4	0	0
LT5	5	0	0
LT6	5	0	0

Lanka. The medakas or ricefishes (Adrianichthyidae) commonly associated with rice fields in other Asian countries do not occur frequently in this habitat in Sri Lanka.

2.6.3 Pools. Small pools accumulating in depressions during rains, or charged by springs, are not uncommon (Figure 2.18). These are usually inhabited by airbreathing fishes, such as *Anabas testudineus, Heteropneustes fossilis* and the smaller species of *Channa*, which can tolerate low levels of dissolved oxygen and in some cases disperse overland from one body of water to another. Pools in rivers that have ceased to flow during the dry season are an important refuge for fishes.

2.6.4 Villus. 'Villus' are small lakes of extent up to about 5 ha situated in the coastal plains of the dry zone (Figure 2.19b). They seldom exceed 3–4 m in depth, occur in depressions that have been caused by compaction during seasonal flooding, and are charged by ground water at other times of the year. Many villus retain some water even through periods of drought, although most dry up during the dry season. They are, however, important sources of water for a wide range of fauna. The villus of Wilpattu National Park and Chundikulam Sanctuary are, perhaps, the best-known examples of water bodies of this type.

The water of villus is acidic and contains low dissolved oxygen, resulting in it not being hospitable to most species of fish. Prolonged drought and the consequent drying up of villus also tend to destroy fish life. Thus, the villus do not appear to have developed a distinct ichthyofaunal identity, but usually contain freshwater and estuarine fishes that have been washed in by the flooding of nearby rivers during the rains (Senanayake, 1980; pers. obs.).

2.6.5 Reservoirs. In the seven decades since Independence, extensive irrigation and hydro-power schemes have been completed, resulting in large reservoirs, mainly in the central hills (Figure 2.20a). Many of these contain introduced exotic species of fish, some of which have been found to thrive under local conditions—*e.g., Xiphophorus helleri,* the green swordtail, which occurs in large numbers in the Castlereagh Reservoir and neighbouring streams as a result of an accidental introduction in the 1950s (Pethiyagoda, 1991). Despite persistent concerns for the conservation of endemic fishes in the impounded rivers (*e.g., Labeo fisheri, Systomus martenstyni* and *Dawkinsia srilankensis* in the Mahaweli), there remains a dearth of evidence-based population studies. The available evidence seems to suggest, however, that no fish species have, up to now, suffered population crashes as a result of such hydrological alterations.

2.6.6 Estuaries and lagoons. Several estuarine fishes are able to inhabit fresh water permanently or for extended periods. The tidal influence of many estuaries extends well upriver, often in excess of 10 km, and these areas have an import-

Figure 2.21. Caption on opposite page ►

Figure 2.21. Apart from the fishes, the freshwater crabs (***a–d***) of Sri Lanka (Gecarcinucidae) are perhaps the best known group of aquatic animals, with 51 species in seven genera (*Oziotelphusa, Spiralothelphusa, Perbrinckia, Ceylonthelphusa, Mahatha, Clinothelphusa* and *Pastilla*), all but the first two of which are endemic, with the south-western rain forests and hill country harbouring the preponderant majority of species (Bahir *et al.*, 2005). Freshwater shrimps (***e,*** *Caridina:* Atyidae and ***f–h,*** *Macrobrachium:* Palaemonidae) are ubiquitous, but their diversity remains to be assessed. Spiders of the pisaurid genus *Dolomedes* (***i, j***) too, forage underwater, as do the larvae of a minority of Sri Lankan amphibians (***k,*** *Ichthyophis,* Ichthyophiidae), though among metamorphs only one, *Lankanectes* (see Figure 3.14), is known to feed underwater (Pethiyagoda *et al.*, 2014). The freshwater gastropods were most recently reported to comprise some 38 species (Starmuhlner, 1974; Peiris *et al.*, 2015), 12 of them *Paludomus* (Paludomidae) (***l, m***), in addition to two bivalves. Although mayfly nymphs (***n***) occur commonly in the gut of freshwater fishes, little is known of the diversity of Ephemeroptera in Sri Lanka; the Baetidae remain the only well-explored family (Müller-Liebenau & Hubbard, 1985).

ant, independent ichthyofaunal and ecological identity. Lagoons can on occasion have a higher concentration of dissolved minerals than sea water, and this too, results in specialized ecological characteristics. Many small rivers flow into the sea through large, brackish-water lagoons (*e.g.*, 25 km long, 10 km wide, at Puttalam). The present treatment, however, is limited to hololimnic fishes and hence omits estuarine species which occur in freshwaters only adventitiously. Nevertheless, as Sudasinghe *et al.* (2018b) report, even large cyprinids such as *Labeo heladiva* frequent stretches of rivers that lie within the tidal influence.

2.6.7 Wet zone coastal swamps. The coastal swamps of the wet zone have been recognized as valuable habitats, mainly in respect of their vegetation and avifauna (Pinto, 1986). These swamps contain a mix of 'open water' species associated with the coastal floodplain: no fish species show evidence of specialization to this habitat (Nalinda, 1988). These coastal marshlands usually contain mainly brackish-water fishes, although freshwater taxa such as *Aplocheilus*, *Ophichthys* and *Pseudosphromenus* too, occur in them. Less saline areas contain most of the freshwater fishes that occur in the coastal plain.

2.6.8 Hot springs. A collection of fishes made in 1827 allegedly from the thermal springs at Kanniyar, near Trincomalee, by the French explorer August-Adolphe-Marc Reynaud, who recorded the water temperature as 50° C, included both freshwater and marine species: *Lepidocephalichthys thermalis* (Cobitidae), *Puntius thermalis* (Cyprinidae), *Esomus thermoicos* (Danionidae), *Fibramia thermalis* (Apogonidae), *Ambassis thermalis* (Ambassidae). Deraniyagala (1932a) found no fishes in the springs themselves, but recorded *L. thermalis* and *Channa kelaartii* some 30 m downstream, where the water-temperature was 36.5° C (the water-temperature at the source of the springs was 41° C; more recently, Premasiri *et al.*, 2006, recorded a source temperature of 42° C). In any event, no fishes have been reported from the springs since Renaud's initial collection, which seems to have been made from around the tidal influence in a stream in the vicinity of the hot springs, and not from the springs themselves.

2.6.9 Tanks. Sri Lanka lacks perennial natural lakes. Man-made reservoirs comprise the vast majority of the island's inland lentic water bodies (Figure 2.20b). There are some 3000 such tanks* —mostly in the dry zone—intended primarily for the irrigation of rice fields, ranging from 2 ha to more than 80 km^2, totaling an area of some 1700 km^2. A vast majority of tanks is in the dry zone. The irrigated-agriculture civilization of the Anuradhapura and Polonnaruwa periods of Sri Lankan history, 400 BC onwards, resulted in the construction of reservoirs in the dry zone (the oldest recorded large tank being Tissa Wewa in Anuradhapura, with a surface area of 240 ha and a water storage capacity of about 3.7×10^6 m^3, constructed by King Devanampiya Tissa, *ca* 250–210 BCE). While some of these are dams across small rivers, most are earth-filled embankments less than 10 m high, constructed to trap rainwater in shallow depressions. Many of the smaller tanks dry up completely during periods of drought.

Piet & Guruge (1997) found that at Tissa Wewa (mean depth 1.2 m, maximum depth 2.6 m), the Secchi-depth transparency was 130±18 cm, with a diel variation in dissolved oxygen concentration of 6.8–7.7 mg·l^{-1} and a maximum difference of less than 0.4 mg·l^{-1} between bottom and surface.

Although these tanks today form an important refuge for fishes, they have not existed continuously for long enough to have developed a peculiar ichthyofaunal identity: they contain species found also in rivers (Silva & Davies, 1986). Nevertheless, some tanks such as Parakrama Samudraya host abundant populations of fishes such as *Ehirava fluviatilis* and *Hyporhamphus limbatus*, which are almost never recorded from rivers. Given that the dry zone's rivers often desiccate during the annual dry season, the tanks of this region are in effect 'inundated jungles' (Schiemer & Hofer, 1983) that serve as an important refuge for fishes. Today, however, they are dominated (in biomass) by exotic species introduced for the inland fishery (Fernando & de Silva, 1984). Silva & Davies (1986) showed also that the near absence of larval indigenous freshwater fishes from tanks suggests that

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* These reservoirs continue to be referred to as 'tanks', probably an Anglicization of the Portuguese *tanque*, a holdover from that country's colonization of Sri Lanka's coastal districts (1506–1658).

these water bodies are not suitable spawning or nursery habitats for native species.

2.6.10 Water Quality. The quality of surface water in Sri Lanka was discussed by Costa & Starmühlner (1972), Weninger (1972), Radda (1973), Costa (1980), Starmühlner (1984). The water of hill streams is usually slightly acidic (pH 5.8–6.4), soft (0.25–1.5° DH), cool (20°–25° C in daytime) and except during heavy rains, clear. These conditions change as the river approaches the coastal plain, with the water becoming more alkaline, harder and warmer. In streams traversing south-western rain forests, Geisler (1967) found hardness to be in the range 0.19°–1.07° DH, while pH ranged from 6.17–6.68.

In our experience, almost all Sri Lankan freshwater fishes can be reared successfully in an aquarium of soft (<1.5° DH), clear, pH-neutral water in the temperature range 24°–28° C.

2.7 The aquatic fauna

Although Sri Lanka's freshwater fishes are arguably the best studied of the aquatic macrofauna, the island's inland waters contain a remarkable diversity of crabs, shrimps, molluscs and insects (Figure 2.21), with high levels of endemicity. All 51 species of freshwater crabs (Gecarcinucidae), for example, are endemic to Sri Lanka as are five of the seven genera represented on the island (Bahir & Ng, 2005; Bahir & Yeo, 2005; Bahir *et al.*, 2005). The diversity of the remaining aquatic macrofauna, however, largely remains to be assessed, and its taxonomy is, by and large, more than half a century out of date.

2.7.1 Mountain-stream macrofauna. Chertoprud (2019) reported on the macrofauna of mountain streams below ('tropical') and above ('subtropical') the 1500 m contour within an elevation gradient in the range 600–2050 m in the Nuwara Eliya region of the central highlands. He inventoried a total of 133 taxa, mostly identified to genus, of which 120 were the larvae and imago of insects. The dominant fauna in rocky rifts in small streams in both elevation ranges was composed of leptophlebiid and baetid mayflies, hydropsychid and glossosomatid caddisflies, and gecarcinucid crabs. In the tropical zone, this fauna was supplemented by euphaeid dragonflies, whereas in the subtropical zone it was supplemented by *Simulium* black flies and psephenid water beetles.

Within the leaf litter and detritus substratum of streams, Chertoprud (2019) found detritophagous arthropods to dominate: leptophlebiid mayflies *Goerodes* and *Anisocentropus* caddisflies, in addition to more omnivorous or predatory taxa such as crabs, *Phanoperla* plectopterans, *Heliogomphus* dragonflies, and *Polyplectropus* caddisflies. In streams with a gravel / pebble substrate, he recorded burrowing caddisflies (*Marilia mixta*: Odontoceridae), burrowing mayflies (*Ephemera*), limoniid crane-flies (*Hexatoma*), and gomphid dragonflies, together with leptophlebiid mayflies.

Chertoprud (2019) observed that mayflies and gastropods accounted for ~30 and 6.5 percent, respectively, of the metabolism of communities in both zones of the region. Dragonflies accounted for 18.1 percent in the tropical zone but only 1.2 percent in the subtropical zone, in which decapod crustaceans (Atyidae and Gecarcinucidae) represented 8.1 and 7.1 percent of the abundance, respectively. He noted that bivalves and turbellarians were generally rare, with only a single species of each recorded: *Afropisidium* cf. *javanum* (Pisidiidae) and *Dugesia* cf. *nannophallus* (Dugesiidae), respectively.

2.8 The Ecology of dry zone tanks

Owing to the ephemeral nature of most dry-zone rivers, the ecology of that region's freshwater fishes has been studied mainly in tanks. The tanks themselves fall into two categories: shallow, seasonal ones that dry up almost entirely at the peak of the summer drought (*e.g.*, Tissa Wewa in Anuradhapura), and deeper, usually larger ones (*e.g.*, Parakrama Samudraya, at Polonnaruwa) that offer perennial habitats for fishes.

2.8.1 Tissa Wewa. In a sample catch of ~170,000 fish in Tissa Wewa, Piet *et al.* (1995) and Piet *et al.* (1999) found that *Amblypharyngodon grandisquamis* was by far the most abundant indigenous fish species (58.7 %), followed by *Puntius dorsalis* (8.3 %), *P. thermalis* (8.1 %), *Rasbora microcephala* (7.5 %), *Systomus sarana* (2.9 %) and *Hyporhamphus limbatus* (2.2 %).

Piet (1998a,b) found the fish community to be divided into four trophic groups: (1) *A. grandisquamis* (herbivorous/ detritivorous); (2) *P. thermalis, P. dorsalis* and *S. sarana* (benthivorous); (3) *R. microcephala* and *H. limbatus* (zooplanktivorous); and (4) *Glossogobius giuris, Mystus nanus* and *M. gulio* (piscivorous).

Amblypharyngodon grandisquamis subsisted on phytoplankton and detritus at all size-classes, whereas *P. thermalis* consumed zooplankton, detritus and microbenthos, with adults replacing zooplankton with chironomids. Juvenile *Puntius dorsalis* fed mostly on chironomids and microbenthos, with the latter being replaced by gastropods in adults. Gastropods were the primary food also of *S. sarana*, supplemented by macrophytes and fish, which represented about 10 percent of its diet. Adamicka (1983) concluded from the powerful pharyngeal musculature of *S. sarana* that it was adapted to crushing gastropods using its pharyngeal teeth.

Glossogobius giuris showed the most marked trophic shift, with juveniles feeding mostly on chironomids, supplemented with zooplankton and insects, while adults subsisted almost wholly on fish. Juvenile *H. limbatus* fed mainly on cyclopoid copepods and cladocerans, adding calanoid copepods to their diet as adults, while juvenile *Mystus* fed mainly on zooplankton (73 %) and insects (21 %) transitioning to an almost exclusively piscivorous diet as adults. Juvenile *R. microcephala* consumed cladocerans and cyclopoid copepods in equal measure, while aquatic insects represented about half the diet of adults. *Amblypharyngodon grandisquamis*, the most abundant fish in the tank, was the principal prey of the piscivorous species.

Piet (1998a) considered the orientation of the mouth to divide the Tissa Wewa fish assemblage into benthivores (*P. thermalis* and *P. dorsalis*: mouth subterminal) and surface-feeders (*H. limbatus* and *R. dandia*: mouth superior), whereas *Glossogobius* and *Mystus* species occupied the bottom layer, attacking prey upwards. He concluded that the possession of barbels by the tank's carps and catfishes, except the surface-feeders, was advantageous in sensing prey in the turbid waters of the tank, and at night.

Over a 28-month period, Piet (1998b) harvested and enumerated 359,920 fish from Tissa Wewa, analysing the gut contents of 20,492. The environment of the tank changed drastically between high-water and low-water phases. As the drought intensified in September 1992, the water became more turbid, with the Secchi depth declining from 34 cm to just 6 cm. The dry weight of inorganic matter, meanwhile, rose from 22 mg·l^{-1} to 568 mg·l^{-1}, while the mass of detritus and phytoplankton biomass rose 24-fold and 23-fold, respectively.

Table 2.3. The total catch from Parakrama Samudraya in March/April 1980 reported by Schiemer & Hofer (1983). The catch data excluded several species they nevertheless identified, including *Ehirava fluviatilis, Anguilla bicolor, A. bengalensis* and *Hyporhamphus limbatus*.

	kg	percent
Dawkinsia filamentosa	1380	49.7
Puntius dorsalis	468	16.8
Puntius thermalis	585	21.1
Mystus nanus	95	3.4
Rasbora microcephala	70	2.5
Amblypharyngodon grandisquamis	63	2.3
Etroplus suratensis	34	1.2
Glossogobius giuris	33	1.2
Labeo heladiva	12	0.4
Pseudetroplus maculatus	9	0.3
Devario malabaricus	8	0.3
Esomus thermoicos	8	0.3
Mystus zeylanicus	4	0.1
Ompok ceylonensis	3	0.1
Systomus sarana	3	0.1
Mastacembelus armatus	3	0.1

As the water level fell, all species—including the predatory goby and catfishes—showed a decrease in body mass. The proportion of the pelagic *A. grandisquamis, H. limbatus*, and *R. microcephala* decreased from about two thirds of the catch to almost zero, while the proportion of small fishes (<10 cm) fell from 73 percent to just 22 percent. Bottom-dwelling species such as *P. thermalis, P. dorsalis, S. sarana* and the catfishes were more successful in surviving the drought than pelagic species, such as *A. grandisquamis, R. microcephala* and *H. limbatus*. Piet (1998b) attributed this to the ability of the former to protect their gill epithelia from the high density of suspended matter in the water column through mucus secretion.

The commencement of the second intermonsoonal rains in October, however, saw a rapid recovery of the fish population, with the pre-drought demography established within just three months. Water turbidity fell rapidly, the Secchi depth increasing from 6 to 127 cm. The improved visibility appeared to benefit *G. giuris*, the abundance of which rose rapidly compared to its fellow piscivores. The catfishes, which are nocturnal and apparently more dependent on sensing prey by means of their barbels, were, however, unaffected by the improved visibility.

2.8.2 Parakrama Samudraya. The fish community at Parakrama Samudraya, a 25 km^2 reservoir near Polonnaruwa, although including the species reported by Piet (1998a,b) from Tissa Wewa, is much more diverse. Unlike Tissa Wewa, Parakrama Samudraya retains water year-round. Schiemer & Hofer (1983) described the reservoir as 'an inundated jungle, the submerged trees of which provide a structure for a rich Aufwuchs community.' The bottom of the lake is rich in organic matter (20 percent of sediment dry weight).

Here, Schiemer & Hofer (1983) found *Dawkinsia filamentosa* to be the most abundant species (Table 2.3). Whereas *Amblypharyngodon grandisquamis*, the most abundant species in Tissa Wewa, subsisted on phytoplankton and detritus, *D. filamentosa* in Parakrama Samudraya, though omnivorous, subsisted largely on macrophytes (principally *Ceratophyllum*) and Aufwuchs. It browsed on the marginal vegetation of the reservoir (Hofer & Schiemer, 1983), syntopically with *Ehirava fluviatilis, Labeo heladiva, Systomus sarana, Rasbora microcephala, Devario malabaricus, Esomus thermoicos, Etroplus suratensis* and *Glossogobius giuris*.

Ehirava fluviatilis and *R. microcephala* were common also in offshore areas, together with *Amblypharyngodon grandisquamis*, *Puntius dorsalis* and *Mystus nanus*. While *D. filamentosa* fed on littoral macrophytes in daytime, the more benthic *P. dorsalis* and *P. thermalis* fed on zoobenthos and sediment that included chironomids, cyclopids, cladocerans and ostracods, in offshore areas. *Puntius dorsalis* was particularly active at night, moving inshore at dusk to forage in areas occupied by *D. filamentosa* during daytime. Thus, *Puntius thermalis* and *P. dorsalis*, which consume similar foods, fed during different time intervals of the day (Schiemer & Hofer, 1983), avoiding competition through resource partitioning in the temporal dimension (Peit & Guruge, 1997).

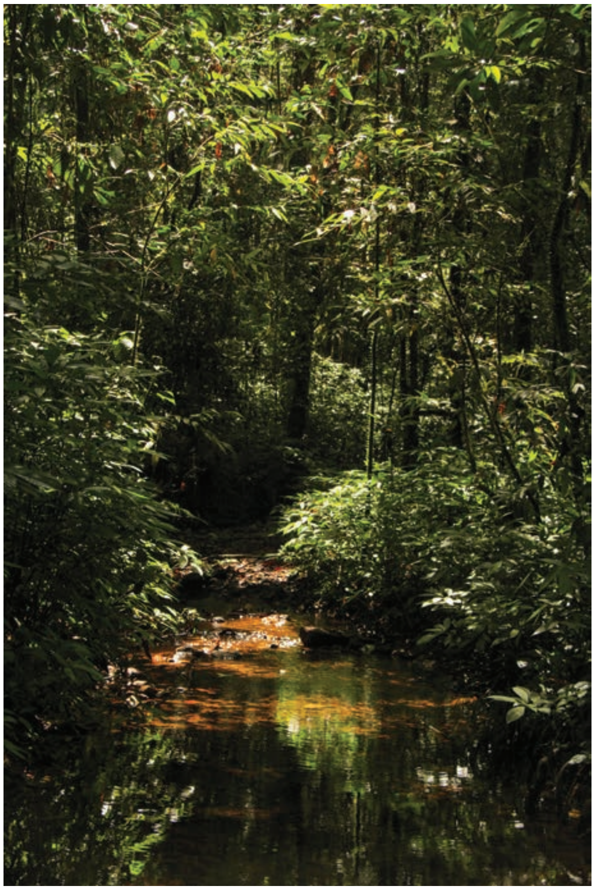

Figure 2.22. The shallow, heavily shaded streams of the wet zone lowlands (here at Atweltota) are among the most important habitats for Sri Lanka's endemic fishes.

Systomus sarana, though uncommon in the reservoir, was found to feed mainly on submerged terrestrial macrophytes and seeds, in addition to insects and small fish, while *Etroplus suratensis* subsisted mainly on detritus, marginal vegetation, trichopterans, chironomids and gastropods.

Weliange & Amarasinghe (2003) concluded that the ichthyofauna of Sri Lanka's dry-zone tanks is composed of stenophagous species which feed on detritus and phytoplankton, and euryphagous species, which exhibit temporal dietary plasticity.

Apart from humans and perhaps piscivorous fishes, Winkler (1983) suggested that cormorants were the greatest predators of the fishes of Parakrama Samudraya, especially the Indian shag, *Phalacrocorax fuscicollis*. These birds hunt among the growths of macrophytes along the margins of the waterbody, preying on the fish feeding there. Winkler (1983) estimated that the ~13,700 Indian shags at the reservoir consumed some 2.3 MT of fish daily, in addition to a lesser toll exacted by Little cormorants (*Microcarbo niger*) and Oriental darters (*Anhinga melanogaster*).

Duncan (1983) reported large numbers of larvae of *Ehirava fluviatilis* and *Hyporhamphus limbatus* in Parakrama Samudraya, implying that these euryhaline species reproduce and complete their life cycle in freshwater. Many of the tank's native fishes, however, migrated to breed further upstream at the onset of the rains. At Diyabeduma, near Parakrama Samudraya, Silva & Davies (1986) observed the fry of *Garra ceylonensis, Labeo heladiva, Puntius thermalis, Puntius dorsalis, Dawkinsia filamentosa, Systomus sarana, Tor khudree, Ompok ceylonensis* and *Wallago attu*, noting that all nine 'actively migrate upstream for spawning before the onset of the north east monsoonal rains'.

2.8.3 Minneriya and Udawalawe. Amarasinghe *et al.* (2014) reported *Amblypharyngodon grandisquamis* to be the most abundant indigenous fish among the 30 species recorded from this ancient reservoir in the island's north-central dry zone, with a mean catch per unit effort of 89 per 100 $m^2 \cdot h^{-1}$, followed by *Puntius thermalis* (20), *Dawkinsia filamentosa* (9) and *Rasbora dandia* (8).

At Udawalawe reservoir in the southern dry zone, the last-mentioned authors again found *Amblypharyngodon grandisquamis* to be the most abundant of the 21 species recorded, with 37 per 100 $m^2 \cdot h^{-1}$, followed by *Dawkinsia filamentosa* (7) and *Rasbora dandia* (2).

2.9 The ecology of lowland streams

The preponderant majority of the island's endemic fishes occurs in streams traversing lowland rain forests (Figure 2.22). In addition to being heavily shaded by the forest canopy, these shallow streams have silt substrates rich in organic matter. Sanjaya *et al.* (2015) found that in a typical lowland rainforest stream, the macrobenthos contained predominantly Hydropsychidae, Helicopsychidae (Trichoptera), Plastisticidae (Odonata), Leptophlebiidae (Ephemeroptera) and Perlidae (Plectoptera). These together accounted for about 65 percent of the individual organisms constituting the macrobenthos, broadly consistent with tropical streams elsewhere in Asia (Jacobsen *et al.*, 2008). Some fishes, such as the ubiquitous species of *Devario*, are surface skimmers, preying on terrestrial arthropods that fall into the water.

Lowland rainforest streams also harbour a rich macroinvertebrate fauna, which includes some 30 species of gecarcinucid crabs, 10 species of atyid shrimps and 30 freshwater gastropods, including about a dozen species of *Paludomus* (De Silva, 1991, 1994; Bahir *et al.*, 2005; Peiris *et al.*, 2015).

Moyle & Senanayake (1984) investigated the ecology of freshwater-fish communities in streams traversing a lowland rain forest (below 122 m elevation) at Kanneliya. These streams contain perhaps the highest number of endemic fishes of any stream habitats in the island. Kortmulder *et al.* (1978) had previously made an ethological study of *Pethia nigrofasciata* in the area, which included the Nanniketa Ela, a stream traversing secondary forest and debouching into the Gin River a short distance downstream. The stream bed consisted of rocks, stones and sand, covered by a thin layer of reddish-brown sediment. These authors also sampled a second similarly forested stream, the Wak Oya (a tributary of the Kelani River), at Waga, a short distance downstream of Labugama.

The stream-water at Kanneliya varied in the range 6.0–7.4 pH, 37–54 $\mu S \cdot cm^{-1}$ conductivity, 4.3–5.5 ppm $CaCO_3$, and 89–94 percent dissolved O_2 concentration, at a water temperature of 24.5–25.3° C, while that at Waga varied in the range 6.1–6.2 pH, 34–61 $\mu S \cdot cm^{-1}$ conductivity, 3.2–4.8 ppm $CaCO_3$, and 78–94 percent O_2 concentration, at a water temperature of 25.5–26.5° C (Kortmulder *et al.*, 1978). Schut *et al.* (1984) found, in mid-hill rainforest streams around Ratnapura and Galle, pH to vary in the range 5.6–6.9, and conductivity 23.1–32.8 $\mu S \cdot cm^{-1}$.

Moyle & Senanayake (1984) recorded the following fish species at Kanneliya (species marked § were encountered too infrequently to warrant inclusion in analyses): *Dawkinsia filamentosa, Devario* sp. (probably *D. micronema*), *Garra ceylonensis, Pethia nigrofasciata, Pe. cumingii*§, *Puntius 'dorsalis' (=Pu. kelumi?), Pu. bimaculatus, Pu. titteya, Rasbora* sp., *Rasboroides pallidus, Systomus pleurotaenia, S. sarana* and *Tor khudree*§ (Cyprinidae); *Schistura notostigma* and *Paracanthocobitis urophthalma*§ (Nemacheilidae); *Lepidocephalichthys thermalis*§ (Cobitidae); *Mystus nanus*§ and/or *M. ankutta* (Bagridae); *Ompok argestes*[§] (Siluridae); *Aplocheilus dayi* (Aplocheilidae); *Xenentodon cancila* (Belonidae); *Belontia signata* (Osphronemidae); *Mastacembelus armatus* (Mastacembelidae); *Sicyopterus lagocephalus*[*] and *Awaous melanocephalus* (Gobiidae); and *Channa orientalis* and *C. kelaartii* (Channidae).

None of the wet-zone ecological studies referenced here (Geisler, 1967; Kortmulder *et al.*, 1978; Moyle & Senanayake, 1984; Schut *et al.*, 1984) recorded *Puntius kamalika*, even by the name by which it was at that time identified: *Pu. amphibius*. The species occurs across the lowlands, where Silva *et al.* (2008) reported it as 'locally common'[†], and is present even in parts of the dry zone.

It appears also that the '*Puntius dorsalis*' reported by Geisler (1967), Moyle & Senanayake (1984) and Schut *et al.* (1984) from their wet-zone study sites might in fact have been—or included—*Pu. kelumi*. The latter species was confused with *Pu. dorsalis* until Pethiyagoda *et al.* (2008a) showed it to be distinct and endemic to the south-western wet zone where, however, *Pu. dorsalis* and *Pu. kelumi* often occur in syntopy.

Weliange *et al.* (2017a) studied water chemistry and macroinvertebrate communities at several sites on the Eswathu Oya, a well-shaded tributary of the Kelani River, in the lowland wet zone (~200 m asl). Here, the stream water varied in temperature from 24–27° C, while pH and conductivity ranged from 5.9–6.8 and 22–25 $\mu S \cdot cm^{-1}$, respectively. Among the benthic macroinvertebrates, Coleoptera (50 %, principally Elmidae and Psephenidae) and Diptera (33 %, principally Chironomidae and Psychodidae) dominated, with Trichoptera (7 %), Ephemeroptera (5 %) and Odonata accounting for most of the remainder. These authors found also that the abundance of macroinvertebrates was inversely proportional to stream discharge, and went on to record 22 species of freshwater fishes in the Eswathu Oya, with substantial variation in the fish communities between sites.

In the sites sampled on the Yan River, at a similar elevation in the dry zone, however, Weliange *et al.* (2017a) recorded water temperatures in the range 25–28° C, pH from 7.1–7.9 and conductivity from 138–721 $\mu S \cdot cm^{-1}$, the last parameter being correlated inversely with stream-water level. Here, the macroinvertebrate community was dominated by Diptera (62 %, principally Chironomidae, Ceratopogonidae and Tanypodinae), followed by Ephemeroptera (16 %, principally Caenidae, Baetidae, and Leptophlebiidae), Trichoptera (7 %), Mollusca (4 %), Coleoptera (3 %), Cladocera (3 %) and Hemiptera (2 %).

In the Yan River sites, Weliange *et al.* (2019) recorded 27 freshwater-fish species, seven of which occurred also in Eswathu Oya (*Dawkinsia filamentosa, Devario malabaricus, Garra ceylonensis, Pethia melanomaculata*[‡]*, Puntius bimaculatus, Rasbora dandia* and *Systomus sarana*). An analysis of gut contents revealed piscivory only in the dry zone community, with the wet zone community subsisting on larval benthic macroinvertebrates, algae, detritus and terrestrial insects. Weliange *et al.* (2017b) found that in the Eswathu Oya, the diversity of prey taxa was higher during periods of low discharge, while the converse prevailed in the Yan River. Further, herbivorous and/or detritivorous fish species, which were rare in Eswathu, were dominant in Yan.

Nevertheless, Weliange *et al.* (2019) observed little dietary overlap between fish species, concluding: 'the higher habitat diversity in the wet-zone stream did not lead to higher species richness, to a higher proportion of specialist feeders, and to a higher number of taxa in the diets of the fish assemblage. The main differences between the fish assemblages in the wet zone as compared with the dry zone were the higher number of endemic species, the lower percentage of specialist feeders, and fish were feeding higher in the food chain.'

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[*] Moyle & Senanayake (1984) recorded '*Sicyopterus halei*', which is a junior synonym of *S. lagocephalus* (Keith *et al*. 2015: 102). Subsequent to their work, however, other sicydiine gobies have been reported from south-western Sri Lanka, such as *S. griseus, Schismatogobius deraniyagalai, Sicyopus jonklaasi* and *Stiphodon martenstyni.* The identity of the species they referred to as '*Sicyopterus halei*' is therefore uncertain.

[†] The survey summarized in Tables 5.1 and 5.2, however, showed *Puntius kamalika* to be an uncommon—if wide ranging—species, more frequently met with in the lowland floodplains than in rainforest streams. It is possible that some of the fish visually identified *in situ* as *Pu. kamalika* by Silva *et al.* (2008) were in fact juvenile *Pu. dorsalis* or *Pu. kelumi*.

[‡] *Pethia melanomaculata* is absent from the wet zone. It is possible that these authors misidentified *P. reval* in Eswathu Oya as *P. melanomaculata*.

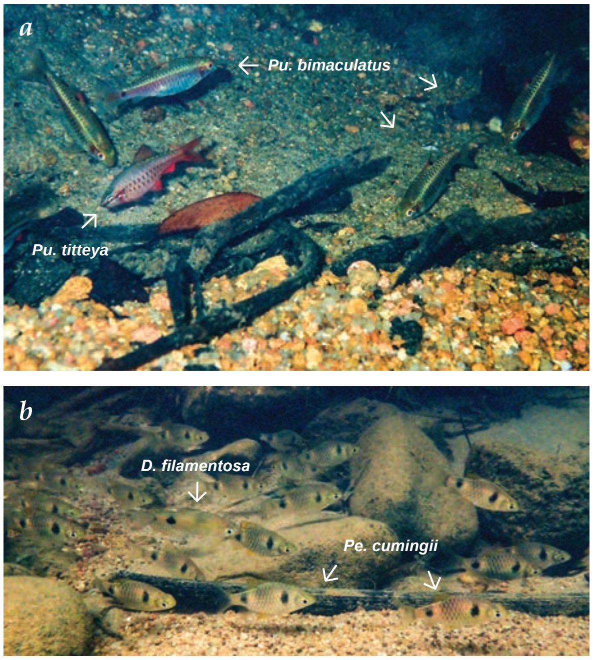

Figure 2.23. ***a,*** As observed by Schut *et al.* (1984), *Puntius titteya* and *P. bimaculatus* show evidence of a close association where they co-occur (the former is confined to the wet-zone lowlands whereas the latter occurs also in the dry zone and also in southern India). The two species also share morphological characters that distinguish them from other species of *Puntius* (Pethiyagoda *et al.*, 2012). ***b,*** The frequent occurrence of juvenile *Dawkinsia filamentosa* among schools of adult *Pethia cumingii* was first observed by Schut *et al.* (1984), perhaps an instance of individuals from different-looking species grouping together to confuse shared predators (Tosh *et al.*, 2006). The juveniles of all species of *Dawkinsia* share a colour pattern consisting of black bars on the side, reminiscent of that in adults of the three species of *Pethia* occurring in the wet zone of Sri Lanka.

2.9.1 Associations. Moyle & Senanayake (1984) found *Puntius titteya, Aplocheilus dayi* and *Channa orientalis* to occur mainly in small, quiet streams, with *P. titteya* almost entirely restricted to relatively undisturbed streams surrounded by dense forest. *Puntius titteya* was often the only fish present in such streams, joined by *A. dayi* and the predatory *C. orientalis* in parts of the stream more subject to anthropogenic influence. Schut *et al.*, (1984), however, found *Pu. titteya* in hill marshes and in trickles and pools[*] in which it favoured parts with minimal current in or near vegetative structures, which it used for both concealment and spawning. They observed *Pu. titteya* in association with *Pu. bimaculatus, B. signata* and *Aplocheilus*.

Schut *et al.* (1984) were struck by the close association between *Pu. titteya* and *Pu. bimaculatus* wherever they co-occurred—'one association, separated from all others' (Figure 2.23a). They noted that the diets of the two species converge as they grow, resulting in adult *Pu. bimaculatus* abandoning their shared habitat for rocky streams as a result of food competition. Here they cohabit with *Devario* spp., which, however, feed mainly on insects such as dipteran larvae. They observed *Pu. bimaculatus* to take cover under stones or overhanging banks when alarmed and noted its association, in addition to *Pu. titteya*, also with *Garra, Devario* and *Rasbora* in rocky streams. *Puntius titteya* was observed to spawn throughout the year, however, while *Pu. bimaculatus* migrated upstream to spawn in inundated grasslands ('marshes') during the rains.

Although not reported on by Moyle & Senanayake (1984), Schut *et al.* (1984) observed *Pe. cumingii* to occur in slow-flowing parts or stagnant pools in or beside the stream, never in fast-flowing water. Here they occupied the whole of the water column, often in association with *Pu. kelumi, Dawkinsia* and *Xenentodon*. Spawning occurred during floods, outside the main streambed, in lateral waters and on the flooded banks.

Dawkinsia filamentosa and *Systomus sarana* were characteristic of larger streams, while *Rasboroides pallidus* and *Xenentodon cancila* were low-gradient pool specialists, the former a potential prey species of the latter.

Schut *et al.* (1984) observed adult *Dawkinsia* in shoals of 50 or more occupying the relatively deeper parts of the stream not structured by large objects such as boulders or tree trunks. They spawned during periods of heavy rain, with their fry co-occurring with the fry of *Pe. cumingii*, with which they remained (or *vice versa*? See Figure 2.23b; Tosh *et al.* 2006) until they were about the same size as sub-adult *Pe. cumingii* (~3 cm total length), after which they shoaled together with conspecific adults.

Schut *et al.* (1984) noted also that *Pe. nigrofasciata* preferred structured parts of the stream, up to 50 cm deep, outside the main current; when disturbed, they hid close to structures or below an overhanging bank. They observed *Pe. nigrofasciata*

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[*] *Puntius titteya* occurs even in streams draining rice paddies in the vicinity of Colombo (pers. obs.).

typically in association with *Pu. kelumi, Rasbora* and *Belontia*. Spawning occurred in marginal shallows in slow-flowing parts of the stream, where streamflow was interrupted by an obstruction such as a log or boulder, but otherwise sunlit.

Systomus pleurotaenia, however, occupied deep (>80 cm), sand-bottomed pits, rapidly taking cover below boulders when alarmed. The species co-occurred with *Garra ceylonensis* and *Pu. kelumi*, and at times with *Devario*. The smallest juveniles encountered were about 3 cm long. These were found in shallow pools between the boulders or swimming together with *Rasbora dandia*, in the shallower parts of the same streams.

In the *Pe. nigrofasciata-S. pleurotaenia-Pu. kelumi* association, Schut *et al.* (1984) observed both *Pe. nigrofasciata* and *Pu. kelumi* to be perennial spawners. However, while *Pu. kelumi* spawned *in situ* in its deep-water haunts, *Pe. nigrofasciata* was seen to migrate as far as several kilometres upstream in search of suitable spawning areas. Occasionally they saw *Pu. kelumi* spawning in typical *Pe. nigrofasciata* spawning grounds. These spawning events were, however, separated temporally, with *Pu. kelumi* spawning early morning, while *Pe. nigrofasciata* did not begin spawning until 3–4 hours after dawn. Schut *et al.* (1984) also revealed from gonadal examination and field observations that *Pu. titteya, Pu. kelumi* and *Pe. nigrofasciata* are largely perennial spawners, while *Pu. bimaculatus, Pu. vittatus* and *Pe. cumingii* spawn mainly during rainy periods.

Although *Pe. nigrofasciata* and *S. pleurotaenia* have similar diets—diatoms and green algae—Schut *et al.* (1984) observed them to occupy different microhabitats even within the same stream. *Puntius kelumi* fed mainly on crustaceans and—especially in the case of individuals larger than 74 mm total length—the foliage of higher plants. Geisler (1967) reported the diet of *P. 'dorsalis'* from south-western wet zone as consisting of diatoms, detritus and Chlorophyceae, very different from the diet of chironomids and microbenthos, with the latter giving way to gastropods in adult *Pu. dorsalis* reported from the dry zone by Piet (1998a), and zoobenthos, chironomids, cyclopids, cladocerans and ostracods reported also from the dry zone by Schiemer & Hofer (1983). This leads us to suspect that the '*Pu. dorsalis*' reported from the wet-zone study sites of Moyle & Senanayake (1984) and Schut *et al.* (1984) were at least in part *Pu. kelumi*.

Schut *et al.* (1984) observed the preferred habitats of *Pu. kelumi* to be highly structured deep pits, well shaded from the sun, with the fish hovering among forked root-systems, entangled branches or logs. In larger streams of depth more than 80 cm, they occurred in pits of ~20 m^2 surface area, though in shallow streams (~50 cm depth) the pits they occupied were as small as ~2 m^2. These authors observed *Pu. kelumi* to spawn within their pits, or where no cover was available, under stones, with fry being encountered in the pits together with adults.

Fishes in higher-gradient streams of slope 9–23° and flow 0.5–2.5 m^{3}s^{-1} included *Schistura, Rasbora, Belontia* and *Garra*. The only species consistently to hold in fast water was *Devario*: other fishes in this habitat took cover in crevices, behind rocks, or in depressions with slower flow. *Awaous* was observed only on sand substrates, while *Sicyopterus* invariably clung to boulders. When disturbed, *Awaous* would bury themselves in the sand, while *Sicyopterus* would flee into deeper, swifter water and cling to the sides of boulders.

While Moyle & Senanayake (1984) did not record *Pu. vittatus* from their study sites, Schut *et al.* (1984) found the species to occur in the shallow waters of marshes and rice paddies. 'In the paddy fields', they noted, 'large numbers gather under the spillways and at other places with flowing water.' Although the species co-occurred with *Rasbora* and *Aplocheilus*, Schut *et al.* (1984) noted that it was not associated with any other species of *Puntius* (then '*Barbus*').

2.9.2 Terrestrial-insect feeders. Six species formed the terrestrial-insect-feeding group: *Rasbora, Rasboroides, Devario, Belontia, Aplocheilus* and *Channa orientalis*. The last two of these appeared to be the most specialized feeders on terrestrial insects, as reflected in both morphology (superior mouth) and habitat (overhanging vegetation). The first four of these fishes were more omnivorous, though terrestrial insects were the largest component of their diets. All four, nevertheless, had considerable amounts of terrestrial debris in their gut. Moyle & Senanayake (1984) inferred from the

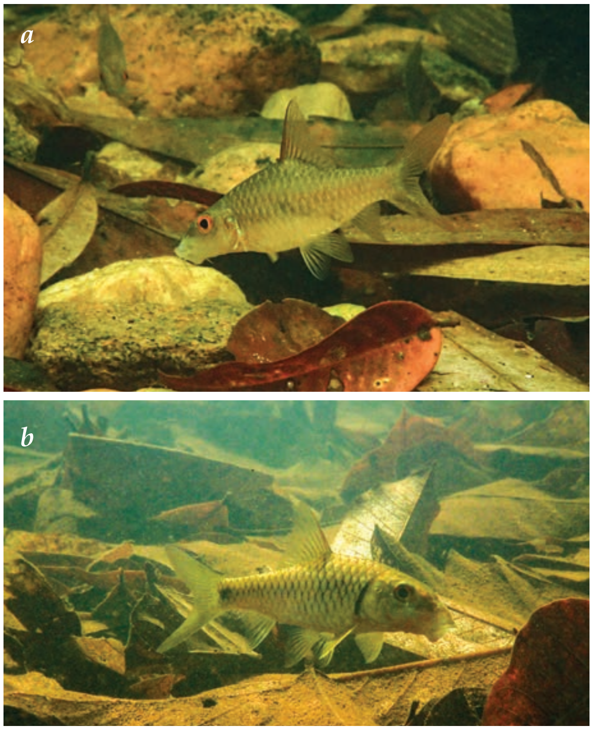

Figure 2.24. The protrusible jaws of ***a,*** *Puntius kelumi* (a species confined to the wet zone) and ***b,*** *P. dorsalis* (which occurs throughout the lowlands of both climatic zones) have been attributed to dietary specialization, with Piet (1998a) noting that in dry zone tanks, *P. dorsalis* used this adaptation to suck in molluscs. Because both species co-occur in the wet zone, and were confused with each other until distinguished by Pethiyagoda *et al.* (2008a), the diets reported for '*Puntius dorsalis*' by Geisler (1967) and Schut *et al.* (1984) may in some instances refer to *Pu. kelumi.*

small, slightly upturned mouth, large paired fins, large eyes and elongate gill rakers of *Rasboroides* that it is adapted for feeding on plankton or small insects at the water's surface.

Schut *et al.* (1984) found *Rasbora* to feed almost entirely on insects (dipteran larvae), as a result of which it does not compete with the species of *Puntius* in these streams. Although it is potentially a trophic competitor of *Devario*, the distributions of the two species are largely different. *Devario* occur mainly in rocky streams with a relatively high gradient, whereas *Rasbora* are widely distributed in habitats ranging from hill streams to the margins of large rivers. Further, our own observations suggest that *Devario* occur mainly toward the centre of the stream, whereas *Rasbora* usually remain close to the sides.

2.9.3 Aquatic-invertebrate predators. Another (morphologically dissimilar) group of six species is specialized in feeding on aquatic invertebrates: *Systomus sarana, Schistura, Xenentodon, Mastacembelus, Channa kelaartii* and *Sicyopterus.* The diets of these six species, however, had only limited overlap with one another. *Schistura* fed on a wide variety of small invertebrates, but especially caseless caddisfly and mayfly larvae. *Mastacembelus* fed on larger invertebrates, such as atyid and palaemonid shrimps, mayfly larvae and trichopterans, while the diet of *Xenentodon* consisted mainly of small fishes and occasional crustaceans captured midwater. Young *Sicyopterus* preyed on mayfly larvae and other small rock-clinging insects, the disproportionately longer intestine of larger individuals suggesting that they transition to a more omnivorous diet as adults (>70 mm total length).

2.9.4 Algae eaters. Another group fed mainly on filamentous green algae and diatoms: *Awaous, Dawkinsia, Pethia nigrofasciata* and *Systomus pleurotaenia*. The three cyprinid species were commonly observed picking at the surface of boulders, logs, or other submerged objects. Moyle & Senanayake (1984) expressed surprise at the dominance of algae in the gut of *Awaous*, assumed to be carnivorous owing to their short intestinal length and the pointed teeth on their pharyngeal bones and jaws.

All species except *D. filamentosa* consistently had small numbers of chironomid midge larvae and the early instars of caddisfly larvae in their guts, presumed to have been ingested with the algae. *Dawkinsia filamentosa*, however, fed mainly on crustaceans, especially as adults, although Hofer & Schiemer (1983) reported them to feed primarily on macrophytes in Parakrama Samudraya, in the dry zone.

Schut *et al.* (1984) and Geisler (1967) observed the diets of *Pe. cumingii* and *Pe. nigrofasciata* to be similar: mostly green algae followed by diatoms in the former, mostly diatoms followed by green algae in the latter. Their microhabitats too, were similar. Though sometimes occurring in syntopy, their schools did not mix; *Pe. nigrofasciata* occupied the mid-region of the water column, while *Pe. cumingii* remained closer to the substrate and usually closer also to the stream margins.

Figure 2.25. Introduced to the Sri Lankan highlands in the 19th century by British sports anglers, rainbow trout (*Oncorhynchus mykiss*) persist in Horton Plains National Park (elevation 2100 m asl).

2.9.5 Detritus and diatom feeders. The cyprinids *Garra ceylonensis, Puntius kelumi, Pu. bimaculatus* and *Pu. titteya* form a detritus- and diatom-feeding guild: fishes that pick (*Pu. bimaculatus, P. titteya*), scrape (*Garra*) or suck (*Pu. dorsalis* and *Pu. kelumi*) algae and organic material from the substrate. *Puntius titteya* was identified by Moyle & Senanayake (1984) as primarily an 'ooze feeder' that incidentally ingested algae and small invertebrates, though Geisler (1967) identified imagos of Diptera and Coleoptera in its diet, in addition to detritus. *Puntius bimaculatus* appeared to be primarily an algae feeder that incidentally ingested detritus. *Puntius kelumi*, which has a subterminal mouth, long maxillary barbels, and closely-spaced gill-rakers—adaptations of a bottom-rover that feeds on small particles— indiscriminately sucked up both diatoms and detritus, using the protrusible jaws of its subterminal mouth (Figure 2.24), while *Pe. nigrofasciata* picked filamentous algae off rocks with its firm terminal mouth.

Systomus pleurotaenia, a streamlined midwater fish, was not unambiguously associated with any of the above four trophic groups: it picked algae from the sides of boulders and logs, especially in fast water, with its terminal mouth.

2.10 The ecology of montane streams

With the possible exception—of *Devario monticola* and a highland population of *Garra ceylonensis* recorded from a stream descending through montane forest at an elevation of 1575 m asl at Bopattalawa—Sri Lanka's hill streams above ~1600 m elevation are notably devoid of indigenous fishes. Kelaart (1852: xxviii), however, noted that in Nuwara Eliya (elevation 1870 m) 'Of fishes only two small species are found.' Kelaart provided no further information on the two species and made no further mention of them elsewhere. Although Deraniyagala (1952: 28) reported *Puntius bimaculatus* from Nuwara Eliya, the survey of Pethiyagoda (1991) failed to record the species there, as did the more recent survey of Sumith *et al.* (2011). Radda (1973) reported *Devario* and *Garra* from an elevation of 1800 m at Maskeliya, but the location he gave (Mocha Dola) is in fact at ~1350 m asl.

Day (1878: 590–591) stated in his account of *Barilius bendelisis,* a South Indian headwater species: 'Found also in Ceylon from whence Dr. Kelaart brought some specimens to the museum of the East India Company [in London]'. In his account of *B. vagra*, a Gangetic species, Day (p. 589) wrote, 'Kelaart sent a Ceylon specimen to the E. I. [East India] Museum.' Day knew the genus well and it is unlikely that he misidentified these fishes. Unfortunately, these specimens do not appear to have been available by the time of Günther's (1868) treatment of *Barilius*, for he omitted to mention them in his accounts of the two species (Kelaart had, in any event, died in 1860: Pethiyagoda & Manamendra-Arachchi, 1997). The presence of *Barilius* in Nuwara Eliya would be surprising given that the genus occurs in the Western Ghats only up to about the elevation of Coorg (Kodagu, Karnataka, at ~1000 m; pers. obs. and Rahul Kumar, pers. comm.) though Day (1878) recorded *Barilius gatensis* up to an elevation of 5000 ft (~1500 m). Whatever fishes did occur in Nuwara Eliya in Kelaart's time (1819–1860), however, probably disappeared in consequence of the introduction of rainbow trout to this area in the late 1880s (Pethiyagoda, 2012a: 173; Figure 2.25).

Prior to the introduction of rainbow trout (*Oncorhynchus mykiss*) to the Nilgiri Hills of southern India, Molesworth & Bryant (1921) reported a Mr Wilson noting the presence of 'stone loach'—presumably a *Balitora*—and *Devario neilgherriensis*, in Parson's Valley. These authors continue, 'In September 1908, *i.e.*, two years after stocking [of rainbow trout] had taken place, Mr. Wilson remarked, apropos of the Parson's Valley stream:–'The decrease of the larger natural fish food is also marked. Crabs and minnows, especially the latter, where once numerous, are now not to be seen.'' Five years later, in 1913, Wilson reported the stunting of trout owing to the lack of natural

Figure 2.26. While the introduction of Rainbow trout to the Sri Lanka *ca* 1890 may have led to the disappearance of freshwater fishes from highland streams, these aquatic habitats continue to host a macro-invertebrate fauna that includes several species of gecarcinucid crabs and this endemic genus of adyid shrimps: *Lancaris* (Cai & Bahir, 2005).

food and recommended culling the population. Rainbow trout have since been widely implicated in freshwater-fish extinctions and population-declines across the world (Welcome, 1988).

Sumith *et al.* (2011) conducted an ichthyological survey of the Uma River, a headwater stream originating from around Nuwara Eliya and traversing an anthropogenic landscape. They found no fish at the highest point sampled, 1865 m, but recorded *Garra ceylonensis* and *Lepidocephalichthys thermalis* from an elevation of 1187 m asl at Perawella, in water with a conductivity of 155 $\mu S \cdot cm^{-1}$ and dissolved oxygen content of 7.5 $mg \cdot l^{-1}$. Lower down, at Medawela (elevation 1100 m), *Puntius bimaculatus* and *Channa kelaartii* too, occurred together with the former two species.

These authors also sampled the Theligam River, a tributary of the Amban River descending through submontane rain forest in the Knuckles Hills. At Etanwala (elevation 807 m), the highest point sampled, they recorded *G. ceylonensis* and *Devario malabaricus*, while lower down, at Illukkumbura (482 m) they found also *Tor khudree, Puntius bimaculatus, Systomus martenstyni* and *Dawkinsia srilankensis*.

In a survey of freshwater fishes on a longitudinal gradient in the upper Walawe River basin, Jinadasa *et al.* (2003) found that from an elevation of 200 m to 2000 m asl, both diversity and abundance declined with altitude, with no indigenous species recorded above an elevation of 1400 m asl.

If specialized hill-stream fishes did exist in Sri Lanka, as Day's record above suggests, it appears they have since disappeared, although populations may yet persist (as in the case of *Devario monticola*) in places not reached by trout. The highest mountain stream in the island, the Belihul River on Horton Plains (2100 m asl) now contains only trout, though in syntopy with an atyiid shrimp, *Lancaris singhalensis* (Figure 2.26), which genus and species are both endemic to Sri Lanka (Cai & Bahir, 2005).

The native fishes that inhabit the hill streams of the third peneplain, up to elevations of about 1600 m asl (no indigenous fishes occur above this), such as *Devario monticola, Garra ceylonensis, Puntius bimaculatus, Rasbora dandia,* and *Schistura* species, are all represented in the lowlands by conspecifics or closely related vicars. It appears that they are relatively recent dispersants into the hills (Sudasinghe *et al.*, 2021a). The species that occur in the next-lower elevation band, 1200–1400 m asl, are all ones that also occur much lower down: *Channa orientalis, Rasbora dandia, Devario malabaricus, Puntius bimaculatus* (see Table 5.2).

2.11 The ecology of mid-hill streams

2.11.1 A translocation experiment. Senanayake & Moyle (1982) observed, 'The present fish fauna of the Second Peneplain streams is depauperate and consists of species that have managed to invade in fairly recent times from the lowland areas, where these same species coexist with many other species, in much more species-rich communities.' The ichthyofauna of the third peneplain is more depauperate still.

In 1981, F. R. Senanayake and P. B. Moyle conceived an experimental project to test whether endemic species threatened in the western lowland wet zone could be translocated, as refugial populations, into highland streams within the Mahaweli basin. Four species native to the south-western wet zone—*Pethia reval* (N=50), *Pe. nigrofasciata* (N=238), *Puntius titteya* (N=174) and *Rasboroides pallidus* (N=136)—were introduced* into tributar-

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* In fact, *Pethia reval* had been introduced to the Mahaweli River around Peradeniya some decades earlier, given that Deraniyagala (1930) recorded it from there. Rodney Jonklaas (pers. comm.) stated that populations of *P. reval* and *P. nigrofasciata* were maintained in a pond in the Royal Botanic Gardens, Peradeniya, and were thought to have escaped when the pond overflowed into the Mahaweli River,

ies of the Mahaweli near Ginigathena (~700–800 m asl), from which basin they were thought to have been absent until then (Wikramanayake & Moyle, 1989; Wikramanayake, 1990a,b).

In their survey four years after the introduction, Wikramanayake & Moyle (1989) found that all four translocated species had not only become established in the host stream but also dispersed into other streams in the area, at least up to upstream impoundments across some of these streams. In addition, they recorded the following fishes from the area: *Puntius bimaculatus, Devario malabaricus, Garra ceylonensis, Rasbora* sp. and *Tor khudree*; *Lepidocephalichthys thermalis*; *Schistura notostigma*; *Belontia signata*; and *Channa orientalis* and *C. kelaartii*.

In 1985–86, E. D. Wikramanayake surveyed the original translocation sites and other streams in the area to assess the efficacy of the translocations. Based on records kept by Moyle, Wikramanayake (1990a) declared the provenance of the introduced species as the Kelani River at Dehiowita for *Pe. reval*, the Kalu River at Kalutara for *Pe. nigrofasciata*, the Kelani [basin] at Parakaduwa for *R. pallidus*, and unknown for *Pu. titteya*.

The diversification of many endemic fish lineages between the river basins of the south-western wet zone was at that time, however, imperfectly appreciated. More recently, two of the species introduced at Ginigathena have each been recognized as comprising a species-pair. *Pethia cumingii* (Kalu River and southwards) was shown to be distinct from *Pe. reval* (Kelani River and north to the Deduru River) by Meegaskumbura *et al.* (2008). The species translocated to Ginigathena is the latter (Sudasinghe *et al*., 2021c).

Meanwhile, Sudasinghe *et al.* (2018a) showed there to be two species of *Rasboroides: R. vaterifloris* (Kelani and Kalu Rivers) and *R. pallidus* (Kalu River and southwards). These authors showed the species of *Rasboroides* introduced* to the Mahaweli near Ginigathena to be *R. pallidus,* originating from the Bentara basin.

2.11.2 Spatial distribution. Wikramanayake & Moyle (1989) found that the new community, after the introduction of *Pe. reval, Pe. nigrofasciata, Pu. titteya* and *R. pallidus,* was similar to the community studied by Moyle & Senanayake (1984) in south-western Sri Lanka, which comprised mostly the same species (or their sibling species).

Here too, in the upper water column, *Devario* were associated with moderate water velocities, while *Rasboroides, Belontia* and *Rasbora*, were associated with slow water. *Rasboroides* consistently occurred in the upper 59–63 percent of the water column, while *Belontia* inhabited the lower 37–54 percent, below *Rasboroides* but above *Rasbora*. The overall relative depth of *Belontia* was the same as for *Rasbora*, though *Belontia* were mostly restricted to deeper water.

In the lower part of the water column, *Garra* and *Tor* were associated with higher water velocities, while *Schistura, Pe. nigrofasciata* and *Pu. bimaculatus* inhabited moderate flow-velocity regions of the streams. Among the benthic associates, *Lepidocephalichthys, Pe. reval* and *Pu. titteya* occurred in slow-flowing water. *Pethia nigrofasciata*, although feeding at the bottom of the water column, engaged in courtship and social displays higher up, while *Pe. cumingii* occurred mostly in relatively shallow water, close to the substratum.

Puntius titteya occurred mostly in shallow water, though moving to deeper regions to browse on submerged rubble, logs and roots, in addition to feeding on the bottom. *Garra, Schistura* and *Lepidocephalichthys* were wholly benthic, though juvenile *Garra* frequently rose to the mid-water column to feed. *Tor* too, kept close to the substrate, though rising higher in fast-flowing or shallow water.

Wikramanayake & Moyle's (1989) data show groups of species to be associated with fast-flowing water (*Garra, Tor, Devario*), others to inhabit regions of moderate flow (*Pe. nigrofasciata, Pu. bimaculatus, Schistura, Rasbora*) and a third group associated with sluggish flow speeds (*Rasboroides, Lepidocephalichthys, Belontia, Pe. cumingii, Pu. titteya*). *Devario* was the only fast-water fish to inhabit the upper part of the water column, *Tor* staying close to the bottom and adult *Garra* on the bottom itself. Of the slow-water species, *Belontia* occurred in pools but always where cover was available, while *Rasboroides* lurked among roots, branches

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adjacent to the Gardens. Given the popularity of both these species as ornamental fishes, it is possible that other undocumented introductions too, could have been made. Owing to the reverence for life in Buddhist societies (Liu *et al*., 2012), such releases are common in Sri Lanka.

* The phylogeography of these and other cyprinid populations is discussed in Chapter 5.

and marginal vegetation and *Lepidocephalichthys, Pe. cumingii* and *Pu. titteya* stayed close to the bottom or margins of the stream.

Channa orientalis and *C. kelaartii* operated as ambush predators, concealed amongst submerged and emergent vegetation along the stream margins.

2.11.3 Trophic guilds – WATER-COLUMN INSECTIVORES. *Rasboroides* and *Devario* comprised the water-column insectivore guild, feeding mostly on larval Ephemeroptera and terrestrial invertebrates. Ants constituted a large proportion of the terrestrial-invertebrate diet component of both species. Seeds and algae represented a smaller proportion of the *Devario* diet.

WATER-COLUMN OMNIVORES. The diet of *Belontia* comprised mostly aquatic insects and crustaceans, with lesser amounts of algae and macrophytes. *Tor* and *Rasbora*, mid- to lower-water omnivores, consumed a wide range of foods, the former more on aquatic insects (especially chironomid larvae) and the latter more on terrestrial insects.

BENTHIC OMNIVORES. *Pethia nigrofasciata, Pu. titteya* and *Lepidocephalichthys* comprised the benthic omnivore guild. Depending on the stream sampled, the diet of *Pethia* consisted either mainly of macrophytes and aquatic insects, or diatoms, algae and aquatic insects, with little plant material. *Puntius titteya* was found to consume plant material, algae, insects (mostly dipteran, ephemeropteran and trichopteran larvae) and crustaceans, while *Lepidocephalichthys* fed mostly on chironomid larvae and filamentous algae.

BENTHIC CARNIVORES. *Channa orientalis, Channa kelaartii* and *Schistura* were benthic carnivores, feeding exclusively on aquatic insects (Coleoptera, Diptera, Ephemeroptera and trichopteran larvae, and Odonata nymphs) and crustaceans.

DIATOM FEEDERS. The diatom feeding guild consisted of *Pu. bimaculatus, Pe. cumingii* and *Garra*. The former two species included also some benthic insects in their diets, though *Garra*, a benthic scraper (Moyle & Senanayake, 1984), fed exclusively on diatoms in addition to some algae.

SUPPLEMENT 2

An ethological detour

The behavioural ecology of Sri Lankan cichlids

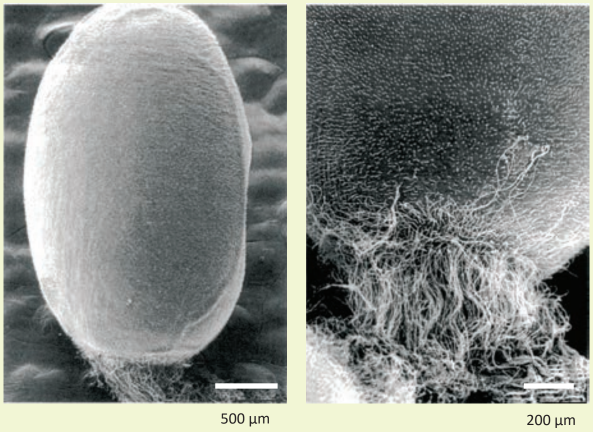
> 'Though cichlids vary widely in form, feeding habits and habitat preference, they have one characteristic in common that sets them apart from members of most other fish families and that is the care of eggs, larvae and young by the parental fish.' — McKaye & McKaye (1977).

Among Sri Lanka's freshwater fishes, the behaviour of the orange chromide, *Pseudetroplus maculatus,* is better understood than that of any other species, thanks largely to the interest of Jack A. Ward (1935–1982), an ethologist who worked in the island for a period of 18 years from the mid-1960s. Records of the orange chromide's behaviour, however, dated to more than a century earlier. Jerdon (1849: 143), for example, had observed, 'The eggs are not very numerous, and are deposited in the mud at the bottom of the stream, and, when hatched, both parents guard their young for many days, vigorously attacking any large fish that pass near them. I have had an opportunity of observing this, as well among fish in confinement as in the streams. When kept along with other species it is very pugnacious, attacking all indiscriminately.'

But it was the ethological observations of Ward, made partly in the field in the Negombo Lagoon and partly in aquarium settings, together with those of his postgraduate students, that shed most light on this fascinating fish. His work is documented in some two-dozen publications that constitute an impressive—and for Sri Lanka unparalleled—body of work save perhaps for that of Koenraad Kortmulder. The following synopsis aims to summarise the main findings of these studies, which were made largely on *P. maculatus* because it is a far less shy fish than *E. suratensis*, on which field observations are much more difficult.

Pseudetroplus maculatus

Reproduction. Ward & Barlow (1967) bred *P. maculatus* in aquariums, noting that spawning occurred seven or eight days after pair-formation. Both parents care for the eggs, which number 140–230 per clutch (Bindu & Padmakumar 2012). The eggs themselves are elliptical, measuring 1.5 mm along their longest dimension, with a thick filament tuft (Figure S2.1) at the pole opposite the micropyle (the small orifice through which spermatozoa enter the egg), which facilitates attachment to the substrate (Stiassny & Mezey 1993). The parents continually fan the clutch using their pectoral (and sometimes also caudal) fins in order to ventilate the eggs by agitating the water around them, orally removing debris and unviable eggs, and protecting the clutch from intruders. Rechten (1980b) compared this behaviour to the thermoregulation of eggs by nesting birds.



Melanie Stiassny

Figure S2.1. The egg of *Pseudetroplus maculatus*. The thick filament tuft at the pole opposite the micropyle facilitates attachment to the substrate (Stiassny & Mezey 1993).

Bindu & Padmakumar (2012) observed that while 97.0–99.5% of eggs benefiting from parental care hatched successfully, only 21.5–50.0% of those separated from the parents did so (for details of captive breeding, see Padmakumar *et al.* 2012). Moreover, parents separated from their eggs would spawn again within two weeks. Significantly, eggs that do not benefit from parental care hatch about 20 hours later than those fanned by parents (Zoran & Ward, 1983). In a later experiment, Sukumaran *et al.* (2017) observed that while parent *E. suratensis* (Figure S2.2) allowed to tend their eggs and fry raised a new clutch about once every three months, the frequency of spawning reduced to 17.6 ± 1.1 days when the parents were repeatedly separated from their eggs. These authors also observed that the inter-spawning interval was significantly lower (32.1 ± 4.4 days) in less saline water (5.4 ± 0.1‰) than in a higher salinity environment (64.4 ± 13.0 days at 27.2 ± 0.8‰).

Zoran & Ward (1983) recorded the eggs to hatch on day 3, following which the parents transferred the young to a pit they had previously excavated in the substrate. The larvae (which authors refer to as wrigglers), remain in this location 5–6 days, during which, however, they are usually transferred between pits by the parents. They become free-swimming fry by day 7, from which time they school tightly around the parents (Figure S2.3), who swim slowly so the young can keep up with them, often retrieving stray fry. When threatened, the parents flicker their dark pelvic fins, a signal that summons the fry.

Both parents cooperate in brood care, one tending the eggs or fry while the other patrols the territory. They alternate these tasks every 1–2 minutes (Rechten, 1980b), demonstrating a high degree of coordination between the mates: only one parent leaves the immediate vicinity of the brood at any given time. 'Presence at the brood may also be a safeguard against raiders in both cases', Rechten (1980b) noted. 'The brood, then, makes high demands on parental time [and] interruptions have a critical length beyond which the odds against brood survival pile up… Two parents are able to overcome such difficulties simply because they can be in two places at once.'

Monogamy. Ward & Samarakoon (1981) suspected *P. maculatus* to be monogamous, a hypothesis elegantly tested by Lamon & Ward (1983), who experimentally induced polygamy by swapping the mates of pairs that had just finished parenting their first brood. They found that while the males' fertilization rate and the females' egg number and total egg mass remained the same over successive spawnings, the lipid content of the eggs declined by almost 30% by the third spawning. The males too, had become much more aggressive by then, while the females showed less motivation to attract a mate (as evidenced, for example, by their quivering displays). 'These factors, coupled with the possible need for biparental care', noted Lamon & Ward (1983), 'demonstrate it is unlikely that a polygamous reproductive tactic ever occurs [in nature] for this species. Missing parents in nature then, are probably not reproducing with new mates but more likely are lost by predation.'


Figure S2.2. The green chromide, *Etroplus suratensis*.


Figure S2.3. Parent *Pseudetroplus maculatus* tending their fry. The flickering of the flexed pectoral fins signals the fry to group close to the parents.

Glancing behaviour of fry. Ward & Barlow (1967) investigated the 'glancing behaviour' of *P. maculatus* fry, a trait they carry into adulthood. From their very first day as free-swimming fry, the young were observed to ram themselves onto the side of their parents' bodies, mostly in the area behind the pectoral fin and the region above the anterior half of the anal fin. During this time, they found that the number of mucus glands in the epidermis of the parent increased by 34%. The fry's glancing behaviour continued until parental care ceased, at the end of the third week of their becoming free-swimming. The parents, who while

Figure S2.4. Colour-pattern variation in *Pseudetroplus maculatus*. Rechten (1980) found the black lateral coloration to vary between the extremes illustrated in ***a*** and ***b***, concluding that the black belly is most probably a mate-directed signal, with individuals tending to be darker after spawning, while smaller fish tend to be darker than larger ones (after Rechten, 1980a). ***c***, The normal ground colour of the fish is brown, while ***d***, 'nursing' adults (on whose skin secretions their young feed) are grey.

nursing the fry had turned a light grey colour (Figure S2.4), would then turn yellow and begin courting over again. The authors found that feeding did not change the glancing rate for young up to 7 days old, but it increased the frequency of glancing 1.6 times for 12-day-old fry, and 2.2 times for 18-day-old fry.

Additionally, Ward & Barlow (1967) observed that fry deprived of such parental care for the first nine days of free-swimming failed to develop normally and suffered high mortality. These authors knew that after decades of failing to raise Discus-fish independently of their parents, Hildemann (1959) had found that the young needed to feed on mucus exuded by the parents. Could the same be true of '*Etroplus*'? To find out, they captured and coated parent *P. maculatus* with a layer of activated-carbon powder and released them back into the aquarium. True enough, fry allowed to glance off the parents were found to have carbon particles in their gut, evidence that the glancing behaviour was associated with mucus-feeding. Ward & Wyman (1967) also found that although 1–2-day free-swimming fry engaged in glancing behaviour, they did not apparently feed off the parents. Clearly, the fry, which were at the same time feeding readily on food such as *Artemia* nauplii offered by the experimenters, were dependent on the nutrients in the parents' mucus: they couldn't survive without it. Indeed, it appears that glancing is essential for maintaining the parent-offspring bond: young *P. maculatus* separated from their parents for 48 hours and then returned were promptly eaten.

Quertermus & Ward (1969) showed that the fry behaviour that Ward & Wyman (1967) had termed 'glancing' in fact comprised two separate activities: glancing *per se*, a posterio-ventrally directed contact action, and micronipping, an anteriodorsally directed mucus-feeding action. The latter authors found that the rates for micronipping and glancing were similar during the first three days of free-swimming, but from days 4–7 micronipping occurred at a higher rate than glancing. After day 7, however, the rate of micronipping declined steadily until day 12 and remained low thereafter. The frequency of glancing, on the other hand, remained at a low rate until day 8 of free-swimming and then rose steadily until day 18.

This 'dichotomy between mouth and body activity', noted Wyman & Ward (1973), is one that 'remains evident throughout the life of this species.' They showed that glancing and micronipping in young *P. maculatus* develop gradually, as the fish age, into 12 discrete behaviours ranging from sibling interactions through territoriality and courtship behaviour.

Coloration and signalling. In another study, Rechten (1980a) examined coloration in *P. maculatus*, noting that the species is sexually monomorphic, with a yellow ground colour superimposed with black markings. One black blotch at the centre of the side is permanent (Figure S2.4a,c), while up to four additional blotches in a longitudinal row appear occasionally (Figure S2.4b,d). The uniform darkening of the entire ventral area, which may appear and disappear within seconds, she found, was a mate-directed signal, with fish tending to be darker after they had spawned, and with smaller individuals tending to be darker than larger ones. Ward & Samarakoon (1981) meanwhile observed that the pelvic fins of *P. maculatus* parents turned black, while Cole & Ward (1969, 1970) showed that the flickering of these fins served as a species-specific signal summoning the fry, especially when the parents were alarmed. Ostrander & Ward (1985) went on to discover that while pelvic-fin flickering was unrelated to courtship, the pelvic fins are, however, necessary also for equidistant placement of eggs when spawning. Interestingly, the pelvic-fin flickering signal of *P. maculatus* was observed by Ward (in McKaye & McKaye, 1977) to be used also by adults to steal ('kidnap') and adopt fry from one another other.

Territoriality and aggression. Wyman & Hotaling (1988) showed experimentally that territoriality in *P. maculatus* is related to the availability of food, but in a quite complex way. Young *P. maculatus* exposed to a restricted food supply showed a marked tendency to be territorial, though as they aged the tendency towards territoriality declined, 'apparently because they had passed downward through the lower threshold for territoriality'. Fry that received larger quantities of food, however, were not notably more territorial because they were above the upper threshold. As fish receiving high quantities of food grew, the food available per gram of body mass decreased and they passed downward through the upper threshold; they then became highly territorial. Fish receiving intermediate quantities of food, however, always defended territories as they progressed from a relatively high food level to a lower level. The authors concluded that 'When food available per gram of fish was low, apparently the benefits of holding a territory (*e.g.*, the assurance of obtaining some food) were outweighed by the costs (*e.g.*, energy spent charging and ramming) and fish did not defend territories. When food was very abundant, apparently the net benefit of territorial behaviour was not higher than the net benefit of being non-territorial and fish were not territorial.'

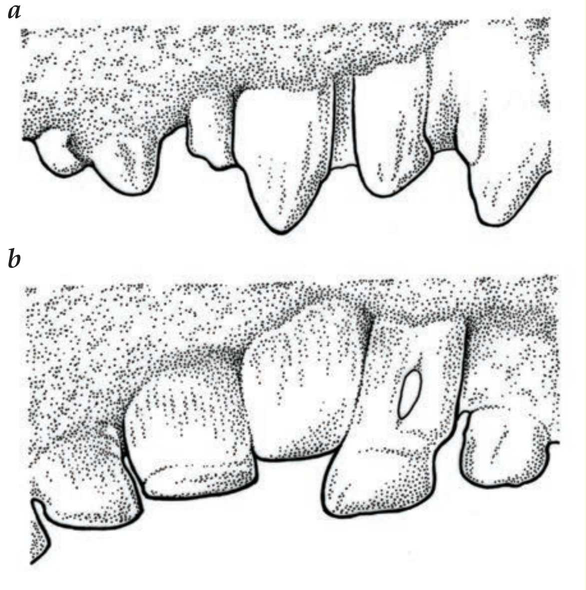
Rasa (1969) observed that individuals of *P. maculatus* that were not yet sexually mature live in schools in which chasing and threatening behaviour is common. With the onset of breeding, however, aggression becomes a prominent part of the behaviour pattern, alongside claiming and defending a territory. During breeding, aggression towards conspecifics, including the 'kissing behaviour' between the breeding pair, becomes frequent, diminishing only with the approach of spawning. 'Courtship here must thus be regarded as an interplay of sexual, flight, and high aggressive motivations,' Rasa (1969) concluded, 'the object of which is to reduce the aggressive tendencies to a point where sexual motivation increases sufficiently to allow spawning to occur… courtship movements in themselves are not sufficient to reduce the overall high aggressive level and this must find outlet in overt aggression toward a conspecific, either an intruding fish or the partner.' Interestingly, this study also found that reproduction was less successful when pairs of *P. maculatus* were bred in isolation from conspecifics: such segregation substantially increased the level of aggression between the mating pair. Sparring with intruding conspecifics appears to be a necessary adjunct to successful reproduction in *P. maculatus*.

Interactions between *P. maculatus* and *E. suratensis*

In July-August 1973 Ward and Wyman spent 300 hours observing *P. maculatus* and *E. suratensis* underwater in Negombo Lagoon, recording their behaviour using ciné cameras*. The paper that resulted from this (Ward & Wyman, 1977) showed that the two species had a much more intricate relationship than their previous laboratory studies had revealed.

Wyman & Ward (1972) had reported a cleaning symbiosis between *E. suratensis* (the host) and *P. maculatus* (the cleaner). The two species occur syntopically almost always, though the latter is vanishingly rare in fast-flowing rivers and streams. *Pseudetroplus maculatus* establishes and defends territories against intruders, whether conspecific or not. When an *E. suratensis* approached one or more adult *P. maculatus* engaged in defending a territory and adopted a head-up orientation while rapidly flickering its pelvic fins, the *P. maculatus* did not attack it. Instead, they approached the *E. suratensis* and slowly moved about, nipping specific areas on its body. Meanwhile, the host flexed its fins and its body took on a dark hue. Such encounters occurred more frequently if the hosts had fungal infections (the authors noted that the dark 'cleaning' coloration enhanced the contrast of the whitish fungi—see also Grutter, 2002: S74), and abated once they had rid themselves of the problem. Wyman & Ward (1972) noted that the cleaning bouts were more frequent early morning and late evening, less so around midday. Ward & Wyman's 1977 study, however, showed that the relationship between the two species transcended a mere cleaning symbiosis, as the following account shows.

Breeding pairs of *P. maculatus* hold territories throughout Negombo Lagoon, especially in shallower water (less than 1 m deep) with an organic sediment, whereas *E. suratensis* occupy areas 1–2 metres deep, with a sandy sediment in which *Halodule* sea-grasses predominate. Each mated pair of *P. maculatus* establish a breeding territory 45–90 cm in diameter, at the centre of which they construct a 3–4 cm deep, 2–3 cm wide pit. These sites were usually concealed by overhanging seagrass leaves or strands of algae. The pair actively defend this territory from conspecifics in adjacent territories, signalling to them with a tail-beating and body-'penduluming' threat behaviour. Their courtship activity, however, consisted of quivering, glancing at and nipping the mate, and lateral and frontal displays (Barlow, 1968, 1970), with spawning occurring around noon on the third day of courtship. *Pseudetroplus maculatus* used the leaves of aquatic plants or a hard surface such as a branch as a substrate for its eggs. Once the eggs hatched, the parents placed the eleutheroembryos (non-feeding larvae still bearing their yolk-sacs) in the central pit within the territory. Unusually for any species of fish, parental care in *P. maculatus* continued until the young had turned adult (*i.e.*, they had acquired their sexually dimorphic coloration of iridescent white bars on the dorsal and ventral tail margins in females, a red eye-spot in males).



Kelum Manamendra-Arachchi

Figure S2.5. Anterior dentition of ***a,*** *Pseudetroplus maculatus*, a piscivore; and ***b,*** *Etroplus suratensis*, an algivore (from Pethiyagoda *et al.*, 2014b).

Ward & Wyman (1977) observed that in the wild too, *E. suratensis* posed 'heads-up' for cleaning by *P. maculatus*, just as they did in the aquarium. This, however, was surprising because while *E. suratensis* is a herbivore with dentition specialized for algal scraping (see Figure S2.5), *P. maculatus* is adapted to piscivory. Indeed, they frequently saw groups of non-breeding *P. maculatus* raiding the nests of *E. suratensis* 'and in seconds consuming

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* The two species are very different in size. In Vembanad Lake (an estuarine lagoon) in Kerala India, Roshni *et al.* (2016) recorded *E. suratensis* to reach a maximum weight of 402 g and total length of 31 cm, while *P. maculatus* reached just 14 g and 9.5 cm.

entire clutches of eggs, free embryos, or early juveniles.' *Etroplus suratensis*, however, appears to have adopted a number of strategies to limit this attrition. First, it protects its eggs by depositing them on the roots of *Halodule* sea-grass, the internodes of which bear galls that resemble its eggs. It appears to do this specifically to address the threat from *P. maculatus*, for where the latter species is absent (*e.g.,* in inland rivers and streams), *E. suratensis* deposit their eggs on an open substrate such as a rock or log, nevertheless defending the site from intruders. At Negombo, raiding parties of *E. maculatus* were forced to spend time searching for eggs among the galls, incurring a delay that improved opportunities for *E. suratensis* to put up a defence. *Pseudetroplus maculatus*, however, raided not only the nests of *E. suratensis*, but also preyed on the eggs and young of their own species.

In the case of *E. suratensis*, however, up to six adults were observed tending a single school of young. Although the non-parent adults remained on the periphery of the school, they were nevertheless micronipped by the young. Ward & Wyman (1977) interpreted this to be an instance of cooperative breeding, in which a group of several adults feeds and tends a single brood. It is not yet known, however, whether the brood comprise the progeny of only one of the accompanying pairs, or whether the parent pairs themselves are related, all of which would have important evolutionary consequences (Wisenden, 1999). As pointed out by Zöttl *et al.* (2013), unrelated subordinate females may provide alloparental care under a 'pay-to-stay' arrangement in which reciprocal commodity-trading (*e.g.,* tending the dominant's offspring in return for protection or access to resources) benefits also the subordinates who invest in the care of the dominants' offspring.

In any event, the young school of *E. suratensis* remains under the protection of the parents and accompanying adults for their first six to eight weeks, by which time they are 2–3 cm long and too big to be ingested by *P. maculatus*. Then, surprisingly, they often join schools of their former enemy and enter into a symbiotic cleaning (rather than predatory) relationship.

What advantage could *P. maculatus*, an egg predator, derive from cleaning *E. suratensis*, the eggs and young of which are its prey? 'The benefit to *P. maculatus*', conjectured Ward & Wyman (1977), 'could be as simple as the survival and reproductive success of sexually mature *E. suratensis*, which in turn provide the eggs and young for the predatory habits of *P. maculatus*.' That, in effect, would be an example of livestock husbandry in the animal world. 'It seems obvious', noted these authors, 'that a few survivors protected by their parents for an extended period of time have the benefit of more experience (*e.g.,* 'an expanded behavioural repertoire': Wyman & Ward 1973) and are more likely to survive than larger numbers of offspring given less parental care.'

Figure S2.6. *Etroplus suratensis*, in a dry-zone river at Madawachchiya.

Etroplus suratensis

Ward & Samarakoon (1981) recorded *E. suratensis* (Figure S2.6) breeding during both the monsoonal and pre-monsoonal periods (most nests were seen in July, fewer in January and April). In brackish water, the fish become sexually mature at a total length of about 80 mm (150 mm in freshwater), and are not sexually dimorphic except in that ripe females are plumper than males (Costa, 1983). Unlike *P. maculatus*, which is a colonial nester (the centre of one nest usually being within 2 metres of the centre of the next), *E. suratensis* nest in isolation, nests being separated by distances of tens of metres. It appears that in areas where *P. maculatus* too, occurs, *E. suratensis* chooses nest sites that contain as few as possible of these predators of their eggs and young. In habitats lacking *Halod-*

ule sea-grass, *E. suratensis* constructs much larger pit-nests, usually more than a metre in diameter and 4–10 cm deep, within which 6–12 small sub-pits 8–l5 mm deep and wide, are excavated, and from which vegetation is cleared by grasping it in the mouth and transporting it away from the nest. In these sub-pits they deposit their eggs (which number 250 to 1,573: Padmakumar *et al*., 2012) on a hard substrate such as a log or rock (where available, they also use vertical substrates such as the face of a submerged boulder). The freshly-laid eggs are yellowish, turning brownish as they develop.

Spawning is usually completed within an hour. While *P. maculatus* parents equally take turns at guarding their nest, the non-guarding parent forages or patrols the area around the nest to deter intrusions by potentially predatory conspecifics. In the case of *E. suratensis*, however, both parents fan the eggs and stand guard over their clutch throughout, without foraging, almost never wandering beyond its perimeter. From here they repulse attempted intrusions by anything (including snorkellers) by charging at them. Ward & Samarakoon (1981) observed that 'Even when unwary hermit crabs entered the territories, they were picked up in the mouth of one of the parents and deposited outside the territory.' The eggs hatch in about 72 hours, following which, as is the case also in *P. maculatus*, the eleutheroembryos are transferred to one of the sub-pits within the territory.

SUPPLEMENT 3

Gymnothorax polyuranodon

The muraenid eel *Gymnothorax polyuranodon* is, after *Stiphodon martenstyni* (see p. 161), the most elusive fish reported from freshwaters in Sri Lanka. Described originally from Seram, in eastern Indonesia, it was until recently known from Sri Lanka from only a single specimen collected in February 1936 from the Kalu River at Kahangama, more than 50 km upstream of the river mouth (Deraniyagala, 1937). A second specimen was discovered in May 2021 in the Gin River at Wakwella.

While Sri Lanka is apparently at the western extremity of its range, *G. polyuranodon* has been reported from islands across the tropical Indo-Pacific eastwards as far as Fiji, including rivers draining the 'wet tropics' region of Australia's Cape York Peninsula in Queensland (Ebner *et al*., 2011). Based on some 36 records, these authors concluded that the species is capable of inhabiting fresh water at all times of the year. While other muraenids such as *Gymnothorax tile* and *Echidna rhodochilus* enter freshwater, they are associated primarily with estuarine habitats. Adult *G. polyuranodon* > 400 mm total length, however, are most frequently encountered in freshwater (salinity < 2.6 ‰) above the tidal influence (Ebner *et al*., 2011). These authors reported adults reaching ~800 mm, with one specimen reported at ~1500 mm total length.

Based on the Sr/Ca ratio of otoliths in four specimens (275–344 mm total length) collected from freshwaters ~13 km upstream of a river mouth in Fiji, Tsukamoto *et al*. (2014) confirmed that *G. polyuranodon* has an early marine phase, followed by an estuarine or freshwater phase after metamorphosis: 'these eels likely had a considerably long residency in either the freshwater or the river estuary after recruitment'. Nothing is known of reproduction in *G. polyuranodon*, though Ebner (2017), who maintained the species in freshwater aquariums for periods of more than a year, was optimistic about prospects for captive breeding owing to relatively low levels of aggression between individuals.

The molecular phylogeny of muraenid eels of Reece *et al.* (2010) showed *G. undulatus*, a species widely distributed in nearshore waters (though never freshwaters) across the Indo-Pacific, to have a sister-group relationship to *G. polyuranodon*. Interestingly, they estimated that the two lineages diverged in the Plio-Pleistocene and perhaps as recently as ~700 kya.

Gymnothorax polyuranodon has not up to now been reported from any country bordering the Bay of Bengal other than Sri Lanka, where both records are from rivers draining rainforested regions in the perhumid south-western wet zone. Several of the records from across the species' range too, are from rainforest habitats, though most authors do not report the climate of the collection localities. If the distribution of adult *G. polyuranodon* are in fact associated with climate, it would add a further layer of complexity to the largely unknown life history of this elusive fish.

Brendan C. Ebner

Figure S3.1. *Gymnothorax polyuranodon,* in aquarium, Queensland, Australia.

3

Sri Lanka's Biogeographic Context

Sri Lanka's rich biodiversity and remarkable endemism give it the appearance of an oceanic island masquerading as a continental one.

3.1 Early biogeographic analysis

3.1.1 Plant biogeography. The arrival in Colombo in September 1506 of Don Lourenço de Almeida, a Portuguese naval captain, quickly developed into that country taking possession of Sri Lanka's maritime regions, as it had done also at Goa, in south-western India (Ferguson, 1907). The colonizers soon began taking an interest in the region's medicinal plants, formalized through the publication in 1563 of Garcia d'Orta's *Coloquies on the simples and drugs of India* and Christóbal Acosta's (1578) *Tractado*. These paved the way for the first comparison of the floras of southwest India and the Dutch East Indies by Jacobus Bontius in his (1642) *De medicina Indorum*.

Between 1678 and 1693, Adriaan van Rheede's *Hortus Malabaricus*, in which 729 species of plants from the southern Western Ghats were depicted, was published. Meanwhile, Paul Hermann, a physician in the employ of the Dutch East India Company between 1672 and 1679, was busy making a herbarium of plants he found in the environs of Colombo, Sri Lanka's capital. This collection came to be described in three works that make up the foundation of Sri Lankan botany: Hermann's (1717) *Musaeum Zeylanicum*, Johannes Burman's (1737) *Thesaurus Zeylanicus* and Carolus Linnaeus's (1747) *Flora Zeylanica*. Collectively, these works facilitated the first comparison of the plants of Sri Lanka and the Western Ghats, which coincidentally, is the region with which the island's flora has its greatest affinity (Pethiyagoda, 2007; Pethiyagoda & Sudasinghe, 2017). Two and a half centuries later, Western Ghats–Sri Lanka came to be recognized as a Global Biodiversity Hotspot (Myers *et al.*, 2000).

The associations between the distribution of plant species within Sri Lanka, and the island's topography and climate, were first investigated, however, by Henry Trimen. Trimen (1886) observed that the flora of the region now referred to as the wet zone (rainfall > 2.5 $m \cdot y^{-1}$) differed from that of the dry zone (rainfall < 1.8 $m \cdot y^{-1}$) not so much because the latter receives less rainfall but because 'the *distribution* of rain through the year has so great an influence on fertility'. He referred, of course, to the temporal distribution of rainfall, rather than the spatial. Of the wet zone*, Trimen continued, 'and in this favoured part there are rarely any long periods without rain. A month's or six weeks' drought in February, March, or April, is the utmost experienced, and this is rarely absolute; during the rest of the year there are frequent showers in nearly every week.'

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* Sri Lanka's wet zone is bounded to the north by the westward extension of the Kangar-Pattani Line (Whitmore, 1984) on the Isthmus of Kra, which marks the northern boundary of the perhumid tropics, with flowering periodicity driven by the southern oscillation (Morley, 2018). Borneo, Sumatra and the perhumid region of the Malay Peninsula too, lie south of the Kangar-Pattani Line. Known also as the Alor Setar–Songkhla Line, this is the northern boundary for aseasonal evergreen tropical forest and the southern boundary for seasonal dry forest. Some 375 plant genera occurring south of it, and 200 occurring north of it, have ranges restricted by this line (Parnell, 2013).

Trimen's (1893–1900) *Handbook to the flora of Ceylon* provided, for the first time, the approximate distribution of each flowering-plant species. This facilitated investigations of phytogeographical relationships, both within Sri Lanka and between the island and the rest of the world. Trimen (1885) himself made a first attempt at this, remarking on the curious distributions of 108 Sri Lankan species in 86 genera that showed greater affinities to the floras of Southeast Asia, Madagascar, Mauritius and the Mascarene Islands, than to those in neighbouring India. Of the 2729 species of flowering plants then recognized as indigenous to Sri Lanka, he observed that as many as 19 genera and 800 species were endemic. The island's Gondwanan past, Earth's climatic history, and Sri Lanka's former terrestrial connections with India during sea-level low-stands were at that time unknown. As a result, Trimen was at a loss to explain the observed disjunctions except by positing ancient land bridges (which had been proposed also by Edward Forbes in 1846 and, more relevantly to the Gondwanan context, by William Thomas Blanford in 1876), for which there was, of course, no evidence at the time.

Notwithstanding these limitations, Trimen's (1886) conclusions regarding the distribution of endemic species within the island were prescient:

> 'And this leads me to mention one of the most remarkable features of the Ceylon flora, *viz.*, the very large number of species which are peculiar to the island, or, as botanists call it, endemic. About 800 species (nearly 30 per cent.) of the whole number found here are, so far as is known, found nowhere else in the world… the most distinct and well-marked of these endemic plants are almost entirely concentrated in this south-west region, which is thus seen to be as peculiar in its flora as in its climatic character. The tree vegetation of the forests above mentioned [*viz.*, Sinharaja, Hiniduma, Neluwa] is almost wholly composed of endemic species, and not a few endemic genera. And it is another significant and remarkable fact, with regard to these, that their affinities and near alliances are with the plants of the Malay Islands and peninsula far more than with the flora of southern India…'

As it happens, the close correspondence between Sri Lanka's wet zone and that of the Malay region is supported also by the more recent analysis of Slik *et al.* (2018). Then, of Sri Lanka's montane flora, Trimen (1886) observed:

> 'In distinction from the low-country vegetation, this hill-flora shows no special affinity with Malaya, while it is really very closely allied to that of the Nilgiri Mountains of S. India… [Figure 3.1]. Less than 400 miles separates the summits of Pidurutalagala, the highest mountain in Ceylon, and Doddabetta in the Nilgiris (and there are half-way houses in the Pulnis and Anamalais). Yet the curious fact presents itself that more than half the species in the Ceylon hills are not found in the Nilgiris or other hills of the Indian Peninsula, but are endemic there, and probably an even larger proportion of Nilgiri species do not extend to Ceylon[*]. The number common to both ranges is only about 200. Yet very nearly all belong to the same genera, which are almost identical for both regions. It is thus possible to make the contradictory assertions that the floras are very similar and very different… Of the genus *Strobilanthes*… the Ceylon hills possess twenty-two peculiar species, and the Nilgiris &c., about twenty nine, whilst only two are found in both regions; of the mountain species of *Impatiens*, there are two common to both ranges, while Ceylon has ten others endemic… If we suppose a common origin for both these hill-floras in the past, or derive the one from the other, the differences now seen in the two districts indicate a sufficient lapse of time since their separation to allow of the evolution under different surroundings of new forms of the rank of species, but not of the superior rank of genera.'

Finally, of the flora of Sri Lanka's northern dry zone he noted:

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[*] Species-endemism in both the Sri Lankan mountains and the Nilgiris is in fact lower than Trimen estimated in the framework of the taxonomy of his time. Suresh & Sukumar (1999) found, for example, that around eight percent of woody species in the Nilgiri shola are shared with Sri Lanka. Their results show, however, that the proportion of shared higher taxa is much greater.

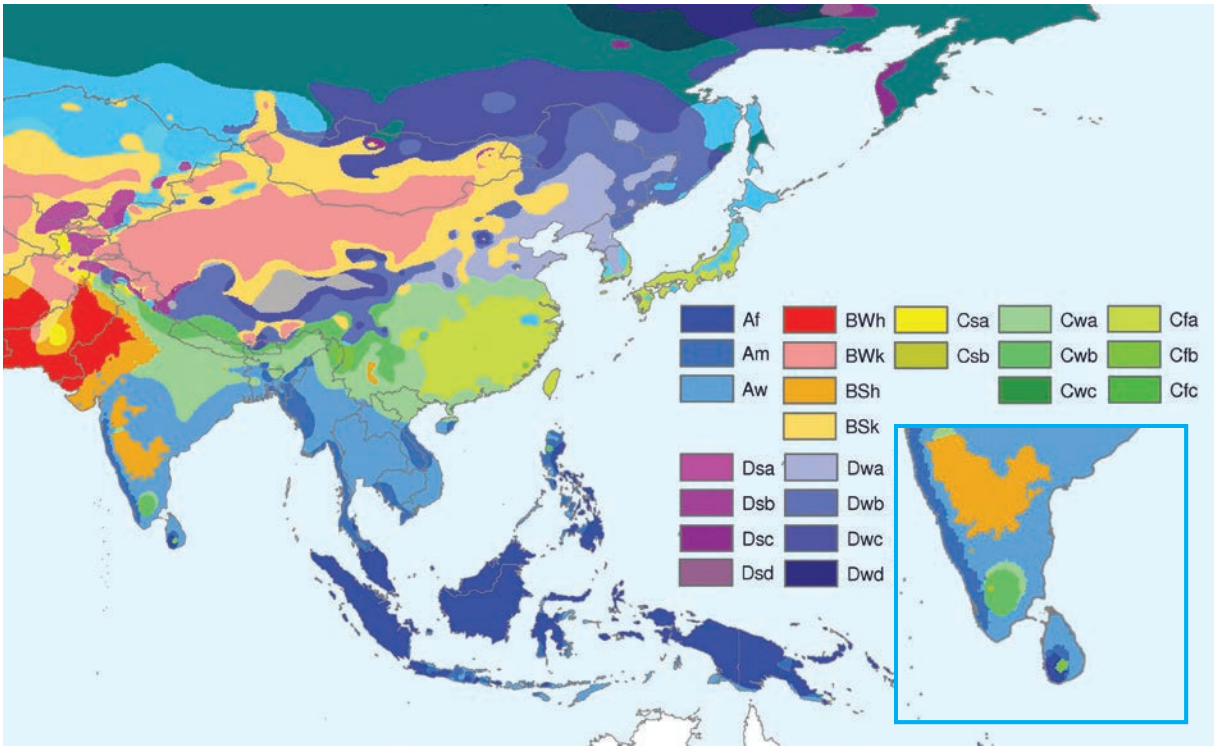

Figure 3.1. Updated Köppen-Geiger climate-type map of eastern and southern Asia (reproduced with permission from Peel *et al.*, 2007: http://people.eng.unimelb.edu.au/mpeel/koppen.html). For the complete key to vegetation types, see table 2 of Peel *et al.*, 2007. The key to the vegetation types relevant to Sri Lanka, India and Southeast Asia is: **A,** tropical **f,** rainforest; **m,** monsoon forest; **w,** savannah. **B,** arid, **W,** desert; **S,** steppe; **h,** hot; **k,** cold. **C,** temperate, **s,** dry summer; **w,** dry winter; **f,** without dry season; **a,** hot summer; **b,** warm summer; **c,** cold summer. Trimen (1885) showed that Sri Lanka's lowland wet zone flora shows its greatest affinity to the rain forests of southern Peninsular Malaysia, Borneo and Sumatra, whereas the montane flora is more similar to that of the highlands of the Western Ghats, and the dry zone flora is nearly identical to that of south-eastern Peninsular India. As seen from this map, these vegetation types correlate closely with climate, with tropical rainforest ocurring nowhere else in South Asia except within Sri Lanka's minute, though biodiversity-rich, perhumid south-western wet zone.

> 'The plants of all this dry district of Ceylon are essentially those of the Carnatic and Coromandel coast of the opposite Indian continent. Nearly all of the species are identical, and there is a much greater similarity between the two countries than between the two climatic districts of Ceylon itself. So far as the flora is concerned, one would think the separation of Ceylon from the mainland (now parted by the very shallow Palk's Strait) to be geologically recent; even the few endemic species in this part of Ceylon are all closely related to the continental ones, and clearly derivable from them or from common ancestors. And the Malayan element, so prevalent in the low country of South-west Ceylon, is here conspicuously absent.'

Trimen (1885) and J. C. Willis (1915) were the earliest workers to recognize the uneven distribution of plant species in Sri Lanka and seek correlations that explained these. By and large, they considered the spatial and temporal distribution of rainfall, together with elevation, to be the primary determinants of plant distributions*. Appreciation of edaphic factors and the concept of plant communities, on which Darwin (1861) had placed considerable emphasis, were largely neglected.

Even by Trimen's time, however, the deforestation of the wet zone had been so extensive that he recognized the problem of understanding, for example, whether a locally-endemic species had a circumscribed range because it was biologically restricted to a single site, or because its natural

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* See Supplement 5, p. 138.

distribution had been decimated. Of the wet-zone lowlands Trimen (1886) observed:

> ‘No doubt the whole of this part of Ceylon was once covered with heavy forest; but most of this has now disappeared, and the country is thickly inhabited. The lower lands are mostly devoted to paddy (*i.e.*, rice) cultivation, and the more elevated parts between are occupied by villages… A few portions of original forest still remain in the tracts of country between Ratnapura and Galle, of which that known as the Singhe-Rajah is the most extensive. Here the true native flora of Ceylon can still be seen unaltered, and is of remarkable interest, as will immediately be shown. The agent of destruction of the forests here has been the indolent and improvident practice of native cultivation known as ‘chena’*, a practice which has prevailed and been continued from a remote antiquity, and by which, for the sake of a single crop of some miserable grain such as Kurakkan (*Eleusine coracana*), the forest growth of centuries is sacrificed.
>
> ‘Native vegetation has also been curiously preserved in a few places which ‘chena’ cultivation has been unable to reach, namely, on the precipitous summits of certain of the small isolated gneiss, rocks, or hills scattered over the south part of the district, such as Hiniduma (or Haycock) and Nillowe Hills. The space on the tops of these rocks is very small and steep, but here, crowded together, are a number of remarkable species mostly peculiar to Ceylon, and in several cases now entirely restricted to the few square yards in question on those isolated spots.’

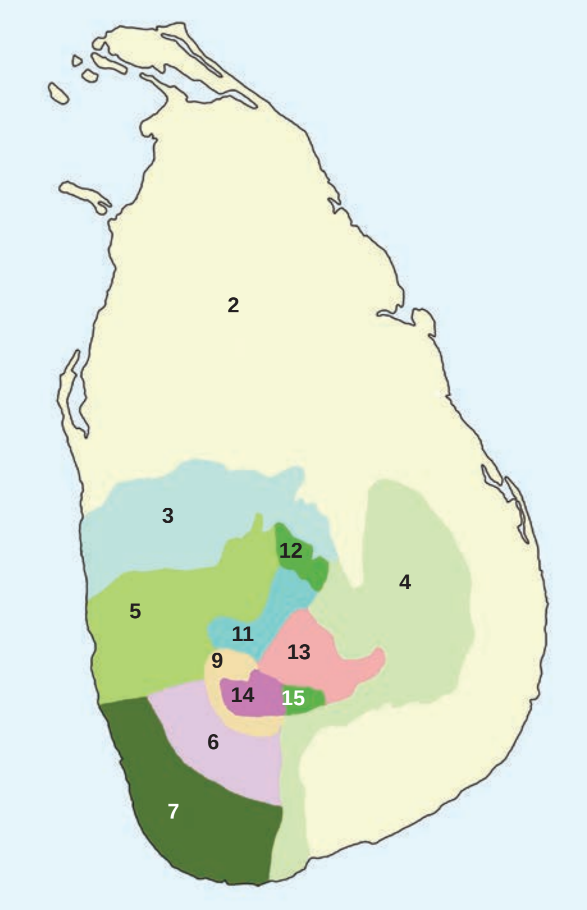

Figure 3.2. Floristic zones of Sri Lanka; adapted from Ashton and Gunatilleke (1987). The zone-numbers are a subset of those of Gaussen *et al.* (1964): 2, dry zone; 3, northern intermediate lowlands; 4, eastern intermediate lowlands; 5, northern wet lowlands; 6, south of Ratnapura - northern Sinharaja; 7, southern Sinharaja-Hiniduma-Kanneliya; 9, foothills of Adam’s Peak north of Ratnapura-Ambagamuwa; 11, Kandy - upper Mahaweli; 12, Knuckles; 13, central mountains - Ramboda - Nuwara Eliya; 14, Adam’s Peak; 15, Horton Plains.

Several authors since Trimen have proposed floristically characteristic forest types for Sri Lanka, identifying distinct floristic provinces (*e.g.*, de Rosayro, 1950; Koelmeyer, 1957; Gaussen *et al.*, 1964; Ashton & Gunatilleke, 1987; Greller & Balasubramaniam, 1993). While varying in detail, the broad regions they propose are largely consistent with the 15 provinces identified by Ashton & Gunatilleke (1987; Figure 3.2), which have been followed by almost all subsequent authors.

Perhaps most notably, Ashton & Gunatilleke (1987) identified several areas of exceptionally high flowering-plant endemism within the island, most importantly the ~10 km wide horseshoe-shaped band of foothills that skirts Adam’s Peak, from Maskeliya in the northwest, south through lowland Ambagamuwa and then eastwards again, through Kuruwita and from there almost to Belihul Oya (Zone 9 in Figure 3.2; see

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* Shifting ‘slash-and-burn’ or swidden cultivation. As pointed out by Ashton and Gunatilleke (1987), however, the peopling of the island’s south-western wet-zone lowlands and the consequent devastation its forests occurred relatively recently, following the retreat of the royal court southwards to Dambadeniya in the thirteenth century.

also Figures 3.3, 3.4). 'The strip as a whole, and the western half in particular,' they noted, 'is the wettest and least seasonal part of the lowlands.'

The second area of high endemism that Ashton & Gunatilleke (1987) recognized extends from the southern block of hills immediately east of Kalutara, running in an arc parallel to the coast, about 30 km inland of it, ending just inland of Hulandawa (Figure 3.4). 'This block', they observed, 'is without doubt floristically the richest area of Ceylon, and indeed of all South Asia.'

Despite a wealth of georeferenced data being available, both from the records of the National Herbarium and the National Conservation Review (Green, 1995), the proposed floristic zones remain to be tested objectively through geospatial analysis*. Nevertheless, the 15 floristic zones recognized by Ashton & Gunatilleke (1987) possess intuitive appeal, and the broad vegetational transition they observed from lowland to hill forest at an elevation of around 1000 m, and from hill to submontane forest at ~1500 m, have found wide utility (*e.g.*, Wikramanayake *et al.*, 2002; Gunatilleke *et al.*, 2008).

3.1.2 Early regional biogeography. 'When we attempt to compare Ceylon with other tropical regions,' noted Trimen (1885), 'the difficulty meets us that there is scarcely any [other] definite area of which the flora has yet been so thoroughly worked out.' While he was right, he omitted to mention (because it no doubt was common knowledge at the time) Joseph Dalton Hooker's (1872–97) encyclopaedic *Flora of British India*, work on which was by then almost complete. Trimen (1885) was thus able to compare the Ceylon and Indian floras, discovering in the process that about a hundred genera of spermatophytes occurring in Ceylon were absent from India; 56 non-endemic genera were absent from India but contained only endemic species in Ceylon; and a further 31 genera were absent from India but contained non-endemic species in Ceylon.

While several of these disjunct taxa have since been discovered in India or shown to be victims of taxonomic error, at least 37 plant genera that occur in Sri Lanka are absent from the peninsula of India, recurring only in Malesia or further afield (Table 3.1). It appears that these taxa once populated the Deccan Peninsula but were extirpated there owing to the prolonged aridification of that region.

Despite barely 25 years having elapsed since the publication of Darwin's *On the origin of species* (1859), it is clear that Trimen (1885) had fully absorbed the implications of that work. For example, as seen from his comparison of the Nilgiri flora with that of the Ceylon hills, he concluded from the fact that nearly all the genera are shared, though about half the species are endemic to each region, that the two floras had been (terrestrially) connected relatively recently. Such a conclusion implies a postulation not only of much lower sea levels but also of a much cooler and less seasonal former climate in the present-day 'dry-zone' of Sri Lanka's northern plains.

Trimen (1885) extended this inference to conclude that should only families (and not genera or species) be shared by two regions, their connection must have been more ancient still, and cited a compelling example:

> 'The two richest and most specialized floras in the world, as already noticed, are those of the [African] Cape and Australia; probably scarcely a genus is common to them, yet the large and well-marked Natural Orders Proteaceae and [Restionaceae] are abundant in each of these far distant regions, and are almost confined entirely to them. This, according to the present views, implies a common focus of origin in a remote past.'

Just as in the case of the Nilgiris and Ceylon Highlands, the mechanism by which Australia and Africa—now separated by 8000 km of ocean—had once been connected was unknown to Trimen; but he deduced that such a connection must once have existed.

3.1.3 Zoogeography. Trimen's (1885) recognition of the close relationship between the floras of Ceylon on the one hand, and of the southern Western Ghats and Indomalaya on the other, had been anticipated for the fauna by Alfred Russell Wallace (1823–1913), just eight years earlier. In his *Geographical distribution of animals*, Wallace (1876) considered Sri Lanka, together with South India, as a

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* But see Perera *et al.* (2019) for an on-going initiative.

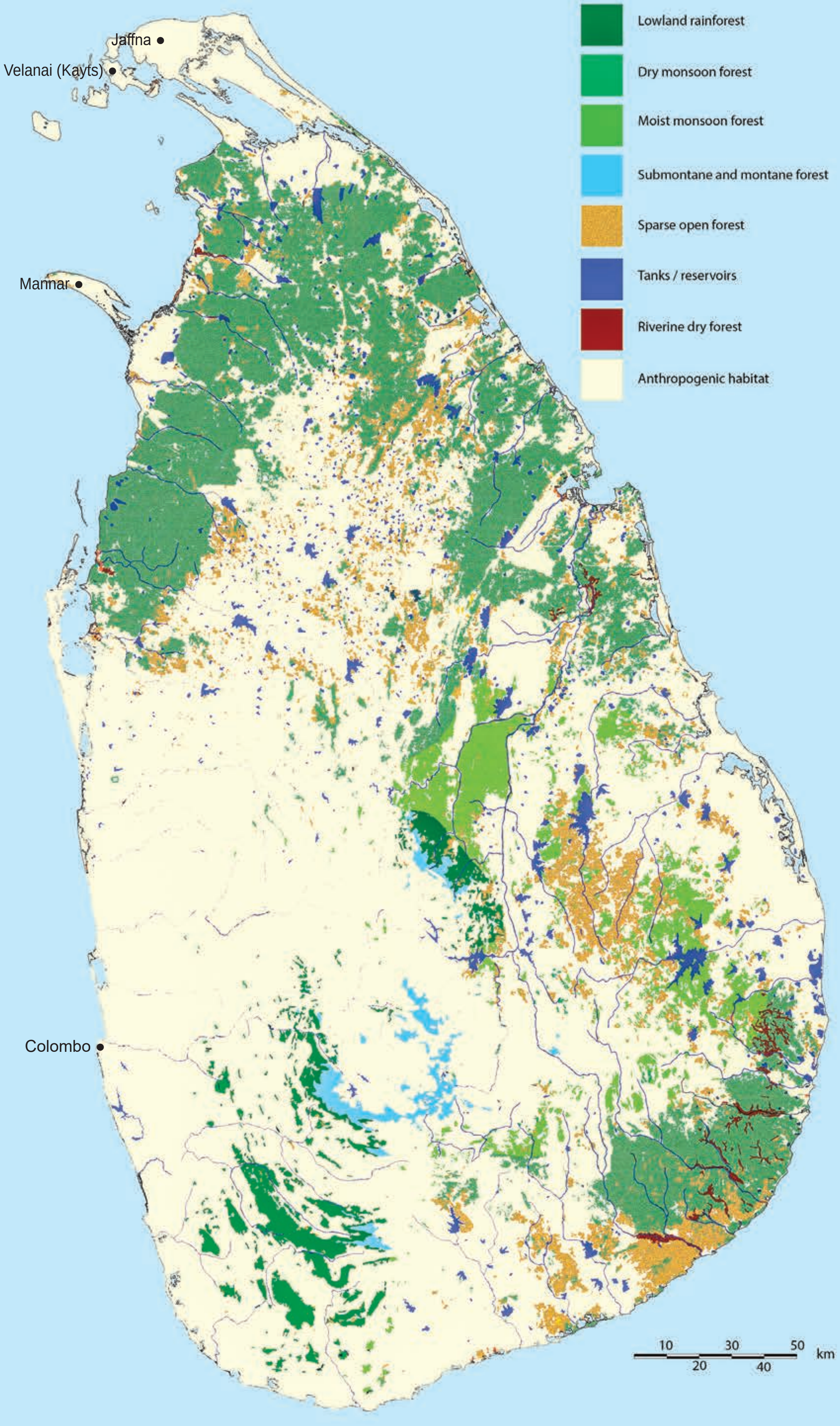

Lowland rainforest
Dry monsoon forest
Moist monsoon forest
Submontane and montane forest
Sparse open forest
Tanks / reservoirs
Riverine dry forest
Anthropogenic habitat
Jaffna
Velanai (Kayts)
Mannar
Colombo
10
30
50
km
20
40

Table 3.1. Genera of plants occurring in Sri Lanka and elsewhere other than the peninsula of India.

Genus	Family	Distribution outside Sri Lanka
Erythrospermum	Achariaceae	Mauritius, China, New Guinea, Samoa, Fiji (Dassanayake & Fosberg, 1980–2006).
Ptyssiglottis	Acanthaceae	Indochina, Sumatra, Java, Borneo, Philippines, New Guinea, Bismarck Archipelago (Hansen, 1992).
Campnosperma	Anacardiaceae	Malesia, tropical Africa, tropical America (Dassanayake & Fosberg, 1980–2006)
Cleghornia	Apocynaceae	Peninsular Malaysia, China (Xu, 1988).
Dischidia	Apocynaceae	Southeast Asia, Malesia,E Himalayas to Taiwan, New Guinea, NE Australia (Dassanayake and Fosberg, 1980–2006).
Ochrosia	Apocynaceae	Indian Ocean to Pacific (Hendrian, 2004; Dassanayake and Fosberg, 1980–2006).
Willughbeia	Apocynaceae	Assam to Philippines (https://wcsp.science.kew.org).
Oncosperma	Arecaceae	Philippines (https://wcsp.science.kew.org).
Rhipsalis	Cactaceae	Americas, Africa, Mascerenes, Sri Lanka (Dassanayake & Fosberg, 1980–2006).
Axinandra	Crypteroniaceae	Borneo and the Malay Peninsula (Rutschmann *et al.*, 2004).
Scirpodendron	Cyperaceae	Northeast India to western Pacific (https://wcsp.science.kew.org).
Tricostularia	Cyperaceae	China to Australia (https://wcsp.science.kew.org).
Cotylelobium	Dipterocarpaceae	South Thailand, Malay Peninsula, Borneo (Dassanayake & Fosberg, 1980–2006)
Adenochlaena	Euphorbiaceae	Comoros, Madagascar (https://wcsp.science.kew.org).
Strongylodon	Fabaceae	Madagascar, Reunion, northeast Australia, New Guinea, Sulawesi, Philippines, western Pacific islands (Huang, 1991).
Crawfurdia	Gentianaceae	China, Vietnam, Burma, Bhutan, Sikkim, NE India (Dassanayake & Fosberg, 1980-2006; Favre *et al.*, 2010).
Hanguana	Hanguanaceae	Malaysia to Micronesia (https://wcsp.science.kew.org).
Glossocarya	Lamiaceae	Myanmar to Queensland, Australia (https://wcsp.science.kew.org).
Hypserpa	Menispermaceae	Indo-Malesia, NE Australia, Caroline Is., New Caledonia, Vanuatu (Forman, 1997)
Allaeanthus	Moraceae	Philippines, Sulawesi, Madagascar (Chung *et al.*, 2017).
Nepenthes	Nepenthaceae	Indomalaya, Seychelles, Madagascar, Assam, Indochina, New Guinea, northern Australia, New Caledonia (Meimberg *et al.*, 2001).
Angraecum	Orchidaceae	Seychelles; tropical and southern Africa (https://wcsp.science.kew.org).
Bromheadia	Orchidaceae	Myanmar, Indochina, Indomalaya, Australia (https://wcsp.science.kew.org).
Cryptostylis	Orchidaceae	Tropical and subtropical Asia, Australia, western Pacific islands (https://wcsp.science.kew.org).
Erythrodes	Orchidaceae	Assam to Philipppines; western Pacific islands (https://wcsp.science.kew.org; Fernando & Ormerod, 2008).
Freycinetia	Pandanaceae	China, Indochina, Indomalaya, Philippines, northeast Australia, Pacific Islands, New Zealand (Dassanayake & Fosberg, 1980-2006; https://wcsp.science.kew.org).
Thuarea	Poaceae	Madagascar to the Pacific (https://wcsp.science.kew.org).
Dichilanthe	Rubiaceae	One species each in Sri Lanka and Borneo (https://wcsp.science.kew.org).
Nauclea	Rubiaceae	Southeast Asia, through Malesia to New Guinea and Australia (https://wcsp.science.kew.org).
Urophyllum	Rubiaceae	Malaysia to Philippines (https://wcsp.science.kew.org).
Dovyalis	Salicaceae	Africa (Sleumer, 1972; Dassanayake & Fosberg, 1980–2006).
Ginalloa	Santalaceae	Andaman Islands across Malesia to Bismark Archipelago (Dassanayake & Fosberg, 1980–2006).
Notothixos	Santalaceae	Malay Peninsula, Indonesia, Australia (Dassanayake & Fosberg, 1980–2006; Bussing, 2000).
Osmelia	Salicaceae	Malay Peninsula to New Guinea (Dassanayake & Fosberg, 1980–2006).
Glenniea	Sapindaceae	Tropical Africa, Madagascar, Malesia (Bürki, 2009).
Phaleria	Thymelaeaceae	Malesia, Micronesia, Samoan Islands, Tonga, Australia (Herber, 2001).
Sciaphila	Triuridaceae	Japan, Solomon Islands (https://wcsp.science.kew.org).

◄ **Figure 3.3**. Distribution of natural vegetation (including secondary-growth forest) in Sri Lanka, based on the map 'Forest Cover of Sri Lanka' (1997), Forest Department, Colombo.

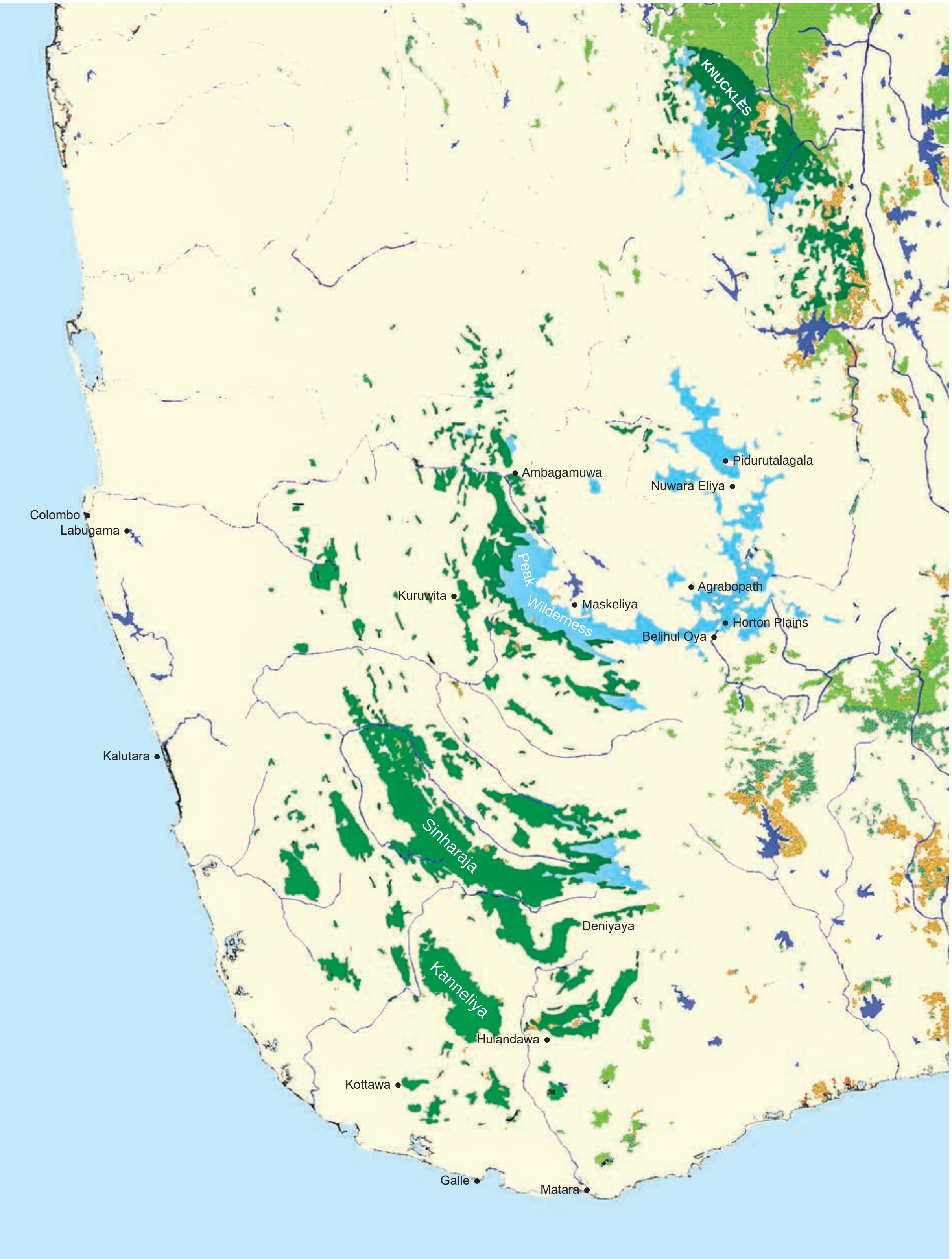


Figure 3.4. Distribution of natural vegetation in the wet south-western quadrant of Sri Lanka (see also Figure 2.5), indicating features mentioned in the text; based on the map 'Forest Cover of Sri Lanka' (1997) published by the Forest Department, Colombo. See Figure 3.3 for key to vegetation colour-codes.

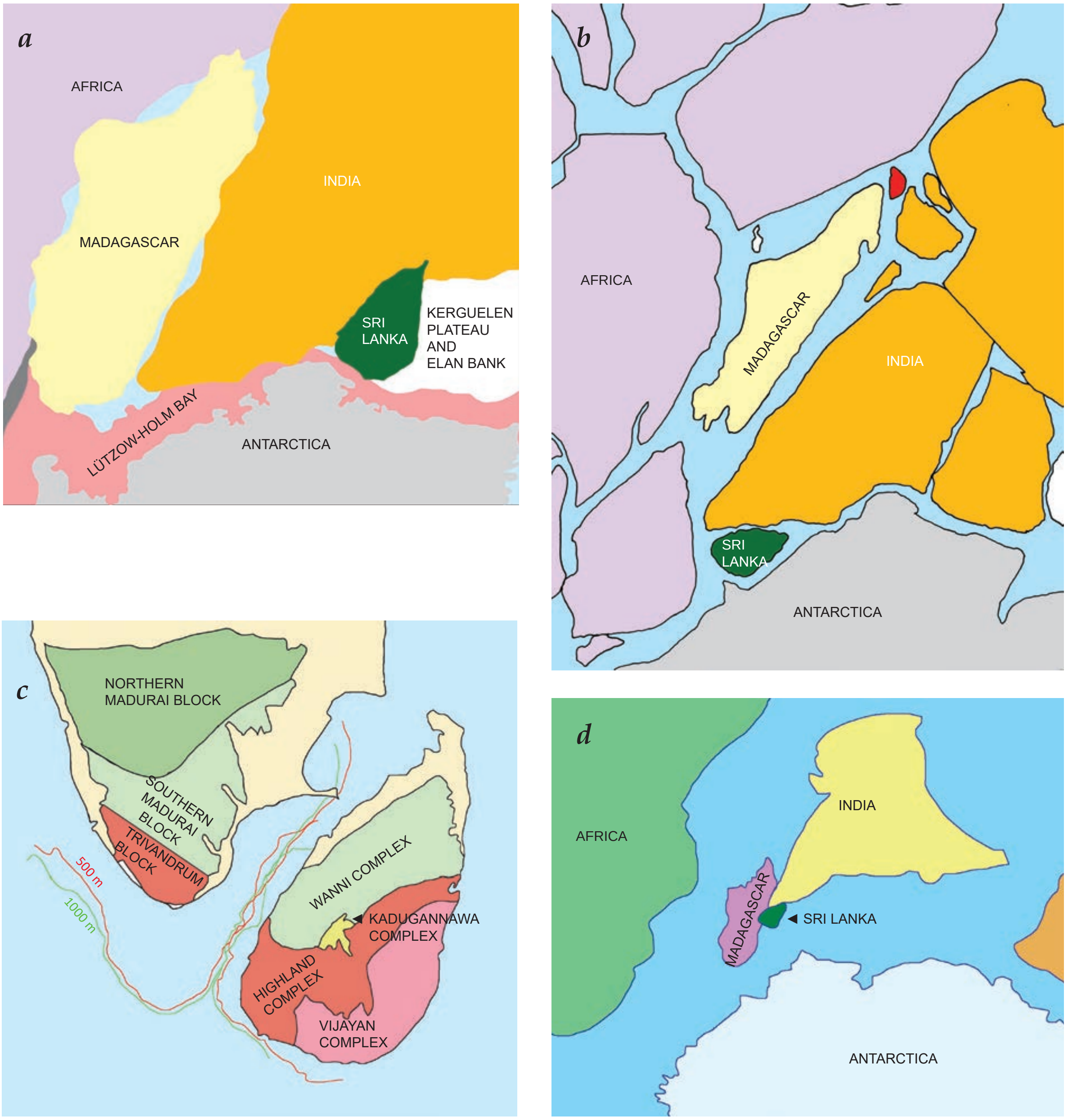
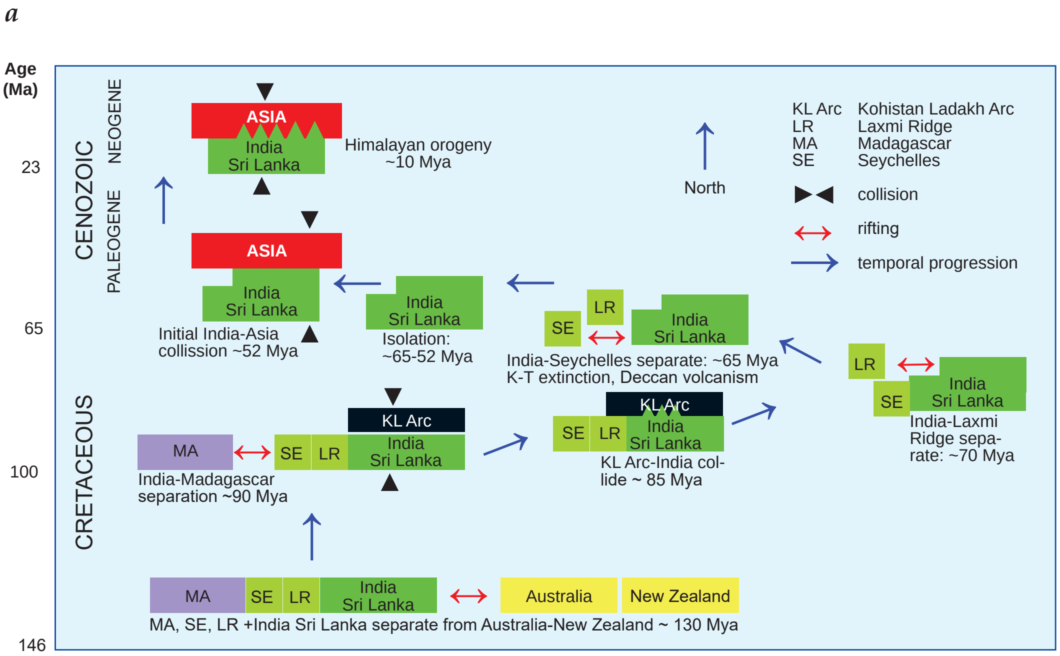
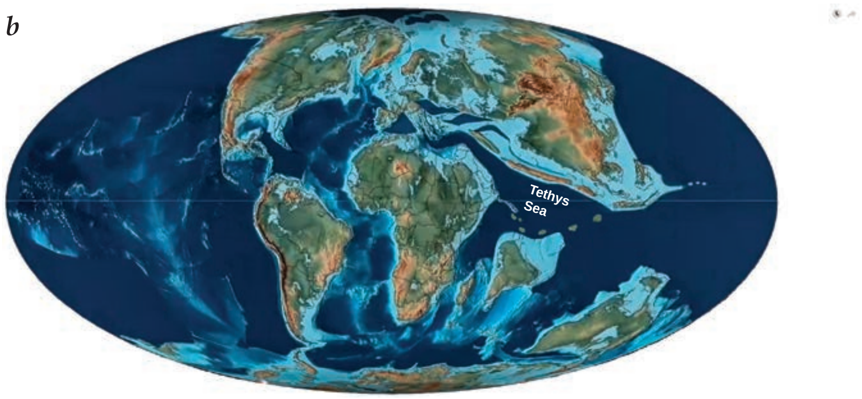
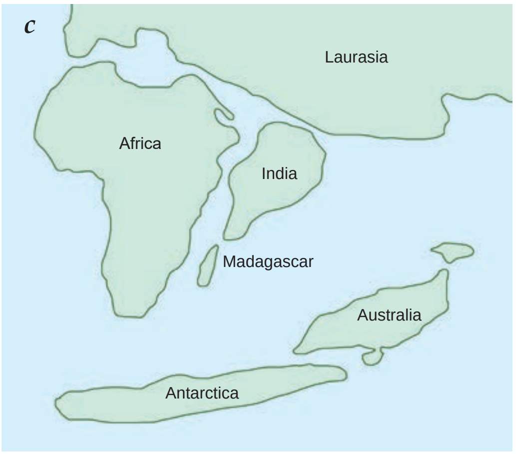


Figure 3.5. The position of Sri Lanka in relation to other Gondwanan landmasses, adapted from the reconstructions of ***a,*** Eagles & König (2008). ***b,*** Reeves (2014) ~168 Mya, with Seychelles indicated in red. This juxtaposition of India-Sri Lanka is broadly supported also by the Paleo-fit reconstruction of Ratheesh-Kumar *et al.,* 2020, at 240 Mya. See Dissanayake & Chandrajith (1999) and McCarthy *et al.* (2007) for alternative—but well-supported—juxtapositions. ***c,*** Paleo-fit of Sri Lanka with respect to India 140 Mya in the construction of Ratheesh-Kumar *et al.* (2020), based on best fit of bathymetric contours and compatibility with correlations with geochronological belts such as the matching of Sri Lanka's Highland and Wanni Complexes with India's Trivandrum and Madurai Blocks, respectively (see also the broadly similar reconstructions of Kitano *et al.*, 2018 and Jain *et al.*, 2020: 134). ***d,*** Juxtaposition of India-Sri Lanka- Madagascar as at 124.8 Mya in the construction of Nguyen *et al.*, 2016.







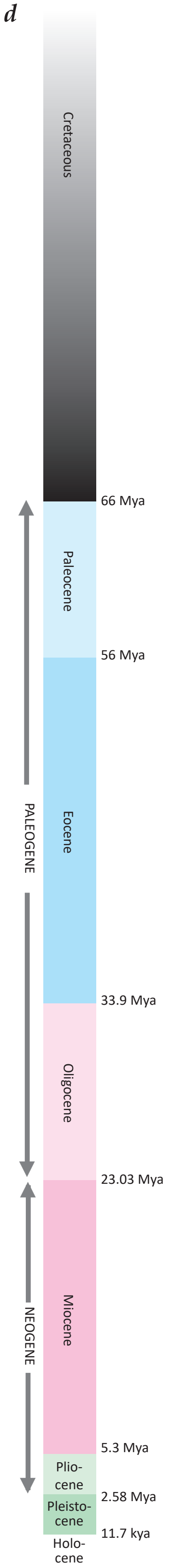
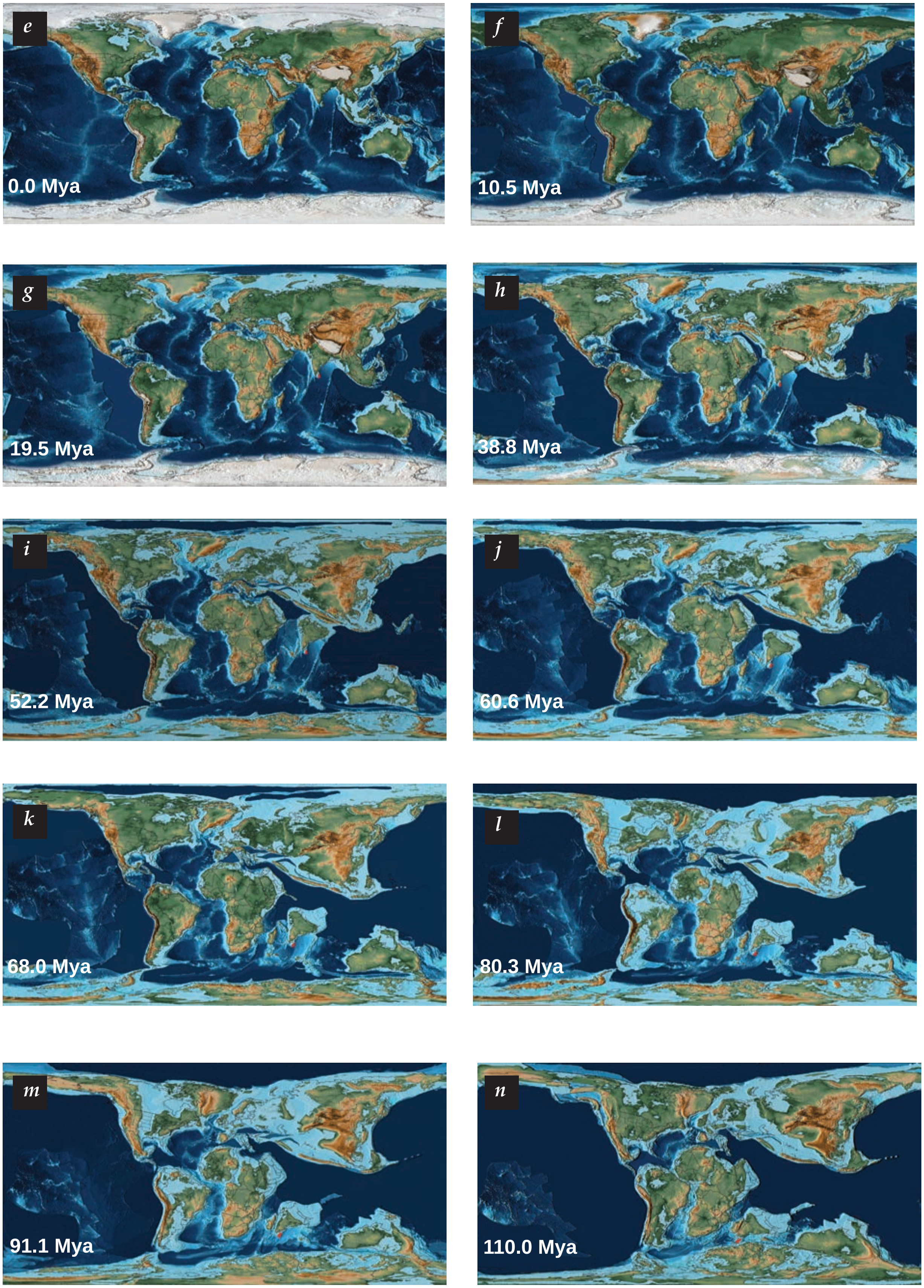


Figure 3.6. ***a,*** One-dimensional schematic of the sequence of rifting and accretion of India–Sri Lanka over the past ~146 My, based on Chatterjee *et al.* (2013). Possible contact of the Kohistan-Ladakh Arc with Africa is not shown. ***b,*** India in relation to Laurasia, Africa and Madagascar at the K-Pg boundary (~66 Mya), from Scotese (2016); ***c,*** The reconstruction of Briggs (2003a), which seeks to account for the biotic connections between India, Laurasia, Africa and Madagascar around the K-Pg boundary, inferred from fossil and molecular-clock analyses, with the Kohistan-Ladakh Island Chain added following Chatterjee *et al.* (2013; Fig. 16); ***d,*** Geochronological time-scale associated with *a*. ***e–p,*** the trajectory of India-Sri Lanka and Africa with respect to Laurasia following the breakup of Gondwana, 132 Mya to present. Possible contact of the Kohistan-Ladakh Arc with Africa is not shown. From C. R. Scotese, PALEOMAP Project (www.scotese.com).


e
0.0 Mya
f
10.5 Mya
g
19.5 Mya
h
38.8 Mya
i
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91.1 Mya
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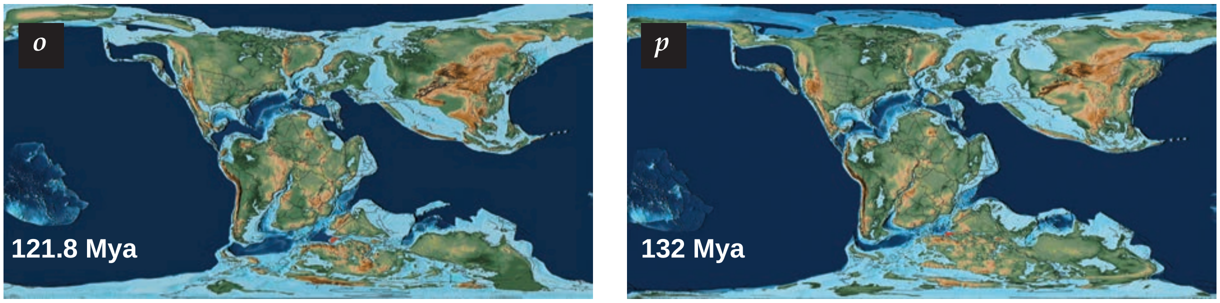
110.0 Mya



◀ For caption, see page 74, Figure 3.6.

distinct sub-region of his Oriental region, thereby recognizing the distinction of the biota of this bloc from that of the rest of India.

Among the few other noteworthy contributors to Sri Lankan zoogeography in the colonial period was Edmund William Hunt Holdsworth (1829–1915), who first described the geographical distribution of bird species within the island, giving detailed locality information. Sidney Dillon Ripley (1949, 1980) added to this work, drawing particular attention to the close connection between the Sri Lankan and Malayan avifaunas, while Aloïs Humbert (1829–1887) was among the earliest workers who sought to explain the similarities of the insular faunas of Sri Lanka and Malesia by positing ancient terrestrial connections, uplift and sea level fluctuations.

Despite these initiatives, zoogeography lagged phytogeography in Sri Lanka by more than a century. The Colombo Museum was opened only in 1877, a year before the Indian Museum in Kolkata. Even after the establishment of the former, there was never a formal attempt to survey the island's zoological wealth as the plants had been. Zoology remained in the province of amateur students of natural history who, for the most part, were eclectic in their objects of study.

3.2 Sri Lanka's tectonic history

3.2.1 Gondwana*. Sri Lanka and India were, together with Madagascar, Africa, South America, Antarctica and Australia, part of the ancient supercontinent of Gondwana. Analyses of gravitational anomalies and geological data show Sri Lanka to have lain within the present-day Cosmonaut's Sea off northeast Antarctica during the early Jurassic, the island's north-south axis inclined about 90° Clockwise of its present orientation (Figure 3.5). Its present-day eastern margin was in contact with Antarctica in the region of Enderby Land, its now-western margin still part of the eastern Indian Peninsula (Eagles & König, 2008; Lal *et al.*, 2009; Gibbons *et al.*, 2013; Reeves, 2014; Ratheesh-Kumar *et al.*, 2020).

3.2.2 Gondwana breakup. By around 180 Mya, however, a more consequential process had begun: the fragmentation of Gondwana. Between 165–118 Mya, a large fragment comprising of Sri Lanka-India, the Laxmi Ridge, Seychelles and Madagascar separated from Antarctica–Australia. Around 132 Mya, about the time to which modern flowering-plant families date (Morley, 2000), Australia and Antarctica broke away from the Madagascar–Seychelles–India subcontinent (Figure 3.6), while Madagascar retained its position with respect to Africa, from which it was now separated by the Mozambique Channel (Reeves, 2014).

As India rifted from Antarctica, Sri Lanka initially retained its position as an integral part of Antarctica. About 128 Mya, however, the India-Sri Lanka rift failed, and Sri Lanka too, separated from Antarctica and followed India on its northward transit. This led to the formation of the microplate of Sri Lanka, which in turn began its anticlockwise rotation with respect to India. Seafloor spreading during this rotation led to the continental extension of the microplate's northern margin: the emergent part of this would become the Palk Isthmus. By ~120 Mya, the Sri Lanka microplate

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* The chronology and sequence of India's 130-My, 9000-km northward drift across the Indian Ocean and its subsequent connections with other Gondwanan terranes and with Asia are fraught with controversy. In this chapter, except where specifically mentioned, we follow the synthesis of Chatterjee *et al.* (2013).

had rotated almost to its current orientation with respect to India (Desa *et al.*, 2018; Ratheesh-Kumar *et al.*, 2020). The region of the Palk Isthmus, meanwhile, appears to have undergone thermal subsidence in the course of the Cenozoic (Premaratne *et al.*, 2016), leading to its inundation during episodes of lowered sea level.

Then, ~90 Mya, with Sri Lanka appended to the Subcontinent's south-eastern margin, India–Seychelles rifted from Madagascar (Storey, 1995; Storey *et al.*, 1995). The eastern coastlines (shelf margins) of present-day Sri Lanka and peninsular India match the geology of the margin of Antarctica from which they rifted (Lal *et al*., 2009). Correspondingly, the western margin of peninsular India is defined by its former Antarctic and Madagascan connectivity (Mandal *et al*., 2017). The northern boundary of the Indian plate, and especially the extent of it that was aerially exposed, is as yet poorly known, and this has resulted in uncertainty regarding its subsequent contacts with Asia and Africa. By the time the India-Madagascar rift occurred (in the Coniacian: ~89–86 Mya), or in any event, before the Cretaceous-Paleogene boundary ~66 Mya, several elements of the African flora had dispersed to the north-bound Indian plate (Storey *et al*., 1995; Morley & Dick, 2003).

3.2.3 Contact with Asia. The subduction of the northern extremity of the Indian craton as it drifted northwards gave rise to the Kohistan–Ladakh Arc of volcanic islands, formed by the obduction of deep oceanic crust to the northwest of the Indian plate. Now sandwiched between the Indian and Asian plates, the Arc appears to have been a wide ridge and/or extensive chain of volcanic islands whose western margin had intermittent contact with East Africa (Chatterjee *et al.,* 2013)*. The subsequent contact between the Kohistan–Ladakh Arc and India appears to have occurred ~85 Mya (Chatterjee *et al*., 2013, 2017), at which time it was at around the latitude of the equator, potentially providing for the exchange of tropical biotas between India and Africa, and perhaps explaining the dispersal from Africa to India of notopterid knife-fishes 105–43 Mya (Lavoué, 2016, 2019; Barby *et al*., 2018), though Gondwanan vicariance cannot yet be ruled out.

Around 70 Mya, the 700 km long Laxmi Ridge, together with the Seychelles, which until then had been part of the north-western Indian plate, began separating from India. By 65 Mya the Seychelles had broken completely away from the Subcontinent.

At about the same time (~66 Mya), around the Cretaceous-Paleogene boundary, coincident with the global 'K-T' extinction that resulted from a meteorite impact on the Yucatán Peninsula in Mexico, India underwent a uniquely violent episode of volcanism. This resulted in the deposition of some one million cubic kilometres of basalt, creating the Deccan Traps across the north-western region of the peninsula, east of present-day Mumbai (Figure 3.7). Chenet *et al.* (2008) estimated that the total volume of SO_2 emitted by the eruptions may have been of the order of that released by the Yucatán impact, and concluded that if several of the eruptions associated with the Deccan larva flows occurred at about the same time, they could by themselves have resulted in a global mass extinction (see also Samant & Mohabey, 2009).

This perhaps explains why so few Gondwanan plant and animal lineages survived into the Paleogene of India and Sri Lanka. Though most pronounced around the Cretaceous-Paleogene boundary, Deccan volcanism began before the meteorite impact (Schoene *et al.,* 2019; Hull *et al.,* 2020) and continued well into the Eocene and perhaps even into the Oligocene (Beane *et al*., 1986), no doubt affecting plant and animal distributions. Nevertheless, the southern Western Ghats (and owing to its remoteness, probably Sri Lanka, too) served as important biodiversity refugia during the upheavals of the Cretaceous-Paleogene extinction as well as those associated with Deccan volcanism (Joshi & Karanth, 2013).

The Indian plate, however—now accreted to the Kohistan–Ladakh Arc—continued its northward drift at 3–5 $cm \cdot y^{-1}$ during most of the Cretaceous, though during the Late Cretaceous to Early Eocene (~67–50 Mya) its northward transit was more rapid.

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* There is convincing biotic evidence for India-Africa / Madagascar connectivity up to the Cretaceous-Paleogene boundary, though the form this took is as yet unknown from geological evidence. Prasad *et al.* (2010) showed, for example, that Indian fossil tetrapods dating to this period show close affinities to African ones. Van Bocxlaer *et al.* (2006) and Chen *et al.* (2019) provided further evidence from amphibians.

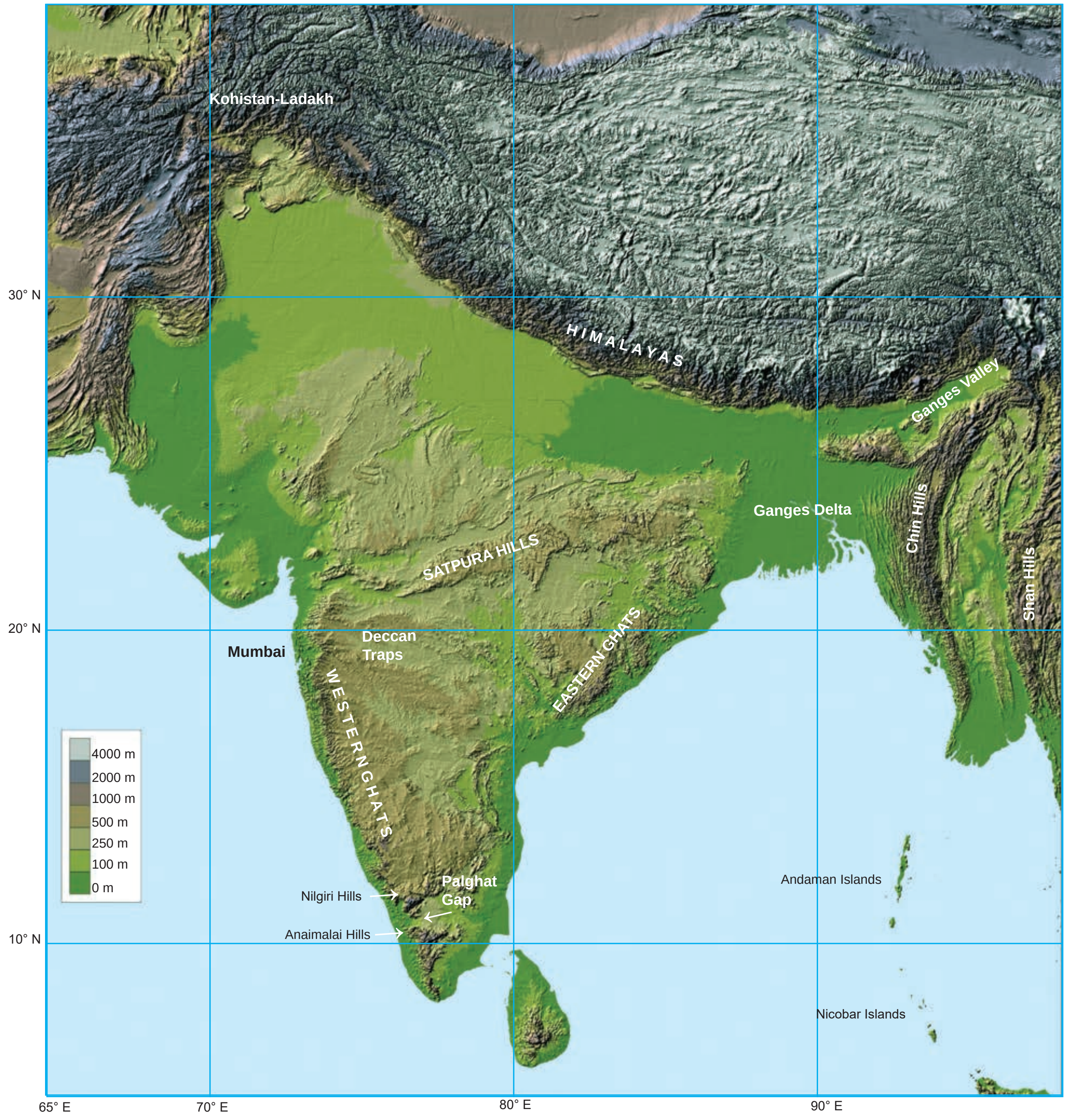

Figure 3.7. Topography of India–Sri Lanka showing physical features referred to in the text, adapted from *www.treehouse-maps.com*.

By the time Deccan volcanism had subsided, India was once more an island. Its collision with Asia in the early Eocene slowed its northward motion to around 5 cm·y^{-1}. The modelling of Ali & Aitchison (2008) suggests a progressive India-Asia contact, with the north-eastern corner of the subcontinent making a glancing contact with Sumatra, thereafter Burma (~57 Mya[*]) and finally with Laurasia. Other authors, however, project a more direct northward approach to Asia (Acton, 1999; Ali & Aitchison, 2008; Klaus *et al.*, 2010; Li *et al.*, 2013). In any event, there was contact between India and Laurasia 59–45 Mya, with dispersal into Asia of 'rainforest' taxa such as Dipterocarpaceae, *Axinandra* and *Trichadenia* and, among animal groups, the heterometrine scorpions and gerrhopilid snakes (Loria & Prendini, 2020; Sidharthan *et al.*, 2021).

The biotic consequences of contact between India and Laursia were arguably more transformative than even the Great American Biotic Interchange that occurred as a result of the closure of the Isthmus of Panama (Bacon *et al.*, 2015). It led to the colonization of Sri Lanka by a largely Asian biota, which supplemented the scant survivors of the island's Gondwanan fauna and flora (see also sections 3.7 and 3.7; Klaus *et al.*, 2016).

3.3 Gondwanan faunal heritage

3.3.1 Asia-Africa connectivity. Biotic connections appear to have been established between the northward-drifting Indian plate and Laurasia well before their final collision. Morley (2018) concluded that immediately prior to its collision with Laurasia, India was characterized by a perhumid climate and a rapidly diversifying megathermal angiosperm flora rooted in Africa. The Kohistan–Ladakh Arc had collided with India along the Indus suture zone by 50.2±1.5 Mya[†], its final accretion with Eurasia being estimated to have occurred ~10 My later, 40.4±1.3 Mya (Bouilhol *et al.*, 2013). Rose *et al.* (2014) show that by the time of the collision with Laurasia, odd-toed ungulates (equids, tapirs, rhinoceroses) were present on India.

The fusion of the African, Arabian and Eurasian terranes, and biotic dispersal between Africa and Asia, show substantial temporal disparities across different taxa. With the collision of the Arabian and Eurasian plates, the Tethys Sea 'closed' during the early Oligocene (Allen & Armstrong, 2008), facilitating the exchange of freshwater fishes by the early Oligocene (Lavoué, 2019). The exchange of large mammals began only with the establishment of the Gomphotherium land bridge around the Oligocene-Miocene boundary, ~23 Mya (Rögl, 1999), connecting Africa with Eurasia across Arabia. By the early Miocene, the rhinoceroses and suids had dispersed into Africa (Patnaik, 2016). This terrestrial dispersal route has persisted since then (Lavoué, 2019), facilitating the entry into India of African freshwater taxa such as the ampullariid gastropod genus *Pila* (Sil *et al.*, 2020). By the Burdigalian (~19 Mya; Rögl, 1999), the African small barbs, whose ancestor had dispersed from Asia, had begun diversifying (Oliver *et al.*, 2015; Ren & Mayden, 2016; Lavoué, 2019; Sudasinghe *et al.*, 2020c). By the early Pliocene, however, aridification and a prolonged dry season combined to increase India's biotic insularity. Except for generalist animals such as elephants, several lineages of which dispersed from Africa to India between the late Miocene and mid-Pleistocene (van der Made, 2010; Barry *et al.*, 2013), dispersal to and from the north, west, and east was inhibited by the Himalayas, the Thar Desert and Chatterjee's Partition, respectively. After that time, only the Western Ghats remained as a reservoir of plants and animals that could disperse to Sri Lanka whenever the Palk Isthmus was emergent, and even then, only when its climate was conducive to such dispersal.

3.3.2 Gondwana reconnection. The connections of the Gondwanan plates, whether with one another or with Asia, and their chronology, is as yet imprecisely understood. The dispersal of ancestral mantellid frogs from Asia to Madagascar at around the

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[*] Or even 60–50 Mya (Yin, 2010; Haproff *et al.*, 2020), while Morley *et al.* (2020) estimate contact between the Indian plate and West Burma 46–40 Mya. Hall (2012) points out, however, that while there is no evidence from Sundaland for contact between the Indian plate and Sumatra during the northward drift of the former, there is evidence for a collision between the Incertus intra-oceanic arc and the northern margin of the Indian plate ~55 Mya. This contact could have provided opportunities for dispersal between India and Malesia in the Early Eocene, possibly via island chains.

[†] Final contact may in fact have occurred as early as 54 Mya: Najman *et al.* (2017).

Cretaceous-Paleogene boundary 66 Mya[*], for example, mandates that there must have been a terrestrial India-Asia and India-Madagascar connection around that time (Yuan *et al.*, 2018), despite India having rifted from Madagascar 23 My prior[†]. The case of the microhylid frogs is more complex still, necessitating multiple ocean crossings or land bridges well after India and Madagascar had rifted (van der Meijden *et al.*, 2007). Although such Asia-Madagascar dispersals at around the Cretaceous-Paleogene boundary remain to be explained, authors such as Briggs (2003a) have argued for a latitudinally much 'longer' subaerial India, positing that the Indian plate at that time spanned almost the entire height of the Tethys, from Madagascar to Laurasia (see Figure 3.6*c*). Even though terrestrial contact with Asia may not have been made until the early Eocene, Spicer *et al.* (2017) argue that powerful seasonally reversing winds, and associated surface ocean currents likely facilitated biotic exchange between India and Eurasia long before the final closure of the Tethys Sea in the Late Eocene (Wang *et al.*, 2020).

The floristic connection[‡] between Madagascar and Southeast Asia (which share 9.1 percent of angiosperm genera) appears even stronger than that between Madagascar and India (6.2 percent). This led Buerki *et al.* (2013) to hypothesize that India could have acted as a land bridge between Madagascar and Asia at some point during the Paleogene. While geological evidence for a direct Late Cretaceous or early Cenozoic freshwater dispersal route between Africa and India (together with Madagascar, Sri Lanka and Seychelles) is still lacking, some freshwater-fish distributions too, appear to mandate such a connection at least between India and Africa (Lavoué, 2019). The channid snakeheads[§], however, seem to have dispersed from Africa to Asia much later (44.5 Mya, 95 % HPD: 47.1–44.5 Mya), somewhat before the climbing perches (Anabantidae; 38.5 Mya, 95 % HPD: 49.4–29.7 Mya) (Wu *et al.*, 2019; see also Britz *et al.*, 2020b, Rüber *et al.*, 2020), though alternative scenarios of Gondwanan vicariance remain tenable.

Figure 3.6a provides a reconstruction based on Chatterjee *et al.* (2013), which is not only consistent with diverse strands of biogeographic knowledge but emphasizes the uncertainties associated with reconstructing, over a time span that exceeds 100 million years and based on the scarcest data, a coherent account of what was essentially a chaotic process. It omits, however, the Paleogene connections between India, Africa and Southeast Asia that are inferred from their shared biotas but for which geological support is as yet lacking.

3.3.3 Invertebrates in the Gondwanan context. The Gondwanan signature in Sri Lanka is faint. The absence of pre-Pleistocene terrestrial fossils, except for the Jurassic palynological record from Tabbowa-Andigama, makes it unclear whether the handful of unambiguously Gondwanan lineages present on the island have persisted there from before the Cretaceous-Paleogene extinction event or immigrated from the Indian mainland since the first terrestrial India–Sri Lanka connection with a perhumid climate occurred, during the Oligocene. Global sea levels fell as much as 50-60 m at the Oligocene Isotope Event 1 (Oi-1) glaciation ~34 Mya (Houben *et al.*, 2012), and 250 m at the Rupellian-Chattian boundary ~28 Mya (Hutchison, 1989; Miller *et al.*, 2005), likely resulting in the emergence of the Palk Isthmus and facilitating terrestrial India–Sri Lanka dispersal. In any event, Sri Lanka appears to have remained mostly subaerial throughout the Cenozoic (see the plaeo-reconstructions by Colorado Plateau Geosystems Inc., 2016).

Among recent studies of the historical biogeography of a groups that includes Sri Lankan taxa,

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[*] Feng *et al.* (2017) estimated the Rhacophoridae-Mantellidae split to have occurred ~55 Mya, while Chen *et al.* (2019) recovered an age of 58.7 (95 % HPD: 62.3–54.2) Mya, and Hime *et al.* (2021) a split in the early Paleogene.

[†] The discovery of a 'rhacophorid' fossil (Rhacophoridae are the sister group of Mantellidae) from the early Eocene of Gujrat, India (Folie *et al.* 2013), appears consistent with such a scenario. In the case of the Mantellidae, given the poor survival abilities of amphibians in saltwater, there is no prospect of invoking oceanic dispersal—or is there not? The occurrence of mantellids on Mayotte in the Comoros, 200 km from the Madagascan coast, representative of apparently separate dispersal events, suggest also that at least some of these frogs are capable of dispersing over substantial marine barriers (Glaw *et al.*, 2019).

[‡] See also Schatz (1996) and Warren *et al.* (2010).

[§] Channidae excludes *Aenigmachanna*, which is now in its own family.

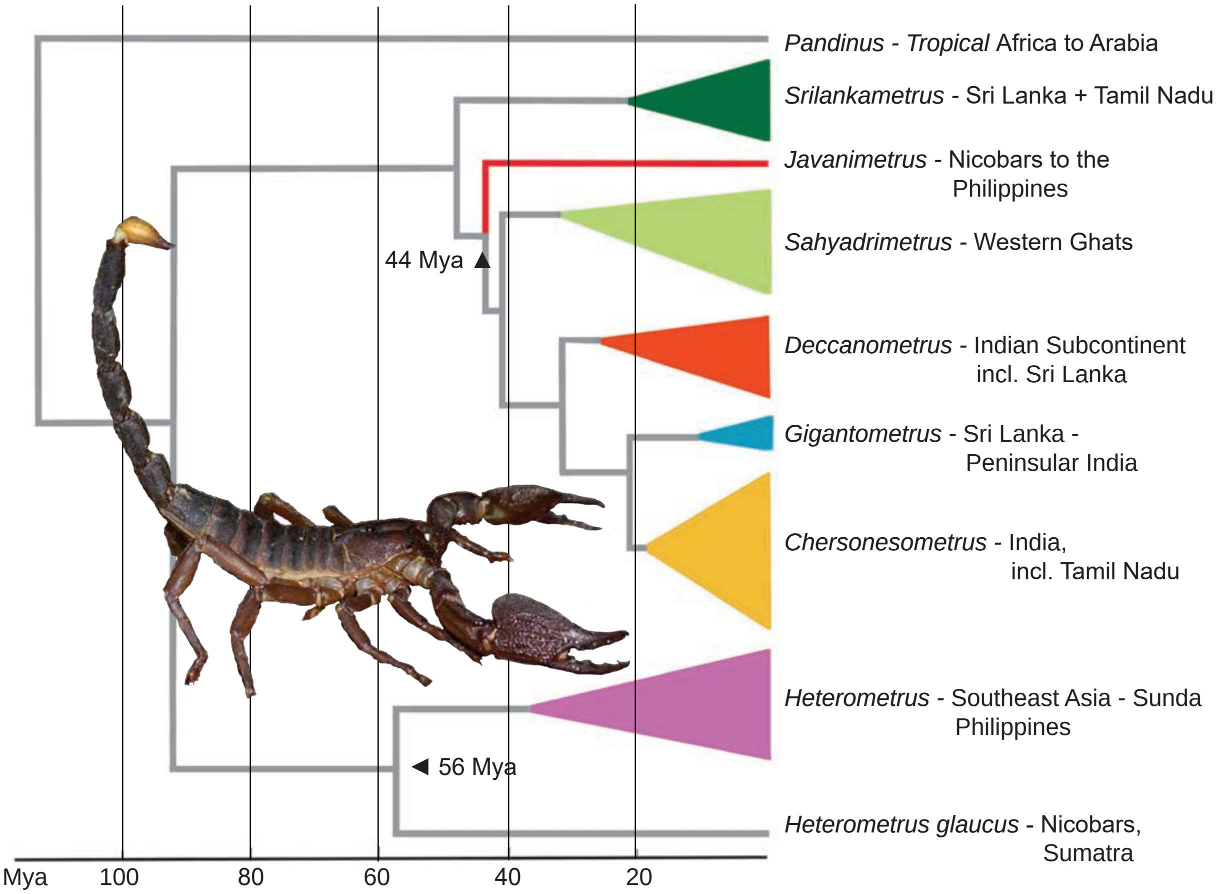


Figure 3.8. Time-calibrated phylogeny of the Asian forest scorpions (Heterometrinae) after Loria & Prendini (2020) (distributions follow Prendini & Loria, 2020). In this construction, the origin of the Heterometrinae on India may have been the result of a vicariance event, when the subcontinent rifted from Antarctica ~135 My, or dispersal from Africa shortly thereafter. Having survived the K-Pg extinction event and Deccan volcanism on India, the ancestor of *Heterometrus glaucus* dispersed to the Sunda region ~56 Mya in the Indian plate's first contact with Asia. A subsequent India-Asia contact ~44 Mya led to the dispersal of the ancestor of *Javanimetrus*. The five Indian and two Southeast Asian genera evidently never crossed Chatterjee's Partition. Inset: *Gigantometrus titanicus* (photo: Tharindu Ranasinghe).

those of Prendini & Lorenzo (2020) and Lorenzo & Prendini (2020) stand out as perhaps the most illustrative. These authors investigated the relationships among the Asian forest scorpions (Heterometrinae), among which six species occur in Sri Lanka, in the genera *Srilankametrus* and *Gigantometrus*. They show the group to have diverged from the African Pandininae in the early Cretaceous, with the rifting of India from Antarctica, following which, having rafted north on the Indian plate, they dispersed to Southeast Asia in the early and mid-Eocene (Figure 3.8).

Prendini & Lorenzo (2020) show all five Sri Lankan species of *Srilankametrus* to be endemic. *Srilankametrus serratus, S. pococki, S. indus* and *S. gravimanus* may represent a monophyletic insular diversification (the lack of the two Indian species, which are confined to Tamil Nadu, in the phylogeny of Loria & Prendini, 2020, do not allow a conclusion). Loria & Prendini (2020) show the Sri Lankan group (excluding *S. yaleensis*, which they lacked) to have an Early Miocene crown age and be basal to the Asian diversification, which includes six further genera.

Despite occurring in the dry-zone lowlands, including the island's arid northern region, and having diverged from their sister group in India in the Eocene, no species of *Srilankametrus* appear

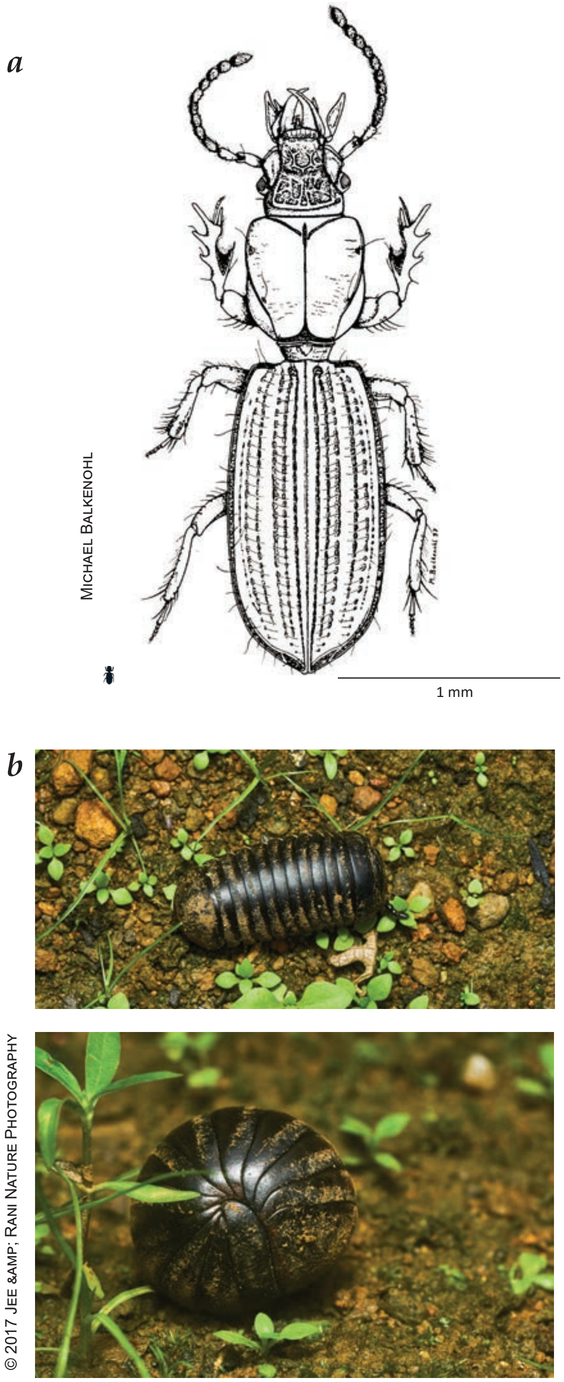


Figure 3.9. ***a,*** *Leleuporella sexangulata*, an endemic species of carabid beetle known only from Yala National Park (Balkenohl, 1997). Except for this one isolated species, the genus is confined to western Africa. The minute replica above-left is approximately the actual size of the beetle. ***b,*** The pill-millipede family Arthrosphaeridae includes three genera: *Zoosphaerium* and *Sphaeromimus,* which are confined to Madagascar, and *Arthrosphaera* (shown here), in Sri Lanka and southern India, a distribution strongly suggestive of Gondwanan vicariance (Wesener *et al.*, 2010; De Zoysa *et al.*, 2016).

Figure 3.10. The spider *Indoetra thisbe*. The distribution in Africa, Madagascar and Sri Lanka of the nephilid spider subfamily Clitaetrinae appears to signal their Gondwanan origin (Kuntner, 2006).

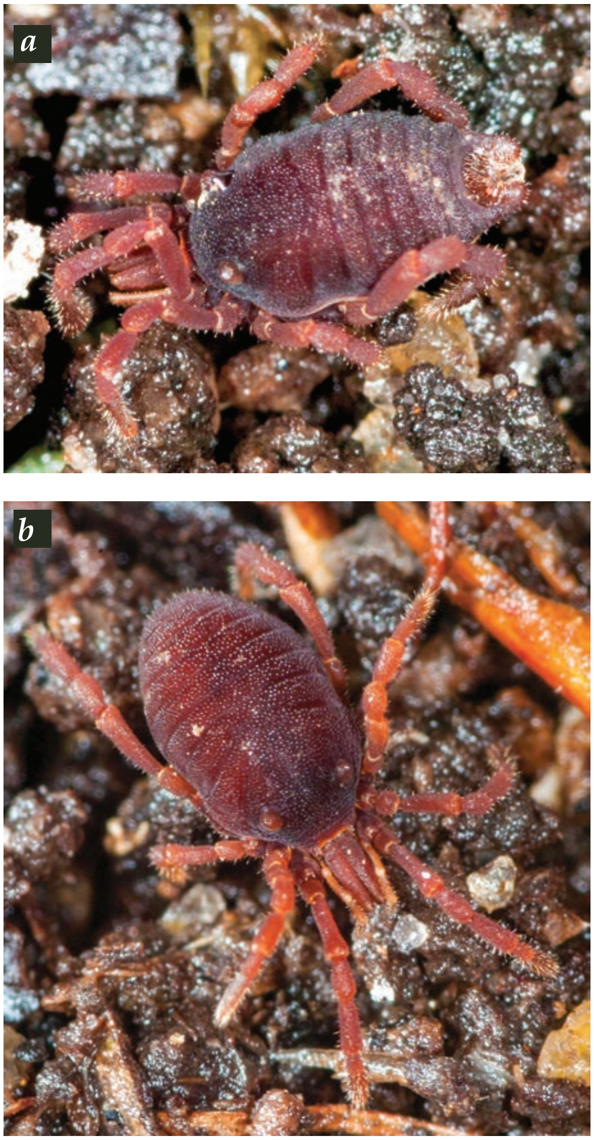
Figure 3.11. *Scoliopsis spinosa.* The sister group of the Sri Lankan and South Indian cascade beetles of the monotypic genus *Scoliopsis* is the Madagascan genus *Tritonus,* strongly indicative of Gondwanan vicariance (Toussaint *et al.*, 2016).

to have crossed the Palk Isthmus. The sixth Sri Lankan species of Heterometrinae, *Gigantometrus titanicus*, also an endemic, diverged from its Indian sister group, represented by *G. swammerdami*, which ranges through the peninsula and beyond, in the mid-Miocene. Neither species crossed the Palk Isthmus since. Further, although an additional pair of Heterometrinae genera, *Chersonesometrus* and *Sahyadrimetrus*, are widely distributed on the Indian peninsula and have representatives in its southernmost region, they too, evidently never crossed the Palk Isthmus to reach Sri Lanka.

Loria & Prendini (2020) estimated the Heterometrinae to have diverged from their African sister group, the Pandininae, with the separation of India-Sri Lanka from Africa ~120 Mya. In this model, Heterometrinae rafted north across the Tethys on the Indian plate, dispersing into Asia after India-Asia contact. The group's distribution illustrates the early contacts between the Indian plate (or elements attached to it) and Asia. The time-calibrated phylogeny presented by these authors recovered a Southeast Asian clade (*Heterometrus*) with a Paleocene crown age, arguably a signal of the earliest contact between India and Laurasia, followed by a further dispersal, this time to Java in the early Eocene.

Restricted to Australia-New Zealand and Sri Lanka-South India, the distribution of the earthworm genus *Notoscolex*[*] and the ant-sized ground-beetles of the genus *Leleuporella* too (Figure 3.9a), are strongly indicative of Gondwanan vicariance (Abhita & Sabu, 2009; Blakemore, 2011). *Leleuporella* is known from only three species: two in western Africa and one, *L. sexangulata*, recorded from Yala National Park in Sri Lanka (Balkenhohl, 1997)[†]. Likewise, the pill-millipedes of the Arthrosphaeridae (Figure 3.9b), a family restricted to Madagascar (*Zoosphaerium*, 55 species; *Sphaeromimus*, two species) and Sri Lanka + South India (*Arthrosphaera*, 40 species), the distribution of which appears to be unambiguously Gondwanan (Wesener *et al.*, 2010; De Zoysa *et al.*, 2016).

A similar distribution is observed also in the basal-most nephilid spider lineage, the Clitaetrinae (Figure 3.10), which occurs only in Africa, Madagascar and Sri Lanka (Kuntner, 2006). Likewise, the monotypic cascade beetle *Scoliopsis spinosa* (Coleoptera, Hydrophilidae, Figure 3.11), restricted to Sri Lanka and the southern Western



Gonzalo Giribet

Gonzalo Giribet

Figure 3.12. The harvestman-spider family Pettalidae is distributed in Australia, Madagascar, New Zealand, southern Africa and southern South America, except for the genus *Pettalus*, which is endemic to Sri Lanka and which contains a rich but as yet incompletely assessed diversification on the island (Boyer *et al.*, 2007; Sharma *et al.*, 2009; Giribet *et al.*, 2016). The species illustrated here is *Pettalus thwaitesi*, ***a***, male; ***b***, female.

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[*] It remains to be demonstrated, however, that the northern and southern-hemisphere species have a sister-group relationship that reflects Gondwanan fragmentation.

[†] It may well be the only species to be known only from the otherwise biodiversity-poor habitat of this national park, in one of the most arid regions of the island.

Ghats, diverged from its Madagascan sister-group *Tritonus* ~90 Mya, strongly indicative of Gondwanan vicariance (Toussaint *et al.*, 2016).

The mayfly genera *Kimminsula* and *Petersula* (Leptophlebiidae) too, belong to a clade confined to Sri Lanka, South India and Madagascar (Sivaramakrishnan, 1984; Hubbard & Peters, 1984). Likewise, the report of the atriplectidid caddisfly genus *Hughscottiella* from Sri Lanka by Chertoprud (2019) suggests a Gondwanan association: the family is otherwise known only from the Seychelles and Australia (Malicky, 1995). A further example is the centipede genus *Ethmostigmus*, which has a single Sri Lankan representative, *E. rubripes spinosus*. The time-calibrated phylogeny of Joshi & Edgecombe (2018) show the distribution of the genus to be explained by Gondwanan vicariance.

In the case of the scolopendrid centipedes of the tribe Otostigmini, Joshi & Karanth (2011) showed that diversification within the genera *Digitipes* and *Rhysida,* which are now confined largely to the Western Ghats, probably occurred on India during the late Cretaceous, suggestive of Gondwanan vicariance (regrettably, no Sri Lankan taxa were included in the study).

A few additional arthropod lineages underscore Sri Lanka's links with pre-fragmentation Gondwana. A time-calibrated molecular phylogeny of the (arachnid) harvestman-family Pettalidae (Boyer *et al*., 2007), which occurs on Sri Lanka, Australia, Madagascar, New Zealand, southern Africa and southern South America, suggests the Sri Lankan group diverged from its Gondwanan sibling-group 160–150 Mya (see Figure 3.12). 'A notable illustration of the importance of vicariance in Cyphophthalmi', noted Boyer *et al.* (2007), 'is that all Sri Lankan species are more closely related to other temperate Gondwanan Cyphophthalmi than to members of the Southeast Asian family Stylocellidae, despite the present-day proximity of Sri Lanka to Thailand, Malaysia and Indonesia… [The] close relationship of Sri Lankan Pettalidae to the species from New Zealand, Australia, South Africa and Chile must be ancient indeed.'

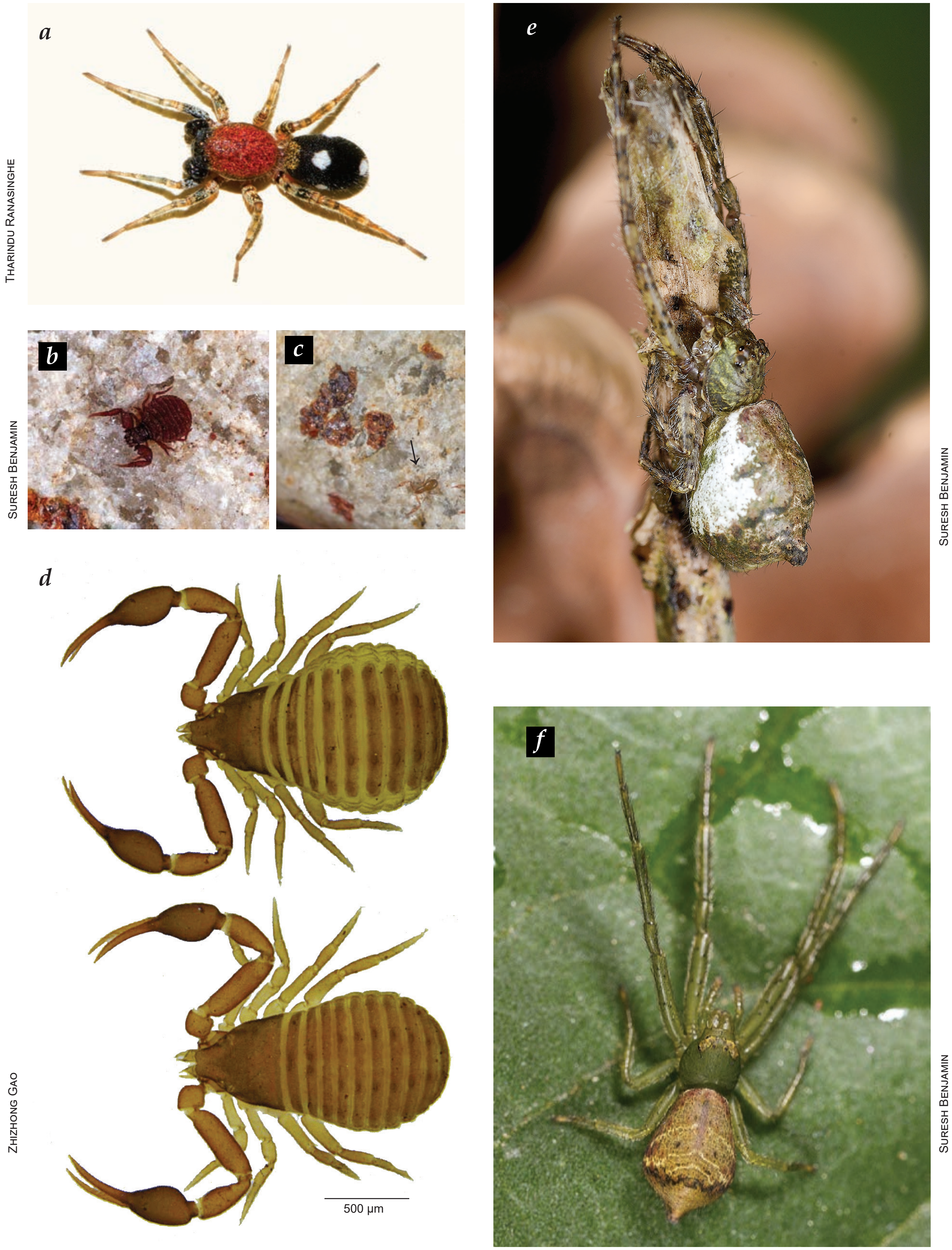
Giribet *et al.* (2016) observed, of the diversification of *Pettalus* in the island, 'Our analyses included representatives of one named species and seven undescribed species from a group that has been diversifying [in Sri Lanka] at least since the Jurassic, long before the Indian subcontinent collided with Southeast Asia' (see also Sharma *et al.,* 2009).

With distributions in Africa, India, Sri Lanka, Madagascar and associated Islands, the mygalomorph spider genera *Scalidognathus, Heligmomerus, Idiops* and *Tigidia* too, support a Mesozoic Gondwanan origin (Mirza *et al.,* 2014). But curious disjunctions persist. The genus *Plesiophrictus*, with 16 species, is concentrated primarily in the Western Ghats and Sri Lanka, but with representatives occurring disjunctively also in Africa and Micronesia (Guadanucci *et al.,* 2011).

Similarly, the velvet ant-mimicking corinnid spider genus *Coenoptychus* has a wide distribution in Sub-Saharan Africa (two species, *C. mutillicus* and *C. tropicalis*), outside of which it occurs only in Sri Lanka and southernmost India (a single species, *C. pulcher:* Paul *et al.,* 2018), suggestive of Gondwanan vicariance, though as yet unverified.

The teloganodid ephemeropteran genus *Indoganodes* represents another such case. Martynov & Palatov (2020) reported from Sri Lanka for the first time: it was until then considered to be confined to the southern Western Ghats. Acknowledging the Gondwanan origin of the Teloganodidae, they inferred a close relationship between *Indoganodes* and *Ephemerellina*, a genus confined to the African tropics.

Figure 3.13 ►. ***a,*** *Coenoptychus pulcher* (Corinnidae), the only member of the genus to occur in Sri Lanka, principally in the dry and intermediate zone. The species occurs also in south India. Both other species in the genus occur in Sub-Saharan Africa. ***b–d,*** The biogeography of the Sri Lankan false-scorpion (Pseudoscorpiones) genera *Faella* (Feaellidae) (Sri Lanka, north-eastern India, Madagascar, Seychelles, Africa, Australia), *Indohya* (Hyidae) (South India, Madagascar, Australia) and *Anagarypus* (Garypidae) (Sri Lanka, Africa, Australia) suggests a Gondwanan history (Harvey, 1996). ***b,*** *Faella indica,* and ***c,*** *Indohya chamberlini,* in life; ***d,*** *Geogarypus longidigitatus* (Geogarypidae; female above, male below), a pseudoscorpion species recorded from Sri Lanka, and then from Thailand to Oceania, is apparently absent in peninsular India, where the genus itself is represented by other species (Harvey, 2000; Gao & Zhang, 2013; Novák & Harvey, 2018). ***e,*** *Tmarus viridomaculatus,* and ***f,*** *Tmarus manojkaushalyai*. Crab-spiders of the genera *Thomisius* and *Tmarus* (Thomisidae) have an apparently Gondwanan distribution. Arachchi & Benjamin (2019) showed that the sister-group of the Sri Lankan diversification of *Tmarus* is Madagascan.



◀ **Figure 3.13**. See caption on previous page.


Kumudu Wijesooriya

Figure 3.14. *Acavus phoenix.* The landsnail family Acavidae is restricted to Sri Lanka, Madagascar and the Seychelles. The genus *Acavus* is endemic to Sri Lanka, with its sister-group, which includes *Ampelita* and *Helicophanta,* confined to Madagascar (Herbert *et al.*, 2015).

Figure 3.15. *Lankanectes corrugatus* (Nyctibatrachidae), which is unusual among anurans in possessing a pair of fang-like processes on its lower jaw, and capturing prey underwater (Pethiyagoda *et al.*, 2014a; Herrel *et al.*, 2019).

Figure 3.16. Skinks of the endemic Sri Lankan genus *Nessia* are characterized by their snake-like habitus and greatly reduced or altogether absent limbs. Nine species are known from the island's wet zone (Batuwita & Edirisinghe, 2017). The relationships of the genus are as yet unresolved.

The report of a new species of arid-adapted goblin spider, *Cavisternum bom* (Oonopidae), by Ranasinghe & Benjamin (2018) from Mandaitivu, a low-lying island about 1 km offshore of Jaffna, represents the first record of that genus from outside Australia. Mandaitivu was almost certainly inundated during the Holocene marine transgressions (see p. 121; also Figure 3.65b), which appears to predict a wider distribution of this spider in northern Sri Lanka and perhaps south-eastern India as well. The same authors also recorded another oonopid spider genus, *Grymeus*, from Sri Lanka for the first time; it has a wide distribution in the island's northern region. It too, was previously considered to be confined to Australia.

Other arthropods that represent Gondwanan lineages in Sri Lanka include the pseudoscorpion genera *Faella* (Sri Lanka, Madagascar, Seychelles, Africa, Australia), *Indohya* (Sri Lanka, Madagascar, Australia) and *Anagarypus* (Sri Lanka, Africa, Australia), none of which are reported from peninsular India (Harvey, 1996): see Figure 3.13a–c. Although not dated, the diversification on Sri Lanka of the thomisid crab-spider genera *Thomisius* and *Tmarus* (Arachchi & Benjamin, 2019; Figure 3.13d,e) too, appears to signal Gondwanan origins given the distribution of the family as a whole.

Another notable Gondwanan relict on Sri Lanka is the acavid snail genus *Acavus* (Figure 3.14), the sister-group of which occurs on Madagascar (Herbert *et al.*, 2015), the family Acavidae itself being restricted to Sri Lanka, Madagascar and the Seychelles. An estimate of the divergence times between the Madagascan, Seychelles and Sri Lankan Acavidae remains, however, to be made.

3.3.4 Gondwanan vertebrate fauna. In the absence of a fossil record, Sri Lanka retains only the scantest traces of its pre-breakup faunal and floral heritage. On India*, however, some groups of freshwater fishes such as the stygobitic snakehead family Aenigmachannidae, recently reported from the Western Ghats, signal a Gondwanan origin, albeit ambiguously (Britz *et al.*, 2020).

In the case of Notopteridae, Barby *et al.* (2018) estimated a divergence time of 120–80 Mya between

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* For reviews of the Gondwanan signature in India's fossil record, see Parmar *et al.* (2020) and Karanth (2021).

the Asian and African clades, which they thought inconsistent with the rifting of India from Antarctica 135 Mya, as inferred from Scotese (2014) and Ali & Aitchison (2008). Jokat *et al.* (2021) show that the final rifting of the Indian plate from Antarctica occurred as recently as ~112 Mya, however, leaving Gondwanan vicariance as a tenable scenario for the biogeography of knifefishes.

Among amphibians, the lineage that is most unambiguously Gondwanan is represented by the Nasikabatrachidae, which are restricted to the moist forests of the Western Ghats (Janani *et al.*, 2017). The sister-group of Nasikabatrachidae, the Sooglossidae, are a Seychelles endemic (Biju & Bossuyt, 2003; see also p. 11: Figure S1.3).

Apart from the Aenigmachannidae, Chikilidae and Nasikabatrachidae, among extant nonvolant Indian vertebrates, only the snake family Gerrhopilidae (see Figure 3.46) unambiguously dates to the Cretaceous (Vidal *et al.,* 2010; Sidharthan *et al.,* 2021). Interestingly, both Gerrhopilidae and Nasikabatrachidae are comprised entirely of troglobionts. Taken together with the stygobitic Aenigmachannidae, this suggests that a subterranean environment may have favoured survival through the Cretaceous-Paleogene mass extinction and perturbations caused by Deccan volcanism (Karanth, 2021). Although the Gerrhopilidae are represented by several species in Sri Lanka, they are yet to be subjected to molecular analysis.

Kamei *et al*. (2012) dated the divergence between the endemic Indian caecilian family Chikilidae and its African sister group, Herpelidae, to ~140 Mya, predating the India-Africa rift. The absence of caecilians in Madagascar, however, would then imply that caecilians were selectively extirpated there some time after it was separated from India ~90 Mya, an event for which no corroboration has been offered up to now[*].

Among Sri Lanka's endemic amphibians, the frog genus *Lankanectes* (Figure 3.15) was considered, together with other Nyctibatrachidae, to have a Gondwanan origin. Bossuyt *et al.* (2006) and Van Bocxlaer *et al.* (2012) estimated it to have diverged from the remaining Nyctibatrachidae, all of which are confined to India, in the Late Cretaceous. More recently, however, Feng *et al.* (2017) have shown Nyctibatrachidae to nest within Asian lineages, from which they diverged at around the Paleocene-Eocene boundary, consistent with India's early contact with Asia.

In any event, four families of amphibians that occur on the Indian Peninsula are unrepresented in Sri Lanka (Caeciliidae, Micrixalidae, Nasikabatrachidae and Ranixalidae), while the island contains just four amphibian genera that are absent from the mainland: *Adenomus* (Bufonidae)*, Lankanectes* (Nyctibatrachidae), *Nannophrys* (Dicroglossidae) and *Taruga* (Rhacophoridae). All four are confined largely to the island's perhumid south-western quadrant, including the montane region. Meanwhile, no fewer than 19 genera of Western Ghats amphibians are absent from Sri Lanka[†]. The inability of some of these groups to disperse to Sri Lanka is inexplicable. The genus *Nyctibatrachus,* for example, contains some 27 species distributed along the length of the Western Ghats, from Gujrat to Tamil Nadu, across a number of distinct climate regimes (Biju *et al.,* 2011).

Although the highly-derived 'limbless' skink genera *Nessia* (Figure 3.16) and *Chalcidoseps*, both of which are endemic to Sri Lanka, have long been considered Gondwanan relicts, neither has yet been subjected to phylogenetic analysis; their relationships remain uncertain.

The origins of other animal groups represented in Sri Lanka, for which Gondwanan origins have been suggested, such as the Chamaeleonidae and lorisiform strepsirrhines, date to the late Eocene, substantially later than the India-Madagascar rift ~90 Mya (Seiffert, 2007; Tolley *et al*., 2013). They evidently reached Sri Lanka after Africa-Asia contact was established in the Oligocene. Meanwhile, Agarwal *et al.* (2020) posited a Gondwanan origin also for the South Asian *Cnemaspis* day-geckos, which they concluded had diversified on the then isolated and northward-drifting

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[*] The absence of caecilians from Madagascar is not by itself conclusive. Loria & Prendini (2020) show the Asian forest-scorpion subfamily Heterometrinae to have a Gondwanan origin, having rafted on India (see 3.3.3). However, these scorpions too, are absent from Madagascar.

[†] *Astrobatrachus, Beddomixalus, Clinotarsus, Gegeneophis, Ghatixalus, Ghatophryne, Indirana, Indotyphlus, Melanobatrachus, Mercurana, Micrixalus, Mysticellus, Nasikabatrachus, Nyctibatrachus, Mysticellus, Pedostibes, Raorchestes, Rhacophorus, Uraeotyphlus, Walkerana, Xanthophryne* (Vijayakumar *et al*., 2019; Dahanukar & Mollur, 2020; Frost *et al.,* 2021).

Indian Plate during the Eocene–Paleocene. There is, however, no evidence to corroborate this conjecture (Karanth, 2021), and Agarwal *et al.* (2021) show the earliest divergence between South and Southeast Asian *Cnemaspis* to have pre-dated India-Asia contact. Nevertheless, the sister-group relationship between the disjunct Northeast Indian *Cnemaspis* cf. *assamensis* and the endemic *Cnemaspis podihuna* clade, which diverged as early as the Oligocene (Agarwal *et al.*, 2021), illustrates the antiquity of the barrier to dispersal presented by the aridification of the Indian Peninsula.

The discovery in Northeast India of an endemic family of caecilians, the Chikilidae, by Kamei *et al.* (2012), which had separated from its African sister group *ca* 140 Mya, in the Jurassic, shows that important discoveries may remain to be made as more taxa are subjected to phylogenetic analysis.

3.3.5 Ancient diversifications. Although their biogeographic affinities remain largely unknown, south-western Sri Lanka contains also several remarkable serpent diversifications. The molecular phylogeny of Sri Lankan snakes of Pyron *et al.* (2013b), for example, found evidence for autochthonous speciation (clades consisting of multiple endemic species) in at least three endemic lineages: *Rhinophis* + *Pseudotyhlops* + *Uropeltis* (Uropeltidae, 14 species[*]), *Aspidura* + *Haplocercus* (Natricinae, 7 species), and Typhlopidae (7 species). They observed that some of the endemic diversity results from allopatric speciation from ancestors which migrated from the mainland, with sister-group relationships between Sri Lankan endemics and their mainland vicars, *e.g.*, in *Balanophis, Boiga, Bungarus, Calliophis, Cercaspis, Chrysopelea, Cylindrophis, Lycodon* and '*Trimeresurus*' (= *Craspedocephalus:* Mallik *et al*., 2021). They concluded that the high diversity of the island's snake fauna could be explained by a combination of species that immigrated recently from India overlayed on older, autochthonous diversifications, though timings for these processes are as yet lacking.

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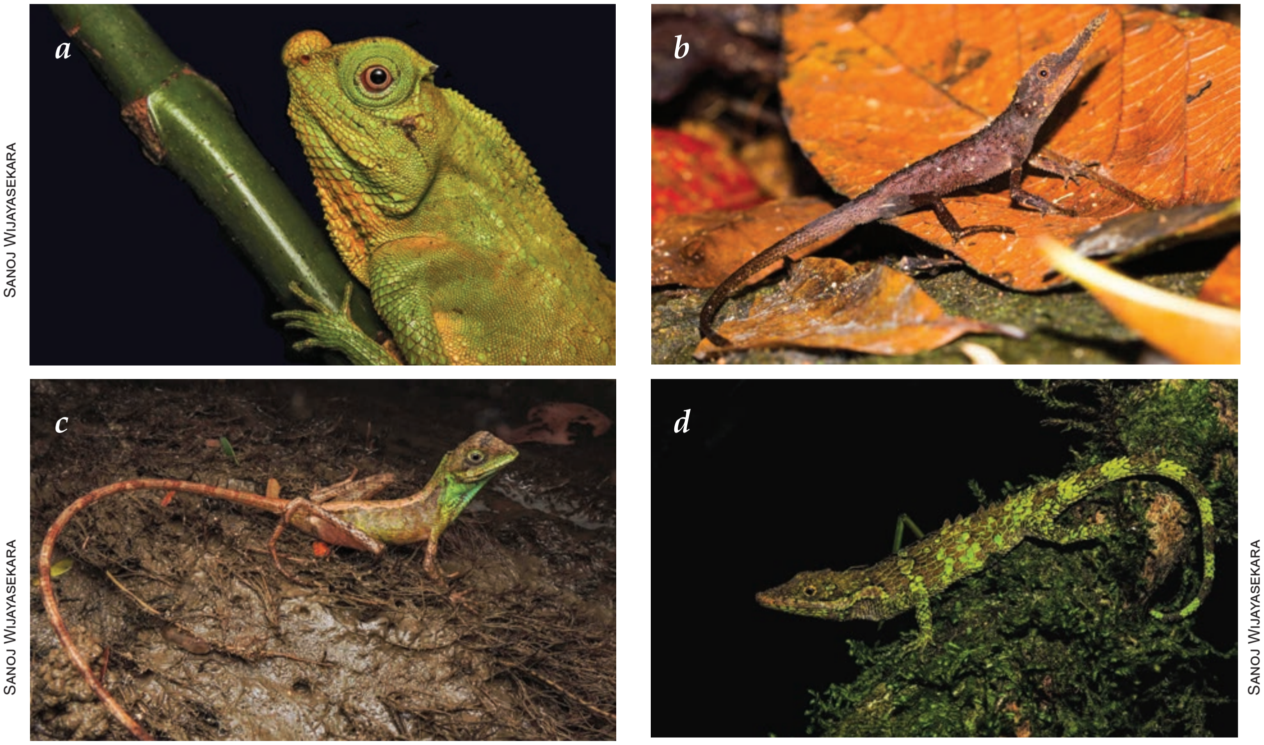
[*] Additional species have since been described: Gower, 2020; Wickramasinghe *et al*., 2017, 2020.



Sanoj Wijayasekara

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Figure 3.17. Representatives of agamid lizard genera endemic to Sri Lanka: ***a,*** *Lyriocephalus scutatus*, ***b,*** *Ceratophora aspera*, ***c,*** *Otocryptis nigristigma* and ***d,*** *Cophotis dumbara*. Originally thought to be Gondwanan (Macey *et al*., 2000), the common ancestor of *Lyriocephalus* + *Ceratophora* + *Cophotis* was later estimated to have dispersed to Sri Lanka in an Eocene India-Asia contact (Grismer *et al*., 2016) and more recently estimated to have an early Oligocene crown age (~27.3 Mya: Karunarathna *et al*., 2020). All 11 included species are restricted largely to wet- and intermediate-zone forests and range from the south-western lowlands to the highest hills, above 2100 m asl.

Other speciose diversifications in the wet zone, such as the *Pseudophilautus* shrub frogs (see Figure 3.70) and the gecarcinucid crabs (see Supplement 3, p. 137) are much more recent (Oligocene and Plio-Pleistocene, respectively) (Meegaskumbura *et al*., 2019; Beenaerts *et al*., 2010).

3.3.6 'Noah's Ark'. The literature contains a number of 'out of India' accounts of Gondwanan biotas rafting northwards to Asia on 'Noah's Ark' India, between the rifting of the Subcontinent from Madagascar ~90 Mya and its collision with Asia ~50 Mya. As Yuan *et al.* (2018) point out, however, there is a dearth of studies of 'nonvolant extant groups that provide substantial evidence for using the Indian Plate as a stepping-stone route among these three plates [Asia, Africa, Madagascar] between 90 and 55 Mya (see also Figure 3.27 and section 4.5). Although several plant and animal groups exhibit sister relationships between India (or Asia) and Madagascar (or Africa), their deep divergences (>90 Mya) attribute this relationship to ancient vicariance coinciding with the breakup of Gondwana.'

Macey *et al.* (2000), for example, identified the Sri Lankan draconine clade comprising of three-agamid lizard genera (*Lyriocephalus, Ceratophora* and *Cophotis*: Figure 3.17) as potentially having rafted to Asia on the Indian plate. Subsequent work (Grismer *et al*., 2016), however, dates the origin of this clade to the early Eocene, via a biogeographic contact with Southeast Asia prior to the Subcontinent's hard collision with Eurasia. The latter study shows that the sister group of the Sri Lankan clade comprises the Sunda clade that comprises of *Aphaniotis, Bronchocela* and *Gonocepahlus*. Karunarathna *et al.* (2020) estimated a later still (Oligocene) crown age for the clade *Lyriocephalus+Ceratophora+Cophotis,* of 27.4 (95 % HPD 31.3–23.3) Mya. For the divergence of the endemic Sri Lankan genus *Otocryptis* from *Sitana,* a genus common to Peninsular India and Sri Lanka, with which it has a sister-group relationship, they estimated a divergence time of ~30.5 Mya. These times are broadly consistent with the dispersal windows recovered by Meegaskumbura *et al*. (2019) for *Pseudophilautus* and Rüber *et al.* (2006) for *Belontia.* These dates are consistent also with the earliest dispersals of freshwater fishes (38 Mya) and amphibians (41 Mya) between Asia and India (Klaus *et al*., 2016).

Joshi *et al.* (2020) presented a convincing case for the out-of-India dispersal into Southeast Asia of the centipede genus *Rhysida,* in which the Southeast Asian species are nested within Indian clades (the genus occurs also on Sri Lanka, which was not included in this study).

The phylogenetic analysis of the ricefishes (Adrianichthyidae) by Yamahira *et al.* (2021) showed *Oryzias setnai* to have a sister-group relationship to all other members of the family, which is distributed across South and Southeast Asia and Malesia. *Oryzias setnai,* however, is confined to fresh and brackish waters in the western littoral of India, parallel to the Western Ghats. Yamahira *et al.* (2021) estimated that Adrianichthyidae separated from the remaining Beloniformes ~89 (95% HPD 107–73) Mya, with *O. setnai* splitting from the remaining Adrianichthyidae 74 (95% HPD 88–60) Mya, prior to the India-Laurasia collison. Based on these dates, taken together with a 52 (95% HPD 60–45) My crown age for the diversification of Adrianichthyidae excluding *O. setnai*, they inferred the family's origin in the northward-drifting Indian plate, with subsequent dispersal eastwards following contact between it and Asia in the early Eocene. If their timing analysis is accurate, this implies that ricefishes originated on the Indian plate.

Garg & Biju (2019) provide another example of a similar distribution and history in the case of the monotypic microhylid frog genus *Mysticellus*, a Western Ghats endemic, and its sister group, *Micryletta,* which has a wide distribution in Southeast Asia. The two clades appear to have diverged ~ 40.6 (95% HPD 51.4–29.1) Mya, consistent with contact between India and Asia in the Eocene.

Molecular analyses over the past few decades have highlighted other possible 'out of India' taxa: *i.e.*, a Gondwanan origin, rafting across the Tethys Sea to India, and then dispersing into Asia during the Eocene. Perhaps the most remarkable of these claims is that of Yuan *et al.* (2018), that the natatanuran frogs as a whole used the Indian Plate to step-stone disperse from Madagascar and Africa to India in at least two events ~65 Mya and ~75 Mya, respectively. A geological mechanism for such dispersal, however, remains speculative, while corroborative evidence from other taxa within these temporal windows remains scant.

Other examples of 'out of India' dispersals include the Dacini fruit-flies (Diptera: Tephritidae: Krosch, 2012), the tropical spider family Ochyroceratidae (Li *et al*., 2020), the knifefishes (Notopteridae: Barby *et al*., 2018), and the Asian arowana (Osteoglossidae: Kumazawa & Nishida, 2000).

Demonstrable instances of India to Asia dispersals of animals following their Eocene contact, as shown above, are few. Instead, the direction of dispersal was largely from Asia to India. In the case of plants, however, the opposite was true. As Morley (2018) show, 'The South-East Asian area was a backwater of angiosperm evolution until the collision of the Indian Plate with Asia during the early Cenozoic'. Among plants, the amaryllidace subfamily Allioideae offer a recently investigated example (Costa *et al*., 2020), in addition to the Dipterocarpaceae, though perhaps more ambiguously (see 3.4.1, below).

3.4 Gondwanan floral heritage

3.4.1 Dipterocarpaceae. No group of angiosperms characterizes the rain forests of Sri Lanka's perhumid south-western lowlands better than the Dipterocarpaceae. Rising to heights above 40 m, these trees often dominate the forest canopy. About 45 species occur in Sri Lanka, all but one of them endemic (Maury-Lechon & Curtet, 1998). Of the seven genera in the island, one (*Stemonoporus*) is endemic and another (*Vateria*) shared with the southern Western Ghats, while a third (*Cotylelobium*) has a disjunct distribution between Sri Lanka to the west, and perhumid peninsular Thailand, Malesia, Sumatra, Lingga, Anabas Islands and Borneo to the east (Dayanandan *et al*., 1999).

The family, however, contains 16 genera and almost 700 species, about half of this diversity occurring on Borneo (Ashton, 1982; Christenhusz & Byng, 2016). The diversity of the group in India, however, is modest.

The Dipterocarpaceae comprise three subfamilies: Dipterocarpoideae (Sri Lanka to New Guinea, with a single disjunct species in the Seychelles); Pakaraimoideae (endemic to tropical South America); and Monotoideae (Africa, Madagascar and tropical South America). Although the global distribution of the family suggests a Gondwanan origin (Ashton, 1969), a convincing model of vicariance remains to be offered. The molecular phylogenies of Gamage *et al*. (2006) and Heckenhauer *et al*. (2017), for example, recovered the Seychelles endemic *Vateriopsis seychellarum* as sister to a clade comprising seven Asian genera, in which *Stemenoporus* has a basal position. The mean divergence time between *V. seychellarum* and its sister group recovered by Hechenhauer *et al*. (2017), however, was only ~35 My. This is at odds with a vicariance framework, which would require a divergence time consistent with the rifting of the Seychelles from its last Gondwanan neighbour, India, ~65 Mya. India-Seychelles vicariance is seen in many other such distributions, among which the amphibian families Nasikabatrachidae and Sooglossidae (see 3.3.4) are perhaps the best known.

According to the time-calibrated phylogeny of Heckenhauer *et al*. (2017), however, that explanation does not hold for the Seychelles Dipterocarpaceae, which must have reached those islands long after they rifted from India, by long-distance dispersal across the Indian Ocean. But *Vateriopsis* has seeds that are unviable in seawater and, having wingless fruits, is incapable of aeolian dispersal, too.

The time-calibrated phylogeny of Heckenhauer *et al*. (2017), recalibrated by Ashton *et al*. (2021), however, recovered a Late Cretaceous tropical African origin for the *Dipterocarpus* clade, with Shoreae becoming established by ~53 Ma at latest. In this model, the *Dipterocarpus* clade first appeared in perhumid equatorial Africa during the Late Cretaceous, although fossils of *Dipterocarpus* wood from India all date to the Neogene (23–2.6 Mya). 'Confidently determined Sarcolaenaceae fossils', note Ashton *et al*. (2021), 'suggest that the sister family to Dipterocarpaceae were able to disperse between Africa and India during the Late Cretaceous [~100–66 Mya]'.

In the case of the Asian dipterocarps too, there is evidence which suggests vicariance between Sri Lanka-India and Madagascar. The phylogenetic and ectomycorrhizal studies of Ducousso *et al*. (2004) and Moyersoen (2006) suggested that the Sarcolaenaceae (endemic to Madagascar) and Asian dipterocarps shared an ectomycorrhizal common ancestor on the Gondwanan India-Madagascar landmass. Phylogenetic evidence too, suggests that the two groups have a proximal common ancestor (Dayanandan *et al*., 1999). However, the time-calibrated phylogeny of Heckenhauer *et al*. (2017) recovered a crown age for the Asian dipterocarps of just ~55 My, which was about when the Indian plate was making its earliest contact with Asia, having rifted from Madagascar ~35 My previously. Further, as Rust *et al*. (2010) and Dutta *et al*. (2011) show from fossil evidence, diperocarps had reached India 53 Mya. But *how* did they do so?

Ashton *et al*. (2021) rejected the hypothesis that Dipterocarpoideae dispersed to India via Madagascar, which invokes a ghost lineage during the Coniacian-Maastrichtian, from which period fossils are lacking. They proposed instead, that Dipterocarpoideae could have dispersed from Africa to India via the Kohistan-Ladakh Island Arc in the late Cretaceous, as did the Sarcolaenaceae (Kapur *et al*., 2017; Morley 2018).

In any event, the Dipterocarpaceae had, from the Early Eocene and up to the Plio-Pleistocene, dispersed widely throughout India (Guleria, 1992; Tiwari *et al*., 2012; Shukla *et al*., 2013) and presumably, Sri Lanka, too. That ancestral dipterocarps inhabited Madagascar prior to its rifting from India 90 Mya too, appears possible (Ducousso *et al*., 2004). The discrepant chronology and exact scenario of dispersal to Asia, however, remain yet to be resolved. Dipterocarps almost certainly entered Asia 'out of India', but how they entered India remains unknown.

Late Cretaceous connectivity between Africa-Madagascar-India-Asia is suggested also by some faunal groups, such as the microhylid, rhacophorid and mantellid frogs (van der Meijden *et al*., 2007; Yuan *et al*., 2018), which remains to be

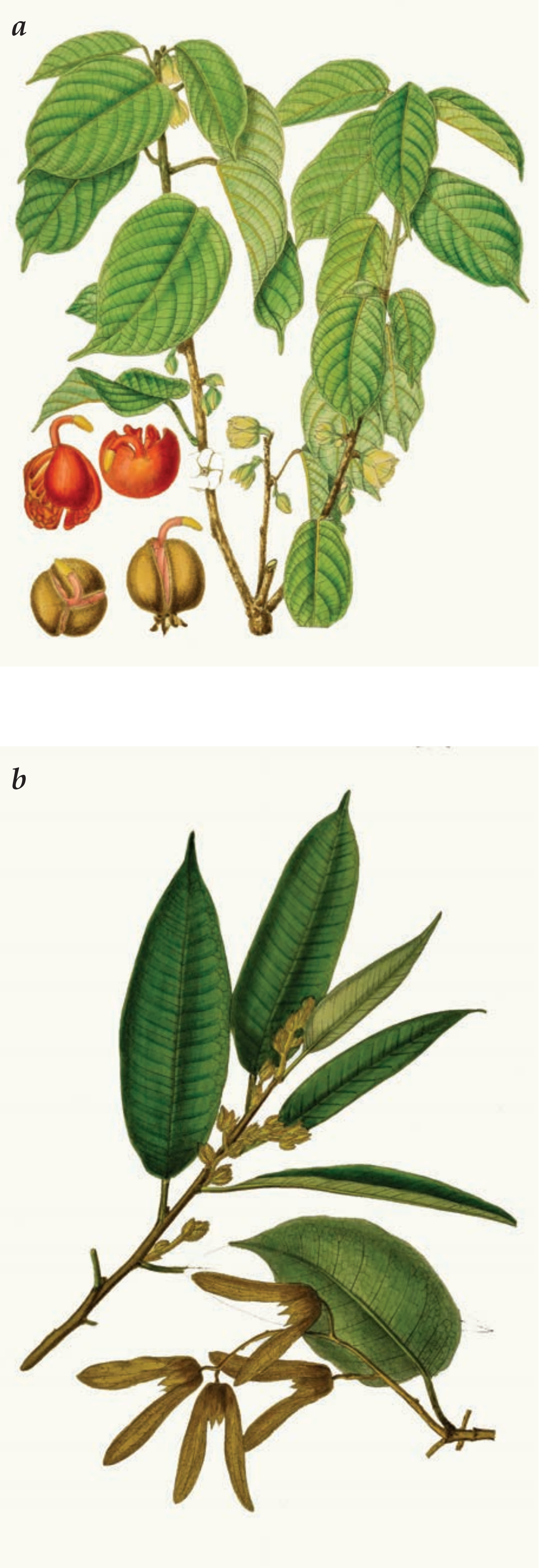

Figure 3.18. Drawings of Sri Lankan dipterocarps by William de Alwis Seneviratne, from Trimen (1893–1900). ***a,*** *Stemonoporus affinis*. The genus, which is endemic to Sri Lanka and is a prominent member of the Mixed Dipterocarp Forests of the wet zone, exhibits a remarkable diversification of some 25 species on the island. ***b,*** *Cotylelobium scabriusculum,* one of six species of the genus in Sri Lanka. The genus is absent from India, recurring in southern Thailand (1 species), the Malay peninsula and Riouw (2 species) and Borneo (3 species). Note the winged fruits.

Himesh D. Jayasinghe

Figure 3.19 *Axinandra zeylanica* (Crypteroniaceae), endemic to the island's south-western rain forests, is the only representative of the genus in Sri Lanka. *Axinandra* is altogether absent from India, recurring only in Southeast Asia, from where three additional species are known, suggestive of a former distribution on the subcontinent, followed by an extirpation.

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Figure 3.20. The genus *Trichadenia* (Achariaceae) is represented by a species (*T. zeylanica*) confined to the humid forests of central and southern Sri Lanka, and two others reported from Borneo eastwards to New Guinea.

Sudath Nanayakkara

Figure 3.21. *Schumacheria alnifolia* (Dilleniaceae). Apart from one circumtropical genus (*Tetracera*), the family exhibits a Gondwanan distribution, with five genera confined to the New World tropics, one in the Old World tropics (*Dillenia,* see Figure 3.22), one (*Schumacheria*) endemic to Sri Lanka, one (*Acrotrema*) in Sri Lanka and the southern Western Gats but then absent until the Malay Peninsula, one (*Didesmandra*) confined to Borneo, one (*Pachynema*) endemic to Australia, and one (*Hibbertia*) restricted to the southern hemisphere, Madagascar, 'across' Australia to Fiji (Dassanayake & Fosberg, 1980–2006).

supported by a convincing geological model (see 3.3.2).

Morley *et al.* (2018) noted that the earliest dispersals of dipterocarps to Southeast Asia possessed winged seeds, the wingless *Vateria, Vateriopsis* and *Stemonoporus* (Figure 3.18a) being restricted to perhumid Sri Lanka and the Seychelles. Pointing to the very old molecular ages (43 and 40 Mya) for the divergence of the winged dipterocarp genera *Cotylelobium* (which occurs in Sri Lanka and perhumid Southeast Asia but not India; Figure 3.18b) and *Dryobalanops* (the Neogene of Kerala and eastern Malesia: Awasthi & Srivastava, 2005), they suggested that these taxa may have dispersed to Southeast Asia during a perhumid phase in the middle Eocene, along the same route as *Axinandra* (Crypteroniaceae, Figure 3.19), *Trichadenia* (Achariaceae, Figure 3.20) and *Dichilanthe*, which too, are disjunct between Sri Lanka and Southeast Asia (Ashton & Gunatilleke, 1987; see also Table 3.1).

The upper Miocene Northeast Indian record of *Shorea* (Khan *et al.*, 2016) too, supports a dispersal to Southeast Asia via the Himalayan foothills. In any event, angiosperms of Indian origin appear in Malesia from ~49 Mya onwards (Gunatilleke *et al.*, 2017) and the Sri Lankan genera associated with a perhumid climate, such as *Stemonoporus* (an endemic) and *Cotylelobium* (disjunct between Sri Lanka and perhumid Southeast Asia) would thus have been present on the Indian Plate prior to contact with Asia.

India-Southeast Asia dispersal probably occurred in the Eocene, when a perhumid climate corridor existed between the two regions (Morley, 2018). This is supported also by the macrofossil record: for example, the tribe Shoreae reached Myanmar by 39.5 Mya (Licht *et al*., 2014) and southern China by 36 Mya (Feng *et al*., 2013).

Until about 6 Mya[*], dipterocarp forests appear to have flourished throughout peninsular India, including the south-eastern region of the peninsula proximal to Sri Lanka (Guleria, 1992; Shukla *et al*., 2013; Morley *et al*., 2018). A total of 31 species are presently recorded from the Subcontinent, just 13 of these from the Western Ghats, in the genera *Dipterocarpus, Vateria* and *Hopea* (Ramesh & Pascal, 1991), all of which occur also in Sri Lanka.

3.4.2 Sri Lanka-India isolation. Evergreen forests persisted throughout the peninsula of India up to the end of the Miocene, when the climate became increasingly seasonal (Patnaik *et al*., 2012). The most important determinant of distribution of these wet evergreen forest is the shorter dry season, rather than high total precipitation (Pascal, 1982; Farooqui *et al*., 2010). From the Eocene-Miocene lignite deposits at Cuddalore in the Cauvery Basin of Tamil Nadu, now an arid region comparable to Sri Lanka's northern dry zone, Guleria (1992) recorded several woody plant genera that are commonly associated with the island's lowland rain forests. These included *Dipterocarpus, Hopea, Calophyllum* and *Mesua*, demonstrating the former occurrence of lowland rain forest in Southteast India. This flora also included several genera of woody plants associated with Malesia, such as *Dryobalanops, Anisoptera* and *Podocarpus.*

From the end of the Miocene, the strengthening monsoon, increasing seasonality and global aridification brought about by the expansion of ice sheets in the northern hemisphere resulted in the progressive aridification of south-eastern India and north-western Sri Lanka, including the region of the Palk Isthmus. This change in climate also confined rain forests to southwestern Sri Lanka and the southernmost region of the Western Ghats (Shukla *et al*., 2013; Morley *et al*., 2018). The shared history of these forests is evidenced by almost a third of Sri Lanka's angiosperm species being shared only with the southern Western Ghats (Bose *et al*., 2016), and some 27 angiosperm genera being confined to Sri Lanka and the southern Western Ghats combined (Nayar & Ahmed, 1984).

The close floral correspondence of the two regions is demonstrated, for example, by the distributions of *Nothopegia* (six species in southern India, one of them present also in Sri Lanka), *Kendrickia* and *Campbellia* (confined to Sri Lanka and the southern Western Ghats), *Memecylon* (a palaeotropical genus with 32 species in Sri Lanka, 30 of them endemic and the other two shared with the southern Western Ghats), and *Humboldtia* (six species in the Western Ghats, and a further one, *H. laurifolia*, endemic to the wet zone of Sri Lanka[†]: Ramachandran *et al*., 2014).

The climate of the south-western Sri Lankan lowlands, like those of Malesia, has remained perhumid at least since the Oligocene, facilitating the persistence of tropical lineages (Renner *et al*., 2010), even if only in greatly reduced refuges during successive glacial maxima, especially the last maximum ~22 kya. The climate that supports the Mixed Dipterocarp Forests of Sri Lanka's south-western lowlands is markedly less seasonal than even that of the wettest forests of peninsular India, recurring once more in Asia only in the low latitudes of Peninsular Malaysia and the Sunda shelf, below the Kangar-Pattani Line (Figure 1.6, and footnote on p. 65).

3.4.3 Floral endemism, vicariance and dispersal. Gondwanan vicariance has been invoked to explain the sister-group relationships between several plant taxa in Sri Lanka and Madagascar and/or the Mascarene-Seychelles islands. The Dillenia-

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[*] The uncertainty results from Dipterocarpaceae not being well recorded by pollen (Bonnefille, 1999).

[†] The inflated, hollow internodes of *Humboldtia laurifolia* serve as domatia to a variety of invertebrate species, including 14 species of ants, four wasps, a bee, two dipterans, three coleopterans, a pseudoscorpion and an annelid (Krombein *et al*., 1999). Despite the proximity of the Sri Lankan species to congeners in southern India, Rickson *et al*. (2003) showed that it hosts a substantially different and richer fauna.

Figure 3.22. *Acrotrema lyratum* (Dilleniaceae), one of seven species (all endemic) in the genus in Sri Lanka. A single species of *Acrotrema* occurs also in southernmost India, and a further one in Myanmar and Thailand. The genus is otherwise absent from India. The drawing, adapted from Trimen (1893–1900), was originally executed by William de Alwis Seneviratne.

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Figure 3.23. *Dillenia triquetra*, a common rainforest tree in the south-western lowlands of Sri Lanka. The genus contains 59 species, with a distribution in Sri Lanka, southern India, Madagascar, Southeast Asia, northern Australia and Fiji. *Dillenia triquetra* is unusual in that it occurs naturally only in Sri Lanka and Madagascar, a distribution that suggests long-distance dispersal rather than Gondwanan vicariance, although the timing and mode of dispersal remains unknown.

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Figure 3.24. *Angraecum zeylanicum*, an orchid that occurs only in Sri Lanka and the Seychelles. Given the late-Miocene crown age of the genus (Farminhão *et al.*, 2021), its occurrence in Sri Lanka apparently results from long-distance dispersal rather than Gondwanan vicariance.

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Figure 3.25. *Chloroxylon swietenia*, the commercially important Ceylon Satinwood tree, with a natural distribution in Madagascar and the dry zones of southern India and Sri Lanka.

ceae, for example, exhibit a strongly Gondwanan distribution (Horn, 2009), with one genus (*Schumacheria,* Figure 3.21) endemic to Sri Lanka and another (*Acrotrema,* Figure 3.22) occurring in Sri Lanka and southern India, and then absent until the Malay Peninsula (Ashton & Gunatilleke, 1987).

Dillenia triquetra (Figure 3.23) exhibits one of the more bizarre distributions among Sri Lanka's rainforest trees: it occurs only in Sri Lanka and Madagascar; other species of *Dillenia*, however, range across Asia, including India. Likewise, the orchid *Angraecum zeylanicum* (Figure 3.24) is restricted to Sri Lanka and the Seychelles, while *Mundulea sericea* (Fabaceae) occurs on Madagascar, South Africa, the southern Western Ghats and Sri Lanka. The distribution of *Chloroxylon swietenia* (Figure 3.25) is no less striking (Madagascar and the dry zones of southern India and Sri Lanka), as is that of *Rhipsalis baccifera.* It, like the other ~50 species in the genus, is confined to tropical South America except for the subspecies *R. b. mauritiana,* which occurs in Africa, Sri Lanka and the Mascarenes. Its presence in Sri Lanka appears to be a combination of natural and historical anthropogenic dispersal (see p. 11: Figure S1.2).

The most tantalizing Gondwanan plant disjunction is perhaps that of *Hortonia* (Monimiaceae, Figure 3.26, a family absent from India), a genus endemic to the island (Ashton, 2014: 391). Ashton (2014: 391) considered might represent 'the only endemic plant taxon with truly ancient origins on Gondwanan India [including Sri Lanka]'. It diverged from the clade that includes genera endemic to Australia-New Zealand (*e.g.*, *Hedycarya*) and South America (*e.g.*, *Hennecartia*) ~71 (84–57) Mya (Renner *et al.*, 2010). Axelrod (1971) suggested that *Hortonia* rafted northwards on the Indian plate (India–Sri Lanka + Madagascar + Seychelles).

The Indian plate, however, separated from Antarctica (which connected Australia and South America: see Figure 3.5) 130–124 Mya, and by 83 Mya, it, together with Sri Lanka, was separated from Antarctica by more than 2000 km of ocean (Gaina *et al.*, 2007; Ali & Aitchison, 2009; Renner, 2010). More recently, based on magnetic and seismic data, Jokat *et al.* (2021) show that Sri Lanka was the final continental part of the Indian plate to separate from Antarctica, ~112 Mya.

If indeed *Hortonia* dispersed from Antarctica to Sri Lanka 71 (84–57) Mya, it would have had to cross a vast marine barrier, presumably along a terrestrial connection that is now submerged* (Figures 3.27, 3.29). This led some authors—originally

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Figure 3.26. *Hortonia angustifolia* (Monimiaceae), one of three species in the genus, which is confined to rain forests of the wet zone. Molecular phylogenies suggest *Hortonia* diverged from its Gondwanan sister group, distributed across Australia, New Zealand and South America ~71 (57–84) Mya (Renner *et al.*, 2010), more than 40 My after India–Sri Lanka-Madagascar had rifted from Australia-New Zealand, mooting the possibility of subsequent land bridges.

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* The mystery of *Hortonia* is reflected also in the palm tribe Eugeissoneae which, having diverged from other Calamoideae on Gondwana, appears to have rafted on India and dispersed into Southeast Asia before becoming extinct on India. But, as Baker & Couvreur (2012a,b) argue, this divergence occurred in the Late Cretaceous, long after the India had separated from Madagascar, leading these authors to acknowledge that connectivity between India and other elements of Gondwana appears to have persisted through the Cretaceous, even though the forms this took are yet to be elucidated.

Figure 3.27 Steppingstones? Emergent subaerial land when sea levels were lower than 135 m below the present level, ~17.5, 30 and 630 kya, based on Warren *et al.* (2010).

Dushantha Wasala
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Figure 3.28. The lichen *Graphis desquamescens* (Graphidaceae), at Horton Plains National Park.

van Steenis (1962), but more recently Masters *et al.* (2006) and Renner *et al.*, (2010)—to moot the possibility of 'steppingstones in the middle of the Indian Ocean'. Buerki *et al.* (2013) too, considered that Madagascar, India, Africa and Australia may have retained connectivity until the end of the Cretaceous, with the Kerguelen Plateau and Antarctica acting as a land bridge between these regions. See Sanmartin & Ronquist (2004), and Voelker & Outlaw (2008) for a fuller discussion; and Bobrov *et al.*, 2017, who suggest an overland route for the ancestral *Hortonia,* north from East Africa across the Arabian Peninsula and along the littoral of the Arabian Sea. Christenhusz *et al.* (2018), however, argue that the pantropical distribution of Monimiaceae was achieved by multiple long-distance dispersal events. Kainulainen *et al.* (2017) give several examples of such dispersal events between Indian Ocean islands such as Madagascar, the Seychelles, Comoros and Mascarenes.

The persistence of *Hortonia* in the island suggests that Sri Lanka continuously harboured perhumid refugia since the Cretaceous. Nevertheless, as pointed out by Ashton (2014: 391), *Hortonia*'s riparian associations too, may have aided its persistence during the island's trans-Tethys transit.

Ali & Aitchison (2008) too, argued that the marine barriers involved were simply too great for steppingstones to be adduced to explain these former linkages. Instead, oceanic or long-distance dispersal has been credibly invoked also to explain several other 'Gondwanan' disjunctions, including the Seychelles Dipterocarpaceae (Heckenhauer *et al.*, 2017) and Asian-African Malmeoideae (Thomas *et al.,* 2015). Weerakoon *et al.* (2019) too, in a comparison of members of the lichen family Graphidaceae between Sri Lanka, Costa Rica and Thailand (selected because these floras were relatively well studied; Figure 3.28), rejected Gondwanan vicariance in favour of long-distance dispersal to explain the recovered relationships.

Likewise, trans-oceanic dispersal via a north-south chain of islands (Figures 3.27, 3.29) has been invoked to explain biotic connectivity during sea-level low-stands, appearing to provide a more robust explanation than vicariance for part of the Madagascan influence evident in the Asian biota, and *vice versa* (Warren *et al.*, 2010; see also Yuan *et al.*, 2018). As seen from section 3.3.6, there are, nevertheless, credible examples of Gondwanan lineages dispersing to Asia and Africa after having rafted across the Tethys Sea on the Indian plate, such as the fig subsection *Urostigma* (Moraceae) (Chantarasuwan *et al.*, 2016).

In the case of several other plant taxa, however, the arguments for Gondwanan vicariance are equivocal. For example, the spurge genus *Adenochlaena* (Euphorbiaceae) is known from two species, *A. leucocephala* on Madagascar and the Comoros, and *A. zeylanica* endemic to Sri Lanka (Radcliffe-Smith, 1973), Figure 3.30. The latter species has not been recorded in Sri Lanka since the 1890s and may now be extinct. The moss genus *Lepidopilidium* (Pilotrichaceae) occurs only in

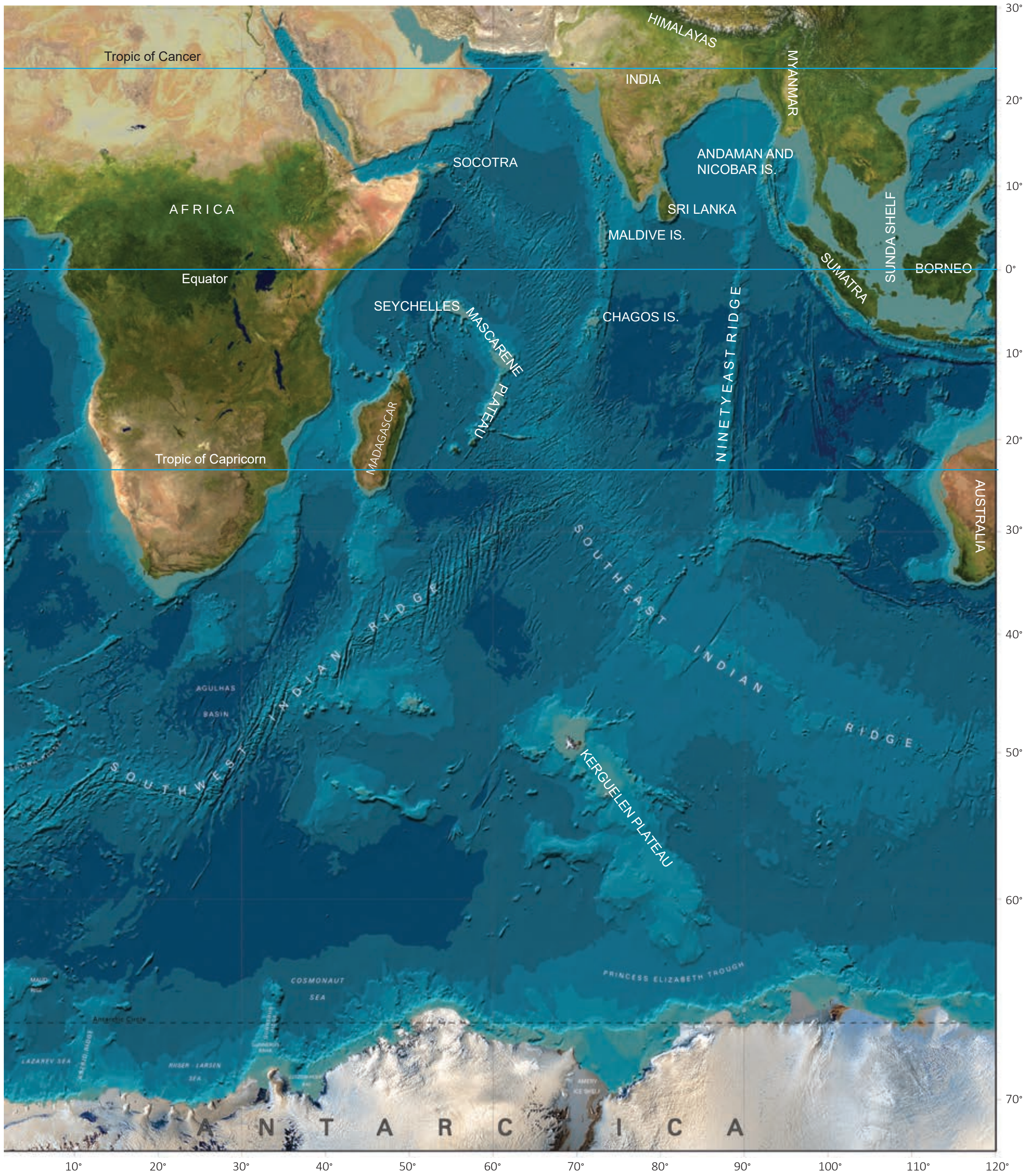

Figure 3.29. Terrestrial and submarine topography of the Indian Ocean basin, with locations mentioned in the text, based on the General Bathymetric Chart of the Oceans (GEBCO), www.gebco.net. Extensive regions such as the Kerguelen Plateau, a submerged 500,000 km^2 microcontinent that rose some 2000 m asl, were subaerial until the early Miocene (Frey *et al.*, 2003). Heard Island, the McDonald Islands and Iles Kerguelen are now the only parts that remain subaerial (Truswell *et al.*, 2005).

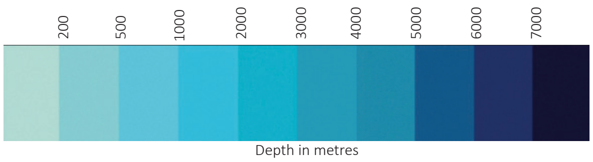

Figure 3.30. *Adenochlaena zeylanica*, a Sri Lankan endemic, drawn by Harmanis de Alwis Seneviratne *ca* 1851–1861, Plate 85 in Trimen (1893–1900). Its only congener, *A. leucocephala*, occurs on Madagascar and the Comoros. The Sri Lankan species has not been collected since 1890 and may now be extinct.


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Figure 3.32. *Cassipourea ceylanica* (Rhizophoraceae), with a distribution in tropical America, Africa and the Mascarene Islands, but with a single species, *C. ceylanica*, present in Sri Lanka and the Western Ghats (Kenfack, 2011).


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Figure 3.31 The pitcher plant *Nepenthes distillatoria*, an endemic which is the only member of the genus and family (*Nepenthes*, Nepenthaceae) represented in Sri Lanka; *Nepenthes* occurs, however, on Madagascar, the Seychelles, Australia, New Caledonia, the Sunda Region and north-eastern India, but is absent from the peninsula of India. The molecular phylogeny of Alamsyah & Ito (2013) showed the Sri Lankan and north Indian species to have a sister-group relationship, the pair in turn being, enigmatically, sister to New Guinean—rather than Sunda—*Nepenthes.*


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Figure 3.33. *Gaertnera walkeri*, a montane-forest shrub. The genus is absent from the Indian Peninsula but occurs in Africa, Madagascar, the Mascarene Islands, and Southeast Asia.

South and Central America, Africa and Sri Lanka (Atwood, 2015); the fern genus *Nesolindsaea* comprises two species, one endemic to Sri Lanka and the other to the Seychelles (Lehtonen *et al.*, 2010); and the pitcher plant genus *Nepenthes* (Nepenthaceae; Figure 3.31) is distributed in Sri Lanka, Madagascar, the Seychelles, north-eastern Australia, New Caledonia and north-eastern India (Meghalaya), with spectacular diversifications on Borneo, Sumatra and the Philippines. It is, however, absent from the Indian Peninsula (Meimberg *et al.*, 2001; Alamsyah & Ito, 2013).

Other taxa with apparently Gondwanan fingerprints—and strikingly disjunct distributions—include the shrub genus *Cassipourea* (Rhizophoraceae, Figure 3.32), which ranges from tropical America to Africa and the Mascarene Islands, but with a single species, *C. ceylanica*, present in Sri Lanka and the Western Ghats (Mesta *et al.*, 2009; Kenfack, 2011)*. Likewise, the genus *Gaertnera* (Rubiaceae, Figure 3.33), which is absent from the Indian Peninsula but has five species endemic to Sri Lanka; it is otherwise distributed in Africa, Madagascar, the Mascarene Islands, and Southeast Asia (Malcomber & Taylor, 2009).

With ~170 species distributed largely in mainland Africa, Madagascar and India–Sri Lanka, the gentian tribe Exaceae shows a typically 'Gondwanan' distribution (Pirie *et al.*, 2015). The genus *Exacum* (Figure 3.34), the distribution of which reflects that of the tribe, has 38 species endemic to Madagascar, two in equatorial Africa, five endemic to Sri Lanka, and a further ~20 in India (Klackenberg, 1983; Yuan *et al.*, 2005; Geethakumary *et al.*, 2016). Whether or not the distribution of *Exacum* is in fact Gondwanan, however, remains controversial, with the time-calibrated molecular phylogeny of Yuan *et al.* (2005) supporting a dispersal scenario, while that of Pirie *et al.* (2015) suggests that vicariance too, is tenable.

Figure 3.34. ***a,*** *Exacum pallidum* and ***b,*** *E. trinervium*, two of the five species of *Exacum* endemic to Sri Lanka. It remains unclear whether the (apparently Gondwanan) distribution of the genus is a result of vicariance or dispersal.

In rare cases, anthropogenic dispersal has been invoked to explain such disjunctions, such as in the Sri Lanka-South India distribution of the treacle palm, *Caryota urens* (Hahn & Sytsma, 1999).

Nevertheless, as pointed out by Raven (1979), the substantial number of tropical Asian plants that dispersed across the Pacific to Hawaiʻi, a distance much greater than the ~3800 km that separate Sri Lanka and Madagascar, indicates that in the case of each observed 'Gondwanan' disjunction, dispersal should be contemplated before vicariance is invoked.† In any event, a credible

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* The distribution of *Vanilla* (Orchidaceae) is likewise enigmatic: having evolved in tropical America it dispersed to Africa 37.8–14.7 Mya and from there to Asia 18.7–3.1 Mya, with a further oversea dispersal to Réunion (Bouetard *et al.*, 2010). The mode of dispersal remains unknown, though rafts of vegetation, wind and migratory birds have all been mooted as possible vectors. The specialized pollinators on which these orchids depend, however, adds a further layer of complexity to modelling their trans-oceanic dispersal (Lubinsky *et al.*, 2006).

† But see Samonds *et al.* (2012), who show that probability of successful marine dispersal between Africa and Madagascar, even by groups capable of dispersal by oversea rafting, decreased after the Paleocene.Further, Ali & Huber (2010) demonstrated that the present pattern of currents in the Mozambique Channel

Figure 3.35 The inflorescence of the palm *Loxococcus rupicola*, the only species in this endemic genus, which occurs on cliffs and rocky outcrops in Sri Lanka's southern rain forests. The sister-group of the genus is represented by the genera *Dransfieldia* and *Heterospathe,* which occur in western New Guinea and Oceania, respectively, and not in Asia (Baker *et al.,* 2011).

vicariance scenario must necessarily be based on topological and temporal congruence.

Moreover, such disjunctions are observed frequently between Asian and southern-hemisphere biotas (Heads, 2012): *e.g.*, the endemic Madagascan palm genus *Tahina*, the sister-group of which, *Kerriodoxa*, is endemic to Thailand (Dransfield *et al.*, 2008); trees of the genus *Allantospermum* (Ixonanthaceae), which are restricted to Madagascar and Malesia (Heads, 2012); and the amphipod genus *Pseudocyphocaris*, which occurs only in Madagascar and New Guinea (Myers & Lowrie, 2009). Additionally, several plant families represented in Madagascar and Southeast Asia are entirely absent from India and Sri Lanka, such as the Cardiopteridaceae, Casuarinaceae, Molluginaceae, Phytolaccaceae, and Saccolomatiaceae (Christenhusz *et al.*, 2018; see Warren *et al.*, 2010, and Buerki *et al.*, 2013, for a fuller discussion).

A particular mystery is the complete absence from Sri Lanka of the Podocarpaceae, a family that was present in the Antarctic Cretaceous and now occurs throughout the Southern Hemisphere and Asia, including the peninsula of India. Klaus & Matzke (2020) show the present distribution of the family to be the result of both Gondwanan vicariance and multiple long-distance dispersal events, which make its absence from Sri Lanka even more enigmatic.

3.5 Trans-Deccan floral disjunctions

The sister-groups of many angiosperm species endemic to Sri Lanka's south-western lowland rain forests, such as the endemic and monotypic palm genus *Loxococcus* (Figure 3.35), the dipterocarp *Hopea brevipetiolaris* and the prominent rainforest tree *Canarium zeylanicum* (Burseraceae, Figure 3.36) too, occur not in India, but in perhumid Southeast Asia and eastwards. Baker & Couvreur (2012a,b) showed that the divergence between *Loxococcus* and its sister group, which ranges from Southeast-Asia to the eastern Pacific, occurred in the late Oligocene or early Miocene, suggestive of an extinction on India thereafter. In the case of *Canarium*, Federman *et al.* (2015) concluded that a long-distance oceanic dispersal occurred, from Asia to Madagascar, though the timing of this event is as yet unknown. That several such Asia-to-Madagascar dispersals too, took place, is clear also from other strands of evidence (Yoder & Nowak, 2006; Buerki *et al.,* 2013). See also Ashton (2014: 421), and Table 3.1 for a list of plant genera occurring in Sri Lanka and Southeast Asia but not in India; and Thorne (1972) for a list of flowering plants disjunct between India+Sri Lanka and Africa+Madagascar.

The orchid *Cryptostylis arachnites* too, has a range which includes Sri Lanka and much of tropical and subtropical Asia, extending even to the western Pacific islands, but excludes the peninsula of India (Figure 3.37). Still other species occur in Sri Lanka and only sparsely or rarely in southern Kerala, being absent from the Deccan Peninsula, only to recur farther afield. For example, *Hypserpa nitida* (Menispermaceae, Figure 3.38) occurs in the lower central hills of Sri Lanka, in Kerala, and then again only in Assam and eastwards to the Philippines; and the commercially-important *Gyrinops*

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was established as long as 20–15 Mya, substantially diminishing the likelihood of transoceanic dispersal to Madagascar from the African mainland. Nevertheless, long-distance dispersal appears to be the only mechanism that explains some remarkable Madagascan disjunctions, such as in the tribe Spermacoceae of Rubiaceae, with colonization taking place not just from Africa but as far afield as the Neotropics (Janssens *et al.,* 2016). Similarly, Bartish *et al.* (2011) show that the sapotace subfamily Chrysophylloideae crossed the Mozambique channel at least three times to reach Madagascar, as did *Euphorbia* (Euphorbiaceae) (Agnarsson & Kuntner, 2012).

Figure 3.36. The flowers of *Canarium zeylanicum*, a prominent endemic of Sri Lanka's lowland rain forests. The genus is absent from the Indian Peninsula but recurs in perhumid Southeast Asia.

Figure 3.38. *Hypserpa nitida* (Manispermaceae), a species restricted to lower elevations in Sri Lanka's central hills and the Western Ghats, then absent from India until Assam, thereafter occurring eastwards to the Philippines.

Figure 3.37. *Cryptostylis arachnites*, an orchid occurring in Sri Lanka and much of tropical and subtropical Asia, extending also to the western Pacific islands, but excluding the peninsula of India.

Figure 3.39. *Gyrinops walla* (Thymelaeaceae), the only one of the nine species in the genus to occur outside the Sunda region. The species is confined to Sri Lanka and the humid forests of southernmost Kerala.

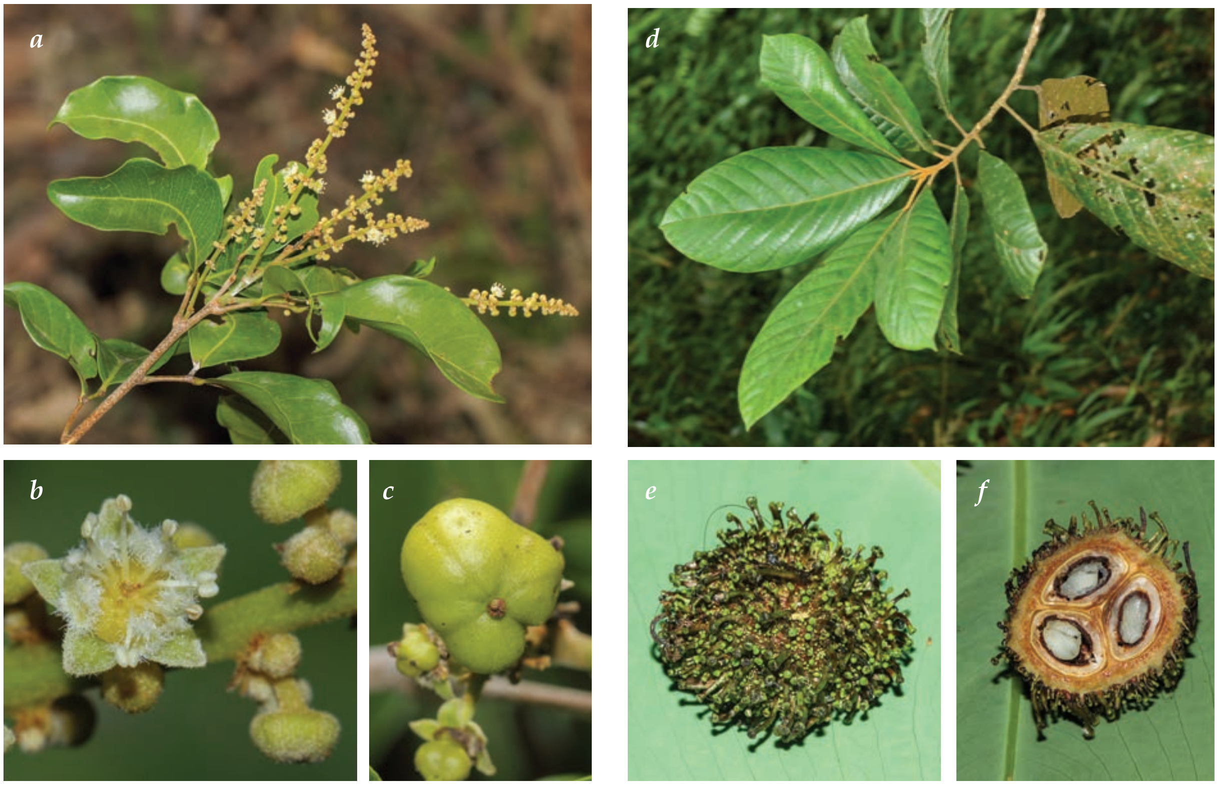

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Figure 3.40. Unexplained distributions. ***a–c,*** *Glenniea unijuga,* a tree endemic to Sri Lanka. The genus contains three species in tropical Africa, one in Madagascar, one in Sri Lanka and three in Malaysia. Unusually among Sri Lankan endemics, *G. unijuga* is absent from the wet zone: it is confined to the intermediate and dry zone, including the arid region around Mannar. Nevertheless, it does not occur in India. ***d–f,*** The leaves and fruit of *Podadenia sapida,* the only member of the genus, which is endemic to Sri Lanka (Webster, 1994). The sister-group of *Podadenia* is *Ptychopyxis*, a genus which ranges from southern Thailand throughout Malesia to New Guinea. The species is altogether absent from intervening India, Bangladesh and Myanmar (Stoops & Welzen, 2013).

walla (Thymelaeaceae, Figure 3.39) is restricted to Sri Lanka and southernmost Kerala, where it is rare; all other species in the genus occur only in Malesia. Another such example is *Agrimonia zeylanica* (Rosaceae), the range of which, except for Sri Lanka, extends from Sikkim and Meghalaya to China and Japan (Chung, 2008)[*].

Several other plant species too, show strikingly disjunct distributions between Sri Lanka and Southeast Asia. *Cleidion nitidum* occurs only in Sri Lanka and the Andaman Islands; *Gironniera parvifolia* is restricted to Sri Lanka, the Malay Peninsula, Sumatra and Borneo; *Horsfieldia irya* is distributed in Sri Lanka, the Andamans and eastwards to the Solomon Islands; *Scutinanthe brunnea* occurs only in the rain forests of Sri Lanka and Malaysia; and *Stylidium uliginosum* is restricted to Sri Lanka (though not reported from the island in the past century) and eastern Asia (Dassanayake & Fosberg, 1980–2006). All are absent from the Indian Peninsula, as are the entire families Stylidiaceae and Monimiaceae (the latter are represented in Sri Lanka by the endemic genus *Hortonia*, with three species). These distributions suggest a widespread extinction across the Indian Peninsula of taxa dependent on a perhumid climate. In the

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[*] Some 35 plant families represented in Sri Lanka and the Western Ghats are absent elsewhere in the Indian Peninsula: Achariaceae, Ancistrocladaceae, Anisophylleaceae, Aquifoliaceae, Buxaceae, Calophyllaceae, Celastraceae, Centroplacaceae, Chrysobalanaceae, Clusiaceae, Connaraceae, Crypteroniaceae, Cyatheaceae, Dichapetalaceae, Equisetaceae, Ericaceae, Flagellariaceae, Geraniaceae, Gleicheniaceae, Haloragaceae, Hymenophyllaceae, Icacinaceae, Isoëtaceae, Marattiaceae, Metteniusaceae, Myristicaceae, Nyssaceae, Passifloraceae, Piperaceae, Proteaceae, Psilotaceae, Sabiaceae, Schisandraceae, Stemonuraceae, and Vahliaceae (data in Buerki *et al.*, 2014; Christenhusz *et al.*, 2018).

southern Western Ghats, however, many plant species which existed during the Palaeogene survived aridification in humid refugia (Farooqui *et al.*, 2010).

Such disjunctions, however, do not always involve wet-zone taxa. The genus *Glenniea* (Sapindaceae), for example, is represented in Sri Lanka by a single species, *G. unijuga* (Figure 3.40), which is widely distributed through the dry and intermediate zones, including Mannar (Dassanayake & Fosberg, 1980–2006). *Glenniea* is absent from India, however, but reported from tropical Africa, Madagascar, Southeast Asia and Malesia (Buerki *et al.*, 2010). Leenhouts (1975) refers to the Sri Lankan *G. unijuga* as a 'missing link' to fill the disjunction between Madagascar and Indo-China that otherwise arises in the genus. Given that it is an arid-adapted species, its absence from India is a mystery.

As is clear from the examples above, the Sri Lankan flora possesses a wealth of taxa whose sister groups are distributed east of Chatterjee's Partition, but which are absent from India (Table 3.1; Ashton & Gunatilleke, 1987; Conti *et al.*, 2002; Rutschmann *et al.*, 2004). So it is that the sister group of the Sri Lankan endemic *Podadenia* (Euphorbiaceae), is *Ptychopyxis*, a genus restricted to Southeast Asia and New Guinea, and absent from India (Stoops & van Welzen, 2013). Like the common ancestor of *Podadenia* and *Ptychopyxis, Axinandra* too, was likely present in India but lost owing to a climate-driven extirpation (Conti *et al.*, 2004; Rutschmann *et al.*, 2004). This may have been associated with the massive extinction of India's Gondwanan elements caused by climatic changes around the Cretaceous-Paleogene boundary ~66 Mya (Conti *et al.*, 2002). But lineages associated with a perhumid climate, such as the Crypteroniaceae mentioned above, must have dispersed to Southeast Asia before such a corridor ceased to exist across Chatterjee's Partition in the early Miocene.

Former biotic connectivity between Sri Lanka-Western Ghats and Southeast Asia is evident also in other groups absent elsewhere across the Indian Peninsula. The genera *Helicia* (Proteaceae; Figure 3.41) and *Aporosa* (Phyllanthaceae), for example, have species endemic to Sri Lanka and to the Nilgiris. But they are absent elsewhere across

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Figure 3.41. *Helicia ceylanica*, an endemic which is the only Sri Lankan representative of the predominantly Southern-Hemisphere family Proteaceae. The genus, which contains some one-hundred species, is represented by a single species (*H. nilagirica*) in the southern Western Ghats, is then widely distributed from Southeast Asia through New Guinea to Australia.

India, to recur from Assam to Southeast Asia. Shukla *et al.* (2016) show *Aporosa* to have evolved on the northward-drifting Indian plate, dispersing to Southeast Asia when India contacted with Laurasia in the Eocene, subsequently being extirpated elsewhere on the Subcontinent as a result of increasingly seasonal climate. The distribution of the tribe Heliciinae—*i.e.*, *Helicia*, in the Sri Lankan wet zone, southern Western Ghats, then Northeast India and across New Guinea to New South Wales, Australia; *Hollandaea*, an Australian endemic; and *Knightia*, a New Zealand endemic) remains to be framed within a context of Gondwanan vicariance or long-distance oceanic dispersal (Barker *et al.*, 2007).

Similarly, *Kadsura heteroclita*, the only South Asian representative of the Schisandraceae, occurs in Sri Lanka and the Western Ghats, but is then absent from the subcontinent until it recurs in Sikkim and then on to eastern China.

The genus *Xylopia* (Annonaceae) has two species endemic to Sri Lanka and a third, *X. parvifolia*, widely distributed across the lowlands of all climatic zones in Sri Lanka as well as southernmost India. The genus, which has a pantropical distribution, is otherwise absent from India (Dassanayake & Fosberg, 1980–2006; Johnson *et al.*, 2013).

Biogeographic conclusions drawn from such disjunctions, however, necessarily depend on sound taxonomy, as the case of *Myristica ceylanica* (Figure 3.42) illustrates.

What is clear from the foregoing examples is that both vicariance events and dispersal corridors acted over long periods of time to produce the diversity of biogeographic patterns seen today (Moyle, 2004; also, for amphibians, Pyron, 2014). Little is known of the history of the extinctions that gave rise to contemporary biogeography.

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Figure 3.42 *Myristica ceylanica*, an endemic species of wild nutmeg widely distributed in Sri Lanka's lowland dry and intermediate zones. It represented a wide disjunction (Sri Lanka – Philippines: Dassanayake & Fosberg, 1980–2006), until the latter population was found to be a distinct—but closely related—species, *M. cumingii,* illustrating the dependence of biogeography on sound taxonomy.

3.6 India-Asia floral exchange

Vegetation simulations (Beerling & Woodward, 2001) suggest that rain forests may have become established in southern India and Sri Lanka by the mid-Cretaceous and persisted until the Deccan Trap volcanism at the Cretaceous-Paleogene boundary (Davis *et al.*, 2005). A perhumid climate appears to have prevailed across the Gangetic Plain thereafter, until the mid-Oligocene, since when Chatterjee's Partition (see Figure 1.6) inhibited biotic exchange between Southeast Asia and Peninsular India (Gunatilleke *et al.*, 2017). From a study of fossil pollen, Prasad *et al.* (2009) revealed a 'striking similarity' between the present flora of the evergreen forest on the western slopes of the Western Ghats and that of the north-eastern and western parts of the Indian subcontinent during the Paleocene to early Eocene (~55–50 Mya).

The exchange of lowland-rainforest taxa between India and Southeast Asia peaked after the middle Eocene and declined to a trickle by the early Oligocene (Ashton, 2014: 391). By then, however, the Indian Peninsula was forested (Guleria, 1992, in Morley, 2018) and Sri Lanka positioned around 15°S (Scotese & Schettino, 2017), within the inter-tropical convergence zone which, at the Mi-1 glaciation 23 Mya, had been displaced southwards (Hyeong *et al.*, 2014).

Current species distribution patterns suggest that a corridor with less than four dry months had ceased to exist between India and Southeast Asia some time prior to ~23 Mya (Ashton, 2014: 412). Seasonal forests continued to provide connectivity between Sri Lanka and Southeast Asia via the Indian Peninsula, however, until the mid-Miocene (Ashton, 2014: 391). Richardson *et al.* (2013) showed, in the case of the sapotace tribe Isonandreae, for example, that Sri Lankan lineages nest within those from Malesia, indicating a Sunda origin and dispersals from Malesia across India and on to Sri Lanka on at least three occasions, ~22.4 Mya, ~19.8 Mya and ~7.7 Mya. It remains open, however, whether the various Sri Lankan lineages arrived overland via India, or by overseas dispersal.

While differences in the periods during which the rates of exchange of the various taxonomic groups peaked (Klaus *et al.*, 2016; see Figure 3.43) may in part be due to the manner in which the molecular clocks for the respective taxa have been calibrated, such differences are consistent also with a scenario in which biotic exchange was modulated by shifts between perhumid, seasonal-tropical and arid climates conducive to particular taxonomic groups during such periods (see Morley, 2012). Biotic exchange may have been progressively attenuated also by the uplift of the Indo-Burman-Ranges since ~40 Mya (Haproff *et al.*, 2020; Morley *et al.*, 2020).

Further, at the time of the early-Eocene biotic exchanges, the axis of the Indian plate was tilted approximately 30° clockwise of its present orientation (Figure 3.5), with present-day central India lying just north of the equator (Morley, 2000: 165). As such, the adjacent regions of India and Southeast Asia that coalesced during this period were probably characterized by similarly perhumid climates (Klaus *et al.*, 2016)*. It should be borne in mind, however, that as much as 4000 km of the northward extension of the Indian plate may have been subducted following its collision with Asia, and that more than a single contact with Asia is likely to have occurred (Zaman & Torii, 1999; Briggs, 2003a; van Hinsbergen *et al.*, 2012; Bouilhol *et al.*, 2013; Hu *et al.*, 2015, 2016).

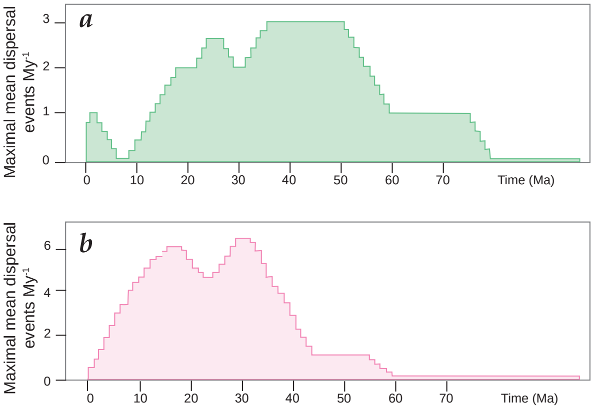

Figure 3.43. Maximal number of dispersal events (MDEs) between Southeast Asia and the Indian Subcontinent per million-year interval (in both directions), after Klaus *et al.* (2016), for ***a***, plants; and ***b***, freshwater fish.

Palynological studies pre-dating the late Pleistocene are lacking for Sri Lanka, however, and the deep history of the island's flora is yet to be revealed. Mandal (2005) and Farooqui *et al.* (2010) show the continued existence, since the Palaeogene, in the Western Ghats and Southeast India, respectively, of rainforest-associates such as *Cullenia* and *Bombax*. This is likely to have been the case also in Sri Lanka.

3.6.1 Chatterjee's Partition and Deccan aridification.

What then, so drastically attenuated the exchange of rainforest species between South and Southeast Asia? Ashton (2014: 411–415) argues that one factor was Chatterjee's Partition, a region extending from the Chin Hills of Myanmar (Figures 1.6, 3.7) westwards to the Gangetic Plain:

> 'The continuing northern movement of Gondwanan India, the rise of the high Himalaya from the early Miocene to heights comparable to the present day, and the consequent inception of the monsoon, resulted in rarer wet tropical corridors between South and East Asia, and exacerbated rainfall seasonality. On the evidence of current species distribution patterns, a corridor with less than four dry months ceased to exist before the origin of

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* There is, however, some evidence that a rainfall seasonality similar to that associated with the present-day South Asian monsoon existed in northern India as early as the beginning of the Eocene, despite the region's near-equatorial position at the time: Spicer *et al.*, 2017.

> the extensive perhumid Sunda lowlands (*c.* 23 Mya). The monsoon has been erratic and even absent over long periods during the last two million years, and the current wet period of high sea levels is likely to be almost as moist as at any time since the Pliocene and earlier… In summary, Chatterjee's Partition is as comparably distinct in relation to the woody and especially the deciduous flora, as Wallace's line, but has not received comparable attention… This lack of research attention may be partly because the partition runs overland, and because it consequently fails to display a distinct zoogeographical signal… It may seem at first truly extraordinary that so many tree families apparently failed to cross the Gangetic Plain.'

Chatterjee's Partition appears to have served as a barrier to the dispersal even of mammals between Sri Lanka-peninsular India to the west, and Southeast Asia to the east: *e.g.*, the tupaiid treeshrew genera *Anathana* (west) and *Tupaia* (east) (Roberts *et al.*, 2011), the sloth bear *Melursus* (west) and sun bear *Helarctos* (east) (Corbet & Hill, 1992), and the primates *Loris* and *Semnopithecus* (west) and *Nycticebus* and *Trachypithecus*, respectively (east) (Karanth, 2010). At least 18 genera of mammals which occur immediately to the east of the partition are absent west of it*. Among the aquatic fauna, Shih *et al.* (2009) showed that the partition applies also to the freshwater crab subfamilies Potaminae (west) and Potamiscinae (east). Heads (2012: 255) pointed implicitly to such a barrier to explain the apparent failure of the mangrove tree *Aglaia cucullata* (Meliaceae), which occurs from the northern shore of the Bay of Bengal to New Guinea, to disperse west of the Ganges delta (the species' range, however, extends substantially southwest of the Ganges Delta: Duke *et al.*, 2010). The barrier appears to have prevented the dispersal between India and Asia also of several reptile and amphibian lineages, which show sister-group relationships on either side, with divergences dating to around the Oligocene-Miocene boundary ~23 Mya (*e.g.*, the *Hypnale* pitvipers in India, *vs Calloselasma* in Southeast Asia: Alencar *et al.*, 2016).


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Figure 3.44. *Persicaria capitata* (Polygonaceae, above), is disjunct between Sri Lanka and the Himalayas, while *P. praetermissa* is confined to montane Sri Lanka, the Himalayas, Southeast Asia and south-eastern Australia.

This partition, taken together with the end-Miocene aridification of the Deccan Plateau, explains also the sister-group disjunctions between species of Dipterocarpaceae on either side: in Sri Lanka-South India to the west, and Southeast Asia to the east. Ashton (2014: 411) identified several such relationships between Sri Lankan (SL) endemics and Southeast Asian (SEA) congeners, including *Dipterocarpus hispidus* (SL) and *D. baudii* (SEA); *D. zeylanicus* (SL) and *D. turbinatus* (SEA); *Hopea brevipetiolaris* (SL) and *H. reticulata* (SEA); *Shorea dyeri* (SL) and *S. guiso* (SEA); and *S. stipularis* (SL) and *S. hypochra* (SEA). Deccan aridification perhaps explains also the distribution of the knotweed, *Persicaria capitata* (Polygonaceae), which is disjunct between Sri Lanka and the Himalayas, while *P. praetermissa* occurs in montane Sri Lanka, the Himalayas, Southeast Asia and south-eastern Australia (Figure 3.44).

Such disjunctions, between vascular-plant genera or even species, between Sri Lanka and/or the Western Ghats to the South and the Himalayan foothills to the north, are common: *e.g.*, *Clematis*, *Eriocapitella rivularis* (Ranunculaceae), *Beilschmie-*

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* *Arctictis, Arctogalidia, Arctonyx, Berylmys, Callosciurus, Cannomys, Catopuma, Dremomys, Hylobates, Leopoldamys, Maxomys, Naeomorhedus, Niviventer, Nycticebus, Pardofelis, Talpa, Tamiops, Tupaia* (Corbet & Hill, 1992).

K. S. Seshadri

Figure 3.45. *Rhacophorus calcadensis,* a species confined to the southern Western Ghats. The genus contains about 85 species, all of which range from north-eastern India to Southeast Asia, apart from four that are endemic to the Western Ghats.

Mendis Wickramasinghe

Figure 3.46. *Gerrhopilus ceylonicus*. The blind-snake family Gerrhopilidae occurs on Sri Lanka and southern Kerala, and is then absent elsewhere in India, though recurring from Thailand to New Guinea. The sister-group of Gerrhopilidae is Madagascan, reflecting the Gondwanan origin of these snakes (Vidal *et al.*, 2010; Sidharthan *et al.*, 2021).

dia, Cinnamomum, Litsea, Ranunculus (Lauraceae), *Geranium nepalense* (Geraniaceae) and *Rhododendron* (Ericaceae); while the sister group of the endemic Sri Lankan genus *Dicellostyles* (Malvaceae) is *Nayariophyton*, which occurs from the Himalayas to southern China but not in the peninsula of India (Paul, 1988). Similarly, the genus *Trigonostemon* (Euphorbiaceae) occurs in the lowland rain forests of Sri Lanka and the southern Western Ghats but is then absent from the Indian peninsula until it recurs in far Northeast India (Yu & van Welzen, 2020).

Pearson & Ghorpade (1989) give examples of similar south-north disjunctions also among tiger beetles (Cicindelidae), within genera such as *Collyris, Neocollyris* and *Tricondyla,* or even within species of *Cicindela.* A similar disjunction is seen also in the scolopendrid centipede genus *Digitipes,* between the Western Ghats to the west and Myanmar to the east (Siriwut *et al.,* 2015).

Sidharthan *et al.* (2021) showed the endemic Western Ghats balitorid genera *Bhavania, Ghatsa* and *Travancoria* form a monophyletic group that is sister the sister group of the Southeast Asian clade that includes *Pseudohomaloptera*. The freshwater-fish family Pristolepididae (see Figure 4.2), is likewise split between the Western Ghats and Thailand to the Malesian region, while absent in between (Britz *et al.,* 2012), a distribution reflected also by the anuran genus *Rhacophorus* (Figure 3.45; Biju *et al.,* 2013). The blind-snake family Gerrhopilidae (Figure 3.46) too, shows a similar distribution in Asia: Sri Lanka and the southern Western Ghats, then absent from the rest of India and recurring from Thailand eastwards to the Philippines and New Guinea (Vidal *et al.,* 2010). With its sister group in Madagascar (Pyron & Wallach, 2014), its distribution reflects Gondwanan vicariance.

Chatterjee's partition finds support also in the analyses of Klaus *et al.* (2016), who show that the exchange of biotas between India and Southeast Asia intensified ~44 Mya, building to a maximum in the Middle Miocene and then decreasing steadily after 14 Mya. Indeed, some Asian taxa, such as the viviparid freshwater snails, may have dispersed from Asia to India as early as 50 Mya (Sil *et al.,* 2019). The analysis of Klaus *et al.* (2016), shows, however, that the dispersal of freshwater fishes peaked around 28 Mya, with another peak around 14 Mya (Figure 3.43). The Indian Peninsula was forested at that time (Guleria, 1992, in Morley, 2018), though the Gangetic plain was becoming increasingly seasonal, presenting a barrier to further dispersal into India of Southeast Asian rainforest associates. The plain's climate served as an ecological barrier to the dispersal from Southeast Asia into India also of several plant families associated with lower montane forests, such as Altingiaceae, Betulaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Nyssaceae and Ulmaceae[*] (Ashton, 2014: 395). The development of this barrier coincides with the emergence of a strongly seasonal climate in northern India followed by a marked expansion of grasslands ~7 Mya (Quade *et al.*, 1989). While the Late Miocene saw the disappearance of rain forests over much of India; these forests withdrew, as refugia, to south-western India and Sri Lanka (Morley, 2000).

3.7 Biotic refugia

The wealth of disjunct distributions between Sri Lanka and the Western Ghats on the one side, and Asia east of Chatterjee's Partition on the other, indicates a widespread extinction of species associated with perhumid forests across the Deccan Plateau, a span of some 2000 km. This left stranded on either side sister groups such as the Microhylid anuran genera *Mysticellus* (Western Ghats) and *Micryletta* (Southeast Asia), which diverged 40.6 (29.1–51.4) Mya (Garg & Biju, 2019) (Figure 3.47), the caecilian genus *Ichthyophis* (Gower *et al.*, 2002) (Figure 3.48), the toad genus *Ansonia,* and the blind-eel genus *Rakthamichthys* (Britz *et al.*, 2020a). The Late Miocene aridification of the Indian Peninsula, especially its eastern side which abuts Sri Lanka, also isolated a wealth of micro-endemic and/or monotypic plant lineages[†] in refugia in Sri Lanka (especially in the south-western wet zone: Figure 2.6) and the Western Ghats,

S. D. Biju

Sonali Garg

Figure 3.47. Garg & Biju (2019) show that the Microhylid genera ***a,*** *Mysticellus* (Western Ghats) and ***b,*** *Micryletta* (Southeast Asia), which exhibit a sister-group relationship, diverged ~41 (51–29) Mya, to diversify on either side of Chatterjee's Partition.

Figure 3.48. The caecilian genus *Ichthyophis* shows a disjunct distribution between Sri Lanka + Western Ghats on one side and Southeast Asia on the other. The molecular analysis of Pyron (2014) recovered a Western Ghats-Southeast Asia clade that is the sister-group of the Sri Lankan clade, with a divergence around the Eocene-Oligocene boundary, ~34 Mya.

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[*] One species of which (*Holoptelea integrifolia*), however, occurs in the arid lowlands of South Asia including the dry zone of Sri Lanka.

[†] Microendemism (narrow-range endemism) in plants may not be a consequence of climate alone; it may be driven by edaphic and other factors. Besides, the distributions of rare species are in any case substantially more aggregated (as opposed to patchy or more dispersed) than common species (Condit *et al.* 2000).

especially south of the Palghat Gap, whose sister groups are in Asia east of Chatterjee's Partition. It was presumably aridification too, that prevented the dispersal to Sri Lanka of some 30 plant genera confined to southern India*. But this was certainly not so in all cases as, for example, the Podocarpaceae (see p. 100).

By the end of the Miocene, rain forests elsewhere in the Indian Peninsula had been reduced to moist valleys in the Eastern Ghats, in which relict patches of tropical evergreen vegetation persist even now, indicative of the former existence of such forests across the entire Peninsula (Ramesh, 2001: 979). The aridification of India may explain the disjunct distribution of taxa such as the *Megachernes* pseudoscorpions. The 23 species in this genus, which is associated with the nests and pelage of small mammals, have a broad range that extends across Asia, from the Black Sea, across the Himalayan foothills to Japan and southwards to eastern Australia. While *Megachernes* is apparently absent from the peninsula of India, a single species occurs in Sri Lanka, living commensally with *Mus mayori*, an endemic mouse associated with rain forests (Harvey *et al.*, 2012).

Another such example is offered by the rover-beetle genus *Labomimus*, which has a single species in Sri Lanka and is then absent from the Indian peninsula, to occur once more eastwards from Northeast India to China (Li & Yin, 2020). The stalk-eyed flies of the genus *Teleopsis* (Diopsidae) are another such case. They occur in Sri Lanka and the southernmost India but are absent elsewhere in India, recurring from Malaysia to China and the Philippines (Feijen & Feijen, 2020).

Numerous genera and species found only in Sri Lanka and the southern Western Ghats too, signal the biotic connection between these two regions. For example, the termite genus *Dicuspiditermes,* which comprises only two species, occurs nowhere else (Amina *et al.*, 2020), as does the copepod genus *Megadiaptomus* (Kulkarni *et al.*, 2018).

The divergence times between Eastern and Western Ghat taxa dependent on perhumid forest, such as the centipede genus *Ethmostigmus* (*ca* 40 My: Joshi & Edgecombe, 2019), the indotyphlid amphibian genus *Gegeneophis* (*ca* 35 My: Gower *et al.*, 2016) and the gecko genus *Geckoella* (32–24 My: Agarwal & Karanth, 2015) suggests, however, that the climate of the lowlands of central peninsular India had become seasonal by the Oligocene, with clear implications for biotic exchange also between the Western Ghats and Sri Lanka since then.

This pattern is paralleled also by a diverse array of vertebrate taxa: the snake genus *Cylindrophis* (Pyron *et al.*, 2013a) (Figure 3.49), the skink genus *Dasia* (Harikrishnan *et al.*, 2012) (Figure 3.50), and among birds, the frogmouth (*Batrachostomus,* Figure 3.52), Asian fairy-bluebird (*Irena puella,* Figure 3.53) and the bulbul genus *Hypsipetes* and (Guptha *et al.*, 2015; Raman, 2006; Shakya & Sheldon, 2017). The nymphalid butterfly genus *Idea* too, shows a similar distribution (Figure 3.54b): Sri Lanka and the Western Ghats, then absent across the width of the Indian peninsula, after which it continues from Myanmar to Malesia (Kitching *et al.*, 1987; Jadhav *et al.*, 2013). In other cases, such as the gliding-snake *Chrysopelea taprobanica* (Figure 3.51), however, such disjunctions inferred in the earlier literature have been shown to be more nuanced (Guptha *et al.*, 2015; Somaweera *et al.*, 2015).

In a few instances, Sri Lanka and the Western Ghats together harbour diversifications whose closest phylogenetic relationships are not with Himalayan lineages, but Sumatran ones, *e.g.*, the *Megarthrus* beetles (Cuccodoro & Liu, 2016; Figure 3.54a).

Such disjunctions are consistent with a model in which, as the intensity of the monsoons abated during glacial maxima, the evergreen rain forests of Sri Lanka retreated to refugia in moist valleys, within the cloud base on hill slopes, and with diurnal cloud-shadow helping to ameliorate desiccation. Farooqui *et al.* (2010) inferred such a scenario also in the Western Ghats. Proximity to the

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* Plant genera confined to southern India (and absent from Sri Lanka) include– Acanthaceae: *Calacanthus, Nilgirianthus, Pleocaulus, Taeniandra, Xenacanthus*; Apiaceae: *Vanasushava*; Apocynaceae: *Baeolepis, Decalepis, Frerea*; Araceae: *Anaphyllum*; Burmanniaceae: *Haplothismia*; Compositae: *Adenoon*, *Lamprochaenium, Nanothamnus*; Cyperaceae: *Ascopholis*; Leguminosae: *Wagatea*; Loranthaceae: *Helicanthes*; Malvaceae: *Erinocarpus*; Myrtaceae: *Meteoromyrtus*; Orchidaceae: *Diplocentrum, Smithsonia*; Orobanchaceae: *Campbellia*; Poaceae: *Bhidea, Indopoa, Limnopoa*; Podostemaceae: *Hydrobryopsis, Indotristicha, Willisia*; Rhizophoraceae: *Blepharistemma*; and Rubiaceae: *Octotropis* (revised from Subramanyam & Nayar, 1974; and Nayar, 1980, restricted to names accepted by theplantlist.org).

Mendis Wickramasinghe

Figure 3.49. The pipe-snake genus *Cylindrophis* (Cylindrophiidae) is represented by a single species, *C. maculatus*, in Sri Lanka's wet and intermediate zones (Mendis Wickramasinghe, pers. comm.), but is then absent from India before recurring in Southeast Asia as a diversification of some one-dozen species (the elevated end of this non-venomous snake is its tail; the head lies beneath, protected by the body).

Mendis Wickramasinghe

Figure 3.50. The arboreal skink genus *Dasia* has a disjunct distribution, with a species each in Sri Lanka and the southern Western Ghats, thereafter absent in India and Myanmar, but recurring from the Nicobar Islands, across Thailand and to the Philippines (Harikrishnan *et al.*, 2012).

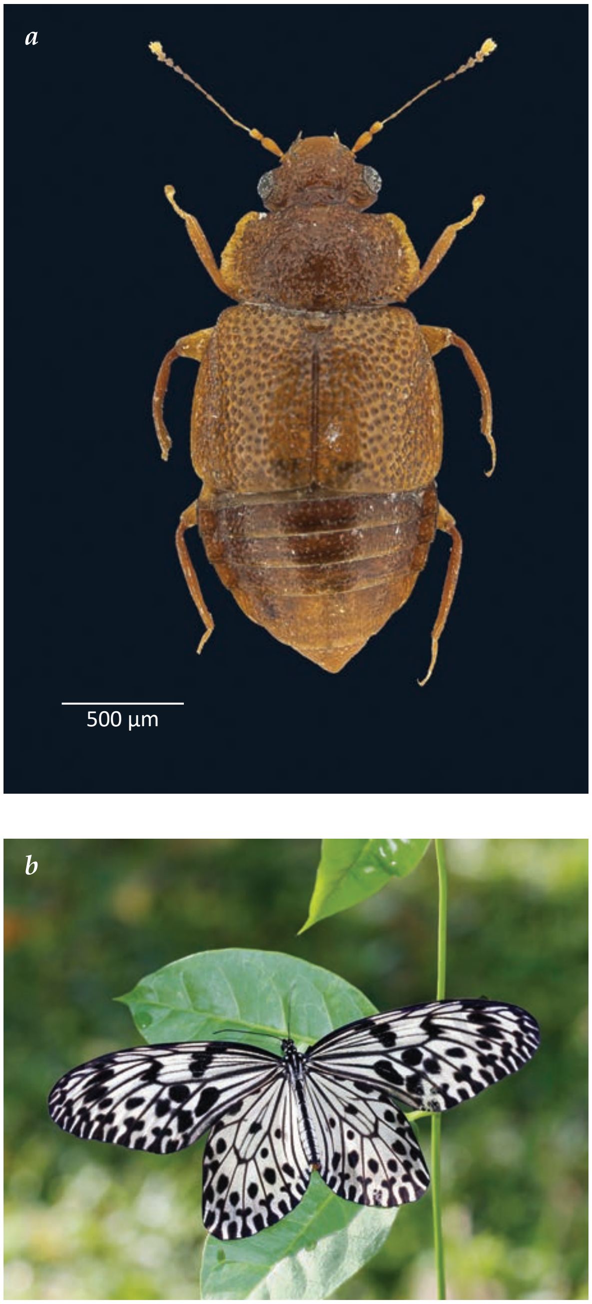
Figure 3.51. The gliding-snake *Chrysopelea taprobanica* occurs in Sri Lanka and then recurs in Andhra Pradesh (Guptha *et al.*, 2015; see also Somaweera *et al.*, 2015).

Ajith Ratnayake

Figure 3.52. The frogmouth genus *Batrachostomus* occurs in humid forest habitats in Sri Lanka and the Western Ghats. It is absent in the rest of India but recurs in the rain forests of Southeast Asia.

Garima Bhatia CC BY-SA 4.0

Figure 3.53. The Asian fairy-bluebird (*Irena puella*) is known in Sri Lanka only from 19th-century records. It is still recorded in the Western Ghats, but not from anywhere else in South Asia, though recurring in Southeast Asia.



Giulio Cuccodoro

Michael van der Poorten

Figure 3.54. ***a*****,** *Megarthrus lanka* (Staphylinidae, Proteininae). Cuccodoro & Liu (2016) show the lineage in Sri Lanka and the Western Ghats to have their closest phylogenetic relationships not with Himalayan (they are absent elsewhere on the peninsula) but Sumatran ones. ***b*****,** Tree nymph butterflies of the genus *Idea* (Nymphalidae) are represented in South Asia by only two species: *I. iasonia*, a Sri Lankan endemic, and *I. malabarica*, which is confined to the Western Ghats. The genus is otherwise absent from India, though recurring from Indomalaya through Southeast Asia. Wallace (1876) pointed to *Idea* (then *Hestia*) as evidence of Sri Lanka's biotic affinity with Malaysia.

ocean (Sri Lanka's western foothills are within 50 km of the sea) and onshore winds too, delivered orographic rainfall helping to maintain refugial rain forests. While overall rainfall declined, mean monthly rainfall in the driest months was sufficient to offset evapotranspiration.

The degree of aridification the island had experienced during the Pleistocene, however, was perhaps dwarfed by the severity and extent of aridification at the Last Glacial Maximum, ~22 kya. Even as low sea levels enhanced the island's subaerial extent (Figure 3.55), humid forests declined to a fraction of their Holocene extent, characterized by more open rain forest, both in the lowlands and the hills (Roberts *et al.*, 2018).

That fraction was, nevertheless, significant. The increasingly pluvial conditions of the Holocene led to rain forests once more expanding their ranges, but the present mix of scattered upper montane rain forest and grassland at Horton Plains, for example, became established as recently as ~2 kya (Premathilake & Gunatilaka, 2013). Meanwhile, lowland evergreen rain forest and Mixed Dipterocarp Forest expanded to fill Sri Lanka's south-western lowlands, where the dry season (rainfall < 100 mm per month) is less than two months' duration or absent altogether.

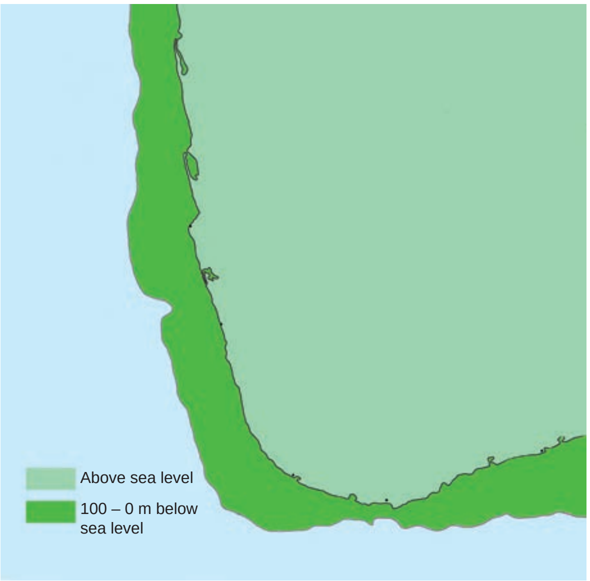


Figure 3.55. The coastline of Sri Lanka's south-western quadrant, which harbours almost all the island's rain forests, and the 100 m isobath, indicating the modest increment in terrestrial extent when sea levels were around this level, most recently from ~26–13 kya.

Fernando (2011) illustrated the potential of small refuges just hundreds of hectares in size to harbour species that are absent from the surrounding landscape. He analyzed the flora of three isolated mountains, Monaragala (1110 m asl), Doluwakanda (660 m asl) and Kokagala (600 m asl), set within the relatively dry lowland plains of the island's 'intermediate' climatic zone (annual rainfall ~1.8–2.5 $\mathrm{m \cdot y^{-1}}$). Despite being embedded in a markedly seasonal landscape, these three mountains were found to harbour 15 percent of the island's endemic angiosperm species, many of which were otherwise restricted to the aseasonal wet zone or other similar mountaintops.

As Roberts *et al.* (2018) show from archaeological sites, the ecotone of the closed-canopy, tropical evergreen rain forests of the wet zone, together with the more seasonal deciduous forests of the intermediate-zone and the dry-adapted jungle and grasslands of the dry zone, similar to that obtaining today, had become established by the end of the Pleistocene (~12 kya) and persisted through to the Iron Age (~3 kya). 'However, while changes in forest extent, particularly during MIS 2 [Marine Isotope Stage 2: 29–14 kya], clearly occurred, faunal, archaeobotanical, and molluscan evidence from the archaeological sites at the Batadomba and Fa Hien rock shelters (Perera, 2010; Perera *et al.*, 2011), as well as direct stable isotope evidence from human fossil-tooth enamel from Batadomba-lena (Roberts *et al.*, 2015, 2017), indicate continuing human reliance on tropical forest resources such as primates and other small semi-arboreal mammals, from 36–3 kya (Roberts *et al.*, 2018).

It is important, nevertheless, to recognize that except for a brief, low-amplitude marine transgressions during the Holocene (Ranasinghe *et al.*, 2013; Yokoyama *et al.*, 2019), Sri Lanka's subaerial extent is now the least it has been since the end of the Miocene (*cf.* Figures 3.59, 3.62). As such, despite the pluvial conditions obtaining at present, the island's biota must be considered to be in a state of refuge. As shown by Cannon (2012) and Cannon *et al.* (2009) for Sundaland, the current extent of evergreen lowland rain forest is among the smallest in terms of total land area over the past million years. The climatic and biodiversity crises of the Anthropocene, then, are compounded by coinciding with a time in which biodiversity is the most vulnerable it has been for the past *ca* one-million years.

Unlike on the Sunda shelf, however, because Sri Lanka's rain forests are restricted to the island's south-western quarter, where the continental margin lies close to the present shoreline (Figure 3.55), the scope for expansion during sea-level low-stands, though substantial, is more limited. While historical marine transgressions and recessions over low-lying terrain in Southeast Asia created opportunities for allopatric speciation and subsequent dispersal as rivers became isolated and then reconnected (Winemiller *et al.*, 2008: 112; de Bruyn *et al.*, 2012), evidence for such a mechanism in the case of Sri Lanka's biota is wanting.

The situation in the Indian Peninsula was arguably less stable, given the lack of a continuously perhumid climate through the Pleistocene. Rain forests shrank substantially everywhere, except in moist and sheltered valleys. While climate warmed and rainfall increased in the Holocene, the refugia expanded as opportunities for dispersal arose once more.

In relation to the Western Ghats, Bose *et al.* (2016) observed, 'the proximity and floristic similarity of the wet forests of… southern Sri Lanka (separated from India only by the Palk Strait)… suggest regular regional exchanges over time, which are expected to have influenced range shifts and speciation events in the endemics.' As we show in this text, however, such exchanges—because they were strongly mediated by climate—were the exception and not the rule.

In the case of the Last Glacial Maximum, proximity may well have helped the aerial dispersal of seeds. But the Palk Isthmus, which bridged the Strait until ~6 kya, was by then hardly a corridor conductive to the dispersal of rainforest species: it was at least as arid as the south-eastern plains of the Indian peninsula.

Although almost a thousand endemic vascular plants survived the Pleistocene in Sri Lanka (many of them with highly restricted distributions: Figure 2.7), the pattern of tree-species richness in the island's rainforest landscapes is suggestive of extinction: unlike elsewhere in Asia, diversity in the rain forests of Sri Lanka's aseasonal wet zone is highest at ~500 m, rather than in the lowlands (Ashton, 2014: 410). Based on palynological data, Flenley (1998) had already suggested that the Last Glacial Maximum witnessed lowland forests being restricted and intermingled with montane elements, consistent with a drier climate that was some 5–10° C cooler than at present. As is the case elsewhere in Asia too, the amplitude of the elevational shifts of vegetation boundaries with climate change is poorly understood also in Sri Lanka (Morley & Flenley, 1987). Shaney *et al.* (2020) estimate, however, that in Sumatra, highland forests retreated 700–750 m at the LGM. Given its similar latitude, a comparable amplitude of retreat could be expected in Sri Lanka, too.

3.8 Insularity driven by Pleistocene climate change

The Last Glacial Maximum (LGM: ~24–18 kya) was, as climate change went in the course of the Pleistocene of Sri Lanka, particularly pernicious. The maps of Ray & Adams (2001) show the expansion of grasslands, while Boivin *et al.* (2013) and Roberts *et al.* (2018) report a substantial shrinkage of megathermal forest and a transition of the lowland rain forests to a more open forest type.

A palynological analysis at Horton Plains, a tropical montane cloud forest at ~2100 m asl elevation, showed the present matrix of upper montane rain forest and (probably anthropogenic) grassland to have been reduced, at the peak of the LGM, to a flora 'characterized mainly by grassland, dry shrub-forest and xerophytic species, with a total lack of upper montane rainforest elements' (Premathilake & Risberg, 2003; Premathilake, 2012; Premathilake & Gunatilaka, 2013; Figure 3.56).

Such episodes of aridification seem to have occurred also in the montane forests of the southern Western Ghats. Bera & Farooqui (2000) made a palynological study of lacustrine sediment pro-

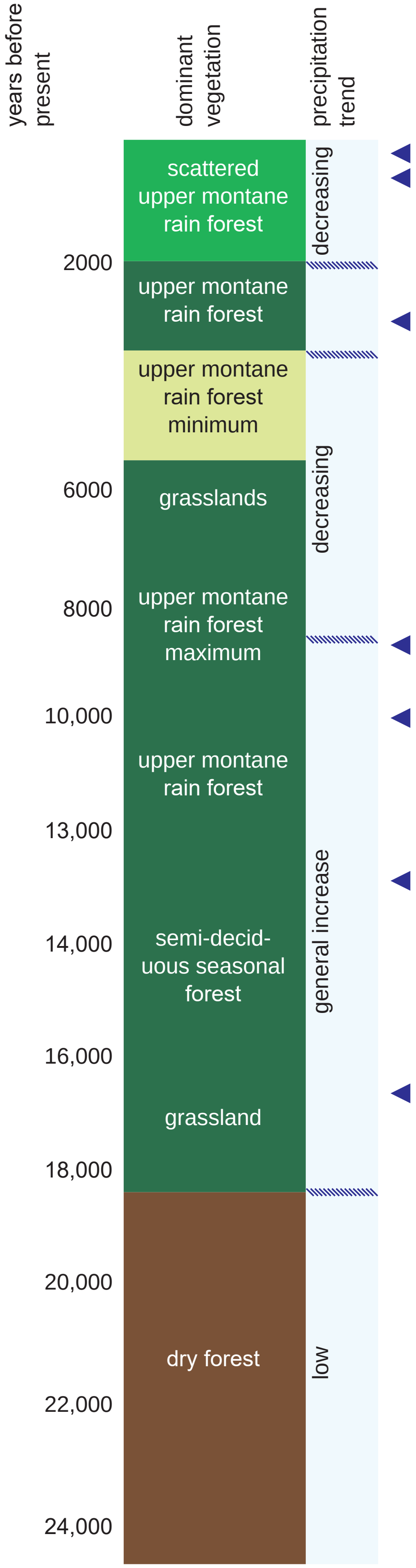


Figure 3.56. General vegetation-type and rainfall in Horton Plains, a 2100 m asl plateau in the central mountains, during the past 24,000 years, inferred from the palynological record (adapted from Premathilake & Risberg, 2003 and Pethiyagoda, 2012). The blue arrowheads indicate peaks in precipitation. Note the marked aridification around the Last Glacial Maximum, ~24–18 kya. Such local fluctuations between arid and humid climates characterize the Holocene of Sri Lanka, for example in the island's Southeast (Ranasinghe *et al.*, 2013), Northwest (Reuter *et al.*, 2020), western wet zone (Gayantha *et al.*, 2020) and north-central region (Premathilake & Caratini, 1994).

files from the Konalar basin and Kuntan shola of the Palni Hills. They showed that following the onset of warm and humid climatic regime, shrub savannah dominated 4000–2300 ya, changing to 'vast stretches of grassland' 2300–1150 ya, indicative of a cold and dry climate. Thereafter, the climate became increasingly warm and less humid.

The pollen record indicates substantially drier conditions also in the Nilgiris 16–22 kya, after which the monsoons returned (Ashton, 2014: 435). Nevertheless, even the Holocene witnessed 'multidecadal to centennial' periods of weak monsoons, for example, in Maharashtra, India, 4.6–3.9 and 2.0–0.6 kya (Prasad *et al.,* 2014). Closer to Sri Lanka, Veena *et al.* (2014) report generally warm and dry conditions 6.8–1.6 kya, though with intense wet phases 6.0–1.7 kya, 1.2–0.8 kya and 440–160 ya at Pookode Lake, Kerala. With an annual rainfall of around 4 m, the lake (770 m asl) now lies within an evergreen (rain) forest characterized by dipterocarps. Clearly, episodes of intense aridification have been frequent in the region.

Roberts *et al.* (2014) showed, from a dated faunal succession accumulated during the past ~200,000 years in the Billasurgam Caves in Andhra Pradesh, India, that 'although local extirpations occurred, the majority of taxa survived or adapted to substantial ecological pressures in fragmented habitats' as the Pleistocene drew to a close. Such, however, was not the case in Sri Lanka. The tiger (*Panthera tigris*), lion (*Panthera leo*)*, hippopotamus (*Hexaprotodon sinhaleyus*), two species of rhinoceroses (*Rhinoceros sinhaleyus* and *R. kagavena*), two species of elephants (*Elephas hysudricus* and *E. namadicus*), the gaur (*Bos gaurus*) and the dhole (*Cuon javanicus*) all disappeared from the island around the LGM (Manamendra-Arachchi *et al.*, 2005 and references therein; Chauhan, 2008) (Figure 3.57). Although their demise might have been hastened by anthropogenic attrition, *H. sapiens* had already been on the island at least since 36 kya (Roberts *et al.*, 2015) and—given the arrival of modern humans in Australia 65 kya (Clarkson *et al.*, 2017)—probably twice that long. Their technologies were likely similar to those in India, where no such extirpations occurred during the LGM (Roberts *et al.*, 2014). Jukar *et al.* (2020) concluded that the large mammals that became extinct in India–Sri Lanka in the late Pleistocene were all endemic to the Subcontinent, and/or had small litters and large intervals between litters, localized distributions and narrow ecological niches.

While extinctions were, no doubt, widespread among species unable to adapt to aridification, a handful of species shows evidence of adaptation to this challenge. Perhaps most remarkable among these are the frogs of the endemic dichroglossine genus *Nannophrys*, which diverged from their sister group *Euphlyctis* + *Hoplobatrachus* in the Oligocene (Roelants *et al.*, 2004; Bossuyt *et al.*, 2006). The genus is known from three species endemic to Sri Lanka, one (*N. ceylonensis,* Figure 3.58) restricted to the rain forests of the perhumid south-western wet zone and the others (*N. marmorata, N. naeyakai*) to scattered locations on the eastern slopes of the Knuckles hills and eastern uplands, respectively. *Nannophrys marmorata* occurs in a region subject to a strongly seasonal climate characterized by high air temperature (21.5–39.2° C), low relative humidity (27–70 %), and strong, desiccating winds (Senanayake *et al.*, 2019). Here, it shows several adaptations to life in perennially-moist rock crevices—wet niches within a dry landscape. These include a strikingly flattened and highly ossified cranium, which serves as a wedge that facilitates squeezing into narrow crevices, and strong, spade-like hindlimbs adapted to thrusting the body into these tight spaces (Senevirathne & Meegaskumbura, 2015). *Nannophrys marmorata* is also one of the very few species of Neobatrachia known to possess free ribs, which too, these authors considered an adaptation to its highly specialized habitat. Senanayake *et al.* (2019) found that *N. marmorata* in rock crevices were able to maintain a body temperature almost 12° C lower

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* Although Kitchener & Dugmore (2000) had argued that peninsular India was a poor habitat for tigers in the Pleistocene, Cooper *et al.* (2016) show that much of the peninsula contained habitats conducive to these big cats. Manamendra-Arachchi *et al.* (2005) argued for the former presence of tigers in Sri Lanka while casting doubt on the earlier identification of Pleistocene fossil bone and tooth fragments as belonging to lions, a species otherwise unknown from the peninsula of India. Although Thapar *et al.* (2013) argue that the lion is an alien species in India, having been introduced to that country in historical times, the review of Jhala *et al.* (2019) suggests, based on historical and molecular evidence, that lions were present in South Asia by 6–4 kya.

Kelum Manamendra-Arachchi

Figure 3.57. Subfossils of extinct Pleistocene mammals from Sri Lanka. ***a,*** gaur (*Bos sinhaleyus*), metacarpal*;* ***b,*** elephant (*Elephas maximus sinhaleyus*), molar*;* ***c,*** dhole (*Cuon javanicus*), lower canine*;* ***d,*** lion (*Panthera leo*), molar*;* ***e, f,*** hippopotamus (*Hexaprotodon sinhaleyus*), molar, lower canine*;* ***g,*** tiger (*Panthera tigris*), middle phallanx*;* ***h,*** elephant (*Hypselephas hysudricus sinhaleyus*), molar fragment*;* ***i,*** Asian straight-tusked elephant (*Palaeoloxodon namadicus sinhaleus*), molar fragment*;* ***j,*** rhinoceros (*Rhinoceros sinhaleyus*), molar*;* and ***k,*** rhinoceros (*R. kagavena*), molar. Images and identifications courtesy of Kelum Manamendra-Arachchi.

Figure 3.58. The frogs of the endemic Sri Lankan genus *Nannophrys*, here *N. ceylonensis*, are adapted to life in moist rock crevices (Senevirathne & Meegaskumbura, 2015). This has enabled *N. marmorata* to occupy this microhabitat and persist in the markedly seasonal climate of the eastern Knuckles hills (Senanayake *et al.*, 2019).

than ambient air temperature outside the crevice.

While the aridification associated with the LGM might have been among the most severe of the Pleistocene desiccation events, the biota that did survive it in Sri Lanka is nevertheless remarkable: a vascular-plant flora of some 3500 species, almost 1000 of which are endemic (Dassanayake & Fosberg, 1980–2006; Gunatilleke & Gunatilleke, 1990; MOE, 2012), together with a rich and diverse fauna that exhibits a high degree of endemism and some spectacular insular Plio-Pleistocene diversifications. These include the *Pseudophilautus* shrub frogs (~76 endemic species: Meegaskumbura *et al.*, 2019; Ellepola *et al.*, 2021) and gecarcinucid crabs (50 endemic species: Beenaerts *et al.*, 2010).

The representation of Sri Lankan vascular plants in time-calibrated molecular phylogenies is scant. Among those available is the remarkable Pliocene diversification of the star-violet genus *Hedyotis* (Rubiaceae, Figure 3.59). Montane Sri Lanka and the Western Ghats possess 25 and 20 endemic species, respectively, in this genus, in addition to about five that are shared between the two regions. Neupane *et al.* (2017) show that there were two successive, independent colonizations by *Hedyotis*. The first pulse of *in situ* diversification took place in the Western Ghats ~8 Mya. The second pulse (~4 Mya), comprising immigrants from Southeast Asia, could not become established in the Western Ghats probably due to niche pre-emption (Silvertown *et al.*, 2005) 'but were able to diversify in the Central Sri Lankan highlands due to the available open niches [there]'.

Wickramasinghe *et al.* (2017) and Lim *et al.* (2019) showed the endemic Sri Lankan Hill white-eye, *Zosterops ceylonensis* (Figure 3.60), to be the sister-group of all other *Zosterops* (some 75 species ranging from Africa to Australia: Lim *et al.*, 2019). Surprisingly, the divergence between *Z. ceylonensis* and its congeners dates to only 1.8 (1.3–2.3) Mya, a remarkably rapid diversification at a time of ecological stress. With *Z. ceylonensis* occupying mainly the highlands above 1300 m asl elevation, the lowlands were subsequently occupied by *Z. palpebrosus*, a migrant that had diverged from its sister population just 190 (310–100) kya. The yellow-eared bulbul, a Sri Lankan highland endemic, shows even longer isolation. Jha *et al.* (2021) show it diverged from its Indian and Southeast Asian sister group in the late Miocene, ~7.5 Mya, with no subsequent diversification in the island.

A similar, but much older, multiple dispersal is represented by the island's five species (Figure 3.61) of nymphalid Bushbrown butterflies of the genus *Mycalesis*: they do not represent an autochthonous diversification but derive from at least three separate founder migrations from India or Southeast Asia in the Late Miocene or the Pliocene (Goonesekera *et al.*, 2019). These authors showed also that the Sri Lankan subspecies *Mycalesis patnia patnia* diverged from its Indian sister-group *M. p. junonia* as long ago as the Late Miocene, and appears to have been isolated since then, despite repeated and prolonged terrestrial connections via the Palk Isthmus.

The degree to which Sri Lanka's rain forests shrank during glacial maxima, however, remains unknown. There is no evidence of a collapse of rainforest biodiversity as was the case, for example, in tropical Africa (Bonnefille, 2011), although its island setting—and its perhumid wet zone itself being in effect an island within the island—negatively influences species diversity (Condit *et al.*, 2000). The effects of Pleistocene climate-change in Sri Lanka may well have been local, exacerbating, for example, the aridity of the island's present-day dry zone and enhancing the extent of open forest in the wet zone. The increased subaerial extent of the island consequent to falling

Figure 3.59. Sri Lanka and the Western Ghats have 25 and 20 endemic species, respectively, of the star-violet genus *Hedyotis* (Rubiaceae), with only two additional species common to the two regions. The Sri Lankan diversification is largely derived from Southeast Asian ancestors which arrived as recently as ~4 Mya (Neupane *et al.*, 2017).

Figure 3.60. The endemic Sri Lanka Hill White-eye, *Zosterops ceylonensis,* which diverged from its ~75 congeners as recently as 1.8 (2.3–1.3) Mya (Wickramasinghe *et al.*, 2017; Lim *et al.*, 2019). The Indian white-eye, *Z. palpebrosus,* which occurs at lower elevations in Sri Lanka, represents a much later migration to the island.

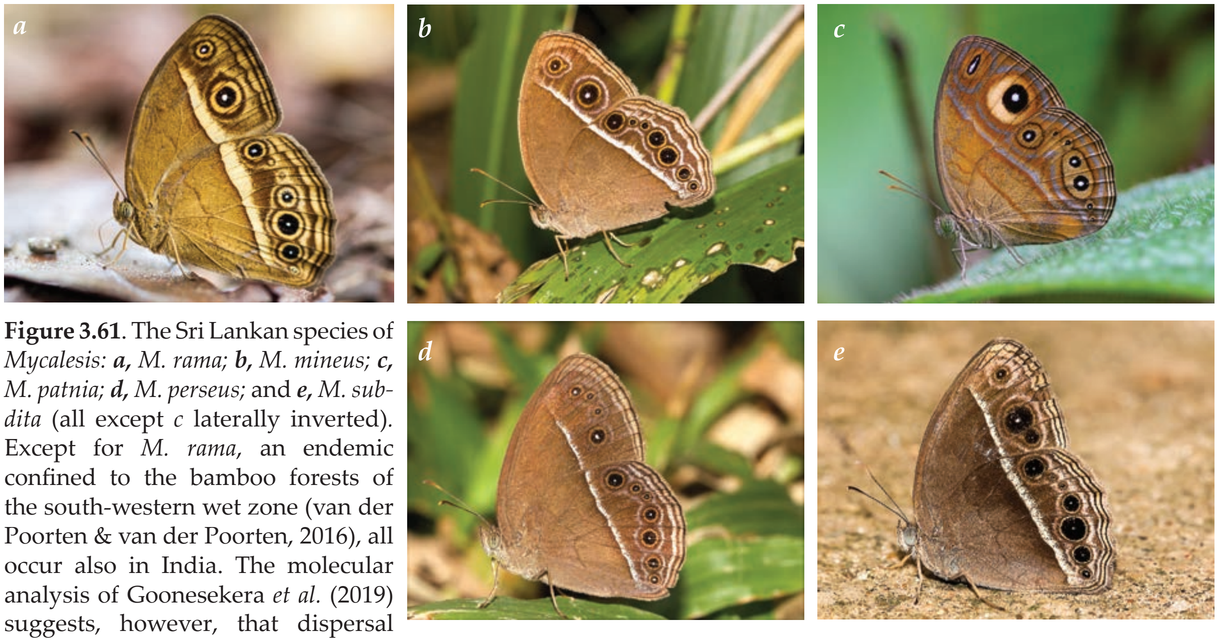

Figure 3.61. The Sri Lankan species of *Mycalesis:* ***a,*** *M. rama;* ***b,*** *M. mineus;* ***c,*** *M. patnia;* ***d,*** *M. perseus;* and ***e,*** *M. subdita* (all except *c* laterally inverted). Except for *M. rama*, an endemic confined to the bamboo forests of the south-western wet zone (van der Poorten & van der Poorten, 2016), all occur also in India. The molecular analysis of Goonesekera *et al.* (2019) suggests, however, that dispersal events between Sri Lanka and the mainland have been rare.

sea level, too, especially in the north, no doubt entailed climatic consequences, for example, by triggering increased convection and upper-level divergence over the island, as was the case also over the Sunda shelf (Bush & Fairbanks, 2003).

The rate at which rain forests were able to expand into land from which the sea had retreated during sea-level low stands too, remains unknown in South Asia. On the Sunda shelf during the Last Glacial Maximum, however, Wang *et al.* (2009) found from examination of pollen and phytoliths in shallow-shelf marine sediment cores, that the exposed shelf had, during sea-level low-stands, been covered with humid vegetation characterized by high proportions of pollen from lowland rain forests and lower-montane rain forests, including rainforest associates such as the *Cyathea* tree ferns. Although the climate, as inferred from the vegetation, was cooler than that obtaining now, no significant decrease in humidity was inferred—at least not to a degree sufficient to inhibit the establishment of rain forest.

3.9 The Palk Isthmus

3.9.1 Geology. The past tectonic juxtaposition of Tamil Nadu and Sri Lanka (Figure 3.5) is inferred from shared Jurassic 'Gondwanan' deposits occurring in the Madras-Chingleput region of India west of the failed rift, and the Tabbowa and Andigama beds of Sri Lanka east of it (Katz, 1978). Although Sri Lanka was then aligned a few degrees clockwise of its presented orientation, its general topography has remained stable since the Oligocene (and likely through the past 130 My: von Blanckenburg *et al.,* 2004). Little surface evidence survives of the island's pre-Jurassic topography, except perhaps for the numerous 'boulder beds' scattered across the lowlands, inferred by Katupotha & Kodituwakku (2015) to have been created by the melting of glaciers following the Karoo Glaciation (360–260 Mya) (see also Chatterjee & Hotton, 1986; Valdiya, 2016: 417). As pointed out by Deraniyagala (1955), however, the disrupted fossiliferous Pliocene and Pleistocene Ratnapura beds present evidence of more recent uplift.

Katz (1978) showed that southeast India and northwest Sri Lanka were once a single structure (Figure 3.5a), separated by subsequent boundary faults and rifting (see 3.2.1). The separation of Sri Lanka from India appears to have begun in the Jurassic, when a series of rifts opened up along the present-day island's west coast, allowing a marine incursion between it and the east coast of southern India (McCune, 1947).

The oldest fossil beds in Sri Lanka are at Tabbowa and Andigama, in the island's northeast, where of carbonaceous shales are distributed over an area of some 30 km^2 and ~500–1000 m deep. Dated to the Middle–Upper Jurassic (175–145 Mya), these contain numerous extinct plants associated with a swamp-forest environment, including the ferns *Cladophlebis*, *Glossopteris* and *Sphenopteris*, the cycadeoids *Nilssonia* and *Otozamites*, and the cycadophytad *Ptilophyllum* (Abeysinghe, 2010; Edirisooriya & Dharmagunawardhane, 2013a,b). This palynoflora is characteristic of the temperate vegetation associated with the Australian Jurassic (Deraniyagala, 1955; Weerakoon *et al.*, 2019).

Weerakoon *et al.* (2019) found the Tabbowa palynoflora to comprise 42 pteridophytes, 24 gymnosperms, five bryophytes and three pteridosperms, dominated by *Araucariacites* and *Callialasporites* conifers (Araucariaceae). They dated the deposit to the Callovian-Kimmeridgian (166–152 Mya), and inferred it to represent an estuarine Southern Hemisphere palaeoenvironment (Tabbowa's elevation is presently ~20 m asl).

Weerakoon *et al*. (2021) dated the Andigama deposit to the Tithonian-Berriasian age (~140–150 Mya). They reported a tree-dominated vegetation that included more than 70 species of cycads, ferns and gymnosperms associated with a freshwater forest-swamp habitat obtaining in a warm, humid environment (Ratnayake & Sampei, 2015).

In any event, the Tabbowa and Andigama deposits suggest that that part of the island's lowlands was subaerial at around the time Sri Lanka-India rifted from Antarctica. The island appears not have been substantially submerged since.

3.9.2 Sea levels. The Oligocene saw, for the first time since the Late Cretaceous, periodic sea level low-stands of 20–30 m below the present level from 28.2–27.7 Mya (Miller *et al.*, 2005, 2020), and as much as 250 m at ~28 Mya (Hutchison, 1989). It may have been this low-stand that gave rise to the first subaerial terrestrial connection between Sri Lanka and the Indian Peninsula since the collision

Madhava Meegaskumbura

Madhava Meegaskumbura

Figure 3.62. The Aruwakkalu fossil bed, part of the north-eastern Miocene Jaffna limestone belt, has yielded a rich harvest of shallow-shelf marine fossils, including bivalves, gastropods and Foramenifera, dated to the Burdigalian, ~20 to ~16 Mya (Epa *et al.*, 2012).

of the Indian plate with Asia in the early Eocene, paving the way for biotic exchange between the two landmasses and, via India, with Southeast Asia.

The Oligocene and early Miocene witnessed a crustal depression of some tens of metres of the region between Sri Lanka and India, as subsidence of Palk Bay progressed (see 3.2.2). As a result, Sri Lanka's north-western littoral, including the isthmus connecting it to India, were inundated and became a shallow-shelf sea (as it is now), resulting in the deposition of the limestone beds that characterize that region (Katz, 1978; Krishnan, 2014). A corresponding limestone belt occurs across the Palk Strait, in the region of Karaikal, near Puducherry in south-eastern India. On the Sri Lanka side, weathered karst limestone[*] occurs in three north-south ridges, in places 80–120 m deep, for example, at Vanathavillu. The limestone bed, which is rich in fossil foraminifera and macro-fossils including corals, rises to ~30 m above present sea level (~65 m above sea level at Aruwakkalu).

The Miocene deposits of the northwest (principally coral, gastropod and bivalve molluscs and the foraminifer *Pseudotaberina malabarica*) have been dated to the Burdigalian (~20–16 Mya) by Epa *et al.* (2012) (Figure 3.62). Parts of this limestone belt are exposed along the northwest Sri Lankan and southeast Indian littoral (Senaratne & Dissanayake, 1982; Cooray, 1995; Wallace, 2016). Miocene marine deposits in south-eastern Sri Lanka, ~20 m above sea level, suggest the subsequent uplift (*e.g.*, at Minihagalkanda in Yala).

In an elegant study, Reuter *et al.* (2021) deduced the major marine incursions in the Palk Bay region since the Oligocene, showing that the Palk Isthmus was inundated, except perhaps for brief intervals, during the period 18–14 Mya, and also in shorter episodes in the earlier and later Miocene. The isthmus has been mostly subaerial, however, for the past 10 My.

The increase in eustatic sea level by almost 50 m[†] at the Miocene-Pliocene boundary 5.3 Mya (Figure 3.63; Cooray, 1984:193; Miller *et al.*, 2005) in any event led to a prolonged biotic disconnection of Sri Lanka from the mainland. There appears to be no geological evidence in Sri Lanka, however, to support the sea level rise of more than 100 m inferred by Bohlen *et al.* (2020) for the Malay Peninsula, or the very high sea levels they propose for almost all of the Miocene-Pliocene (based evidently on Haq *et al.*, 1987). Li & Li (2018), for example, whom too Bohlen *et al.* (2020) cite, show much lower sea levels for this period.

The last interglacial (~120 kya), again saw sea levels rise as much as 24 m above their present level (Figure 3.63a; Miller *et al.*, 2005). Northwest

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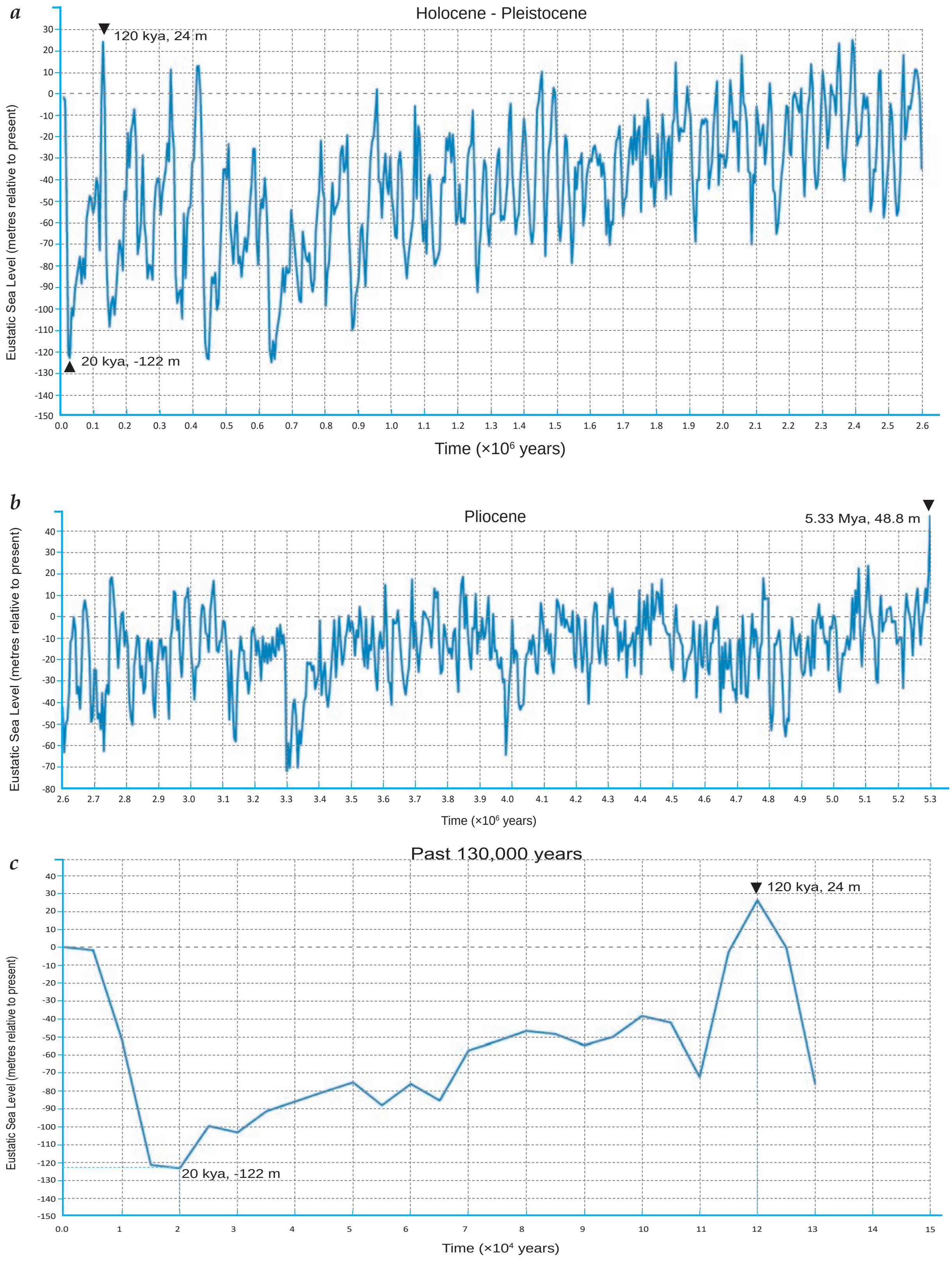
[*] Miocene limestone occupies an area of some 2100 km^2 in north and northeast Sri Lanka, in addition to a smaller deposit at Minihagalkanda in the southeast (Abeysinghe, 2010).

[†] The Pliocene sea-level rise might in fact have been much less: ~10 m, *fide* Bertram *et al.* (2018).


a
Holocene - Pleistocene
120 kya, 24 m
20 kya, -122 m
Eustatic Sea Level (metres relative to present)
30
20
10
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
-100
-110
-120
-130
-140
-150
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
2.4
2.5
2.6
Time (×10⁶ years)
b
Pliocene
5.33 Mya, 48.8 m
Eustatic Sea Level (metres relative to present)
40
30
20
10
0
-10
-20
-30
-40
-50
-60
-70
-80
2.6
2.7
2.8
2.9
3.0
3.1
3.2
3.3
3.4
3.5
3.6
3.7
3.8
3.9
4.0
4.1
4.2
4.3
4.4
4.5
4.6
4.7
4.8
4.9
5.0
5.1
5.2
5.3
Time (×10⁶ years)
c
Past 130,000 years
120 kya, 24 m
20 kya, -122 m
Eustatic Sea Level (metres relative to present)
40
30
20
10
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
-100
-110
-120
-130
-140
-150
0.0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Time (×10⁴ years)

Sri Lanka was thereafter re-submerged during an early Quaternary marine transgression (Wallace, 2016), though coastal areas were inundated also more recently, during the Holocene sea-level high stands of 1.5–5 m above present sea level, 6–5 kya (Sathiamurthy & Voris, 2006; Ranasinghe *et al.*, 2013; Yokoyama *et al.*, 2019)[*]. Adikaram *et al.* (2017) reported trace fossils from the eastern littoral of Sri Lanka formed by (marine or estuarine) polychaetes and *Callianassa* mud-shrimps, suggestive of a Quaternary sea level ~5 m above present mean sea level.

Katupotha (1988) radiocarbon-dated the extensive (now subterranean) reef at Akurala, an inland site north of Hikkaduwa, from where coral skeletons were until recently mined and baked to make lime (calcium carbonate, $CaCO_3$) for the construction industry. Their analysis showed the corals to have been deposited between 6110±80 ya and 5580±80 ya, during which time sea level was ~1 m above present mean sea level (see also Yokoyama *et al.*, 2016, 2019; Ratnayake *et al.*, 2017). Such a Holocene marine transgression is supported also by Brückner (2001) from South India and is consistent with the results of Ranasinghe *et al.* (2013), who found that the mid-Holocene transgression began around 7.3 kya and lasted until ~3 kya[†]. This was much smaller than the transgression 120 kya, of ~ 24 m (Figures 3.63c, 3.65c).

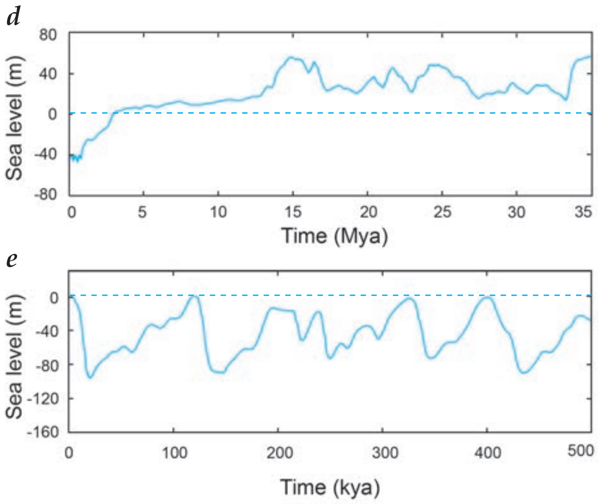


Figure 3.63. ◀ ***a–c,*** Eustatic sea-level curves ***a,*** Holocene-Pleistocene; ***b,*** Pliocene; and ***c,*** past 120,000 years, plotted from the 'backstripped' $\delta^{18}O$ dataset of Miller *et al.* (2005). ▲ ***d,e,*** Broad-scale reconstruction of sea level redrawn from De Boer *et al.* (2010). Based on contemporary bathymetry, a terrestrial connection with India via the Palk Isthmus would have existed whenever sea levels were ~10 m or more below present.

3.9.3 The Palk Isthmus. Sri Lanka is separated from southern India by the ~10 m deep, ~30-km wide Palk Strait (Anonymous, 1977; Rao *et al.*, 2011). The vestiges of the now submerged Palk Isthmus[‡]—'Adam's Bridge'—are visible only as an arc of shoals, sandbanks and reefs that connect Talaimannar, at the end of the Mannar Peninsula, to Dhanushkodi on the south-eastern tip of the Rameshwaram Peninsula of India (Anonymous, 1977; Figure 3.64). The intervening sea is so shallow, often less than a metre in depth, as to be barely navigable even by small craft[§].

Even slightly depressed sea levels were sufficient, however, for a wide terrestrial corridor (the Palk Isthmus) to open up, connecting the island with India, most recently until ~7 kya (Ramasamy & Saravanavel, 2019; inferred also from Rao *et al.*, 2011, and Loveson & Nigam, 2019); Figure 3.65a,c. The Last Glacial Maximum ~22 kya saw sea level fall by 120–134 m (Rohling *et al.*, 1998; Siddall *et al.*, 2003; Lambeck *et al.*, 2014: Figure 3.63), potentially widening the isthmus to almost 200 km

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[*] Three high-stands 1–2.5 m above present sea level have been identified variously at 6240–5130 ya, 5000-4200 ya, 4390–3930 ya and 3280–2270 ya by Katupotha, 2015; Harmsen, 2017; and Reuter *et al.*, 2020.

[†] A shell bed extends some 40 km, from Hungama to Bundala, along the island's southern littoral. This contains mainly bivalves and gastropods associated with estuaries and lagoons. There are also extensive coral limestones (deriving largely from *Acropora*) across the coastal region between Ambalangoda and Matara, most notably around Hikkaduwa (Abeysinghe, 2010).

[‡] The Palk Isthmus appears not to have been referenced in the literature until Sudasinghe *et al.* (2018b) coined the name for it, an allusion to the Palk Strait that now inundates it. This usage was followed also by Reuter *et al.* (2021).

[§] Because it connects the Bay of Bengal to the Arabian Sea (effectively linking India's east and west coasts), the Palk Strait was until the 19th century an important maritime route. Conveniently for the historical Anuradhapura kingdom of Sri Lanka, the principal navigable channel in the strait ran between the mainland and Talaimannar Island, forcing maritime traffic to use it and making the Mantai port there one of the most prosperous in Asia (Carswell *et al.*, 2013).

Figure 3.64. An aerial view of Adam's Bridge, the chain of sandbanks and shoals that are the last vestige of the erstwhile Palk Isthmus that connected Sri Lanka and India during sea-level low-stands, seen from the Sri Lanka side.

(Figure 3.65c) and, subject to climate, facilitating biotic exchange with India via shared drainages and floodplains (Ramasamy & Saravanavel, 2019).

Similar low-stands of up to 145±5 m below present sea level occurred at least six times in the course of the past 500 ky, with each episode lasting up to 50 ky (Warren *et al.*, 2010). Further low-stands of more than 50 m occurred during the Pleistocene (Figure 3.63; Miller *et al.*, 2005, 2020; Warren *et al.*, 2010).

3.9.4 Palk Isthmus ecology. The end of the Miocene witnessed the strengthening of the Asian monsoon system, accompanied by a forest-to-grassland transition on floodplains (Quade *et al.*, 1989)*. The vegetation models of Roberts *et al.* (2018) suggest that during the arid period 71–56 kya the island's tropical wet-zone forests shrank substantially, with the extent of tropical grassland peaking around the glacial maximum 22 kya (Ray & Adams, 2001).

Except perhaps for brief pluvial phases since the Miocene, the region of the Palk Isthmus appears to have experienced a dry season that lasted from four to six months or more, supporting only thorn-forest or savannah vegetation. Pollen cores from the Cauvery Delta reflect an arid climate that was drier than present from 17.8–8.5 kya, as the Palk Isthmus was shrinking owing to sea-level rise (Mohapatra *et al.*, 2019; Figure 3.65c). This was followed by a pluvial phase that lasted about 1.5 ky, with the present climate being established around 3.5 kya.

The repeated inundation of the Palk Isthmus during episodes of elevated sea level too, would have depleted its soils. Thus, if the climate was as arid as it is now, it may have supported only dry savannah; and if less arid, perhaps only herbaceous swamps, as Bird *et al.* (2005) infer for the Sunda shelf.

The situation on the Sunda shelf appears to have been little different, at least during the Pleistocene. As Gorog *et al.* (2004) note, the Pleistocene Sunda shelf was cool, arid and covered mostly by savannah-like vegetation. There too, the Pliocene saw the last of the stable perhumid climate that had characterized that region for millions of years past. "When falling sea levels in the Pleistocene againexposed land bridges among the Sun-

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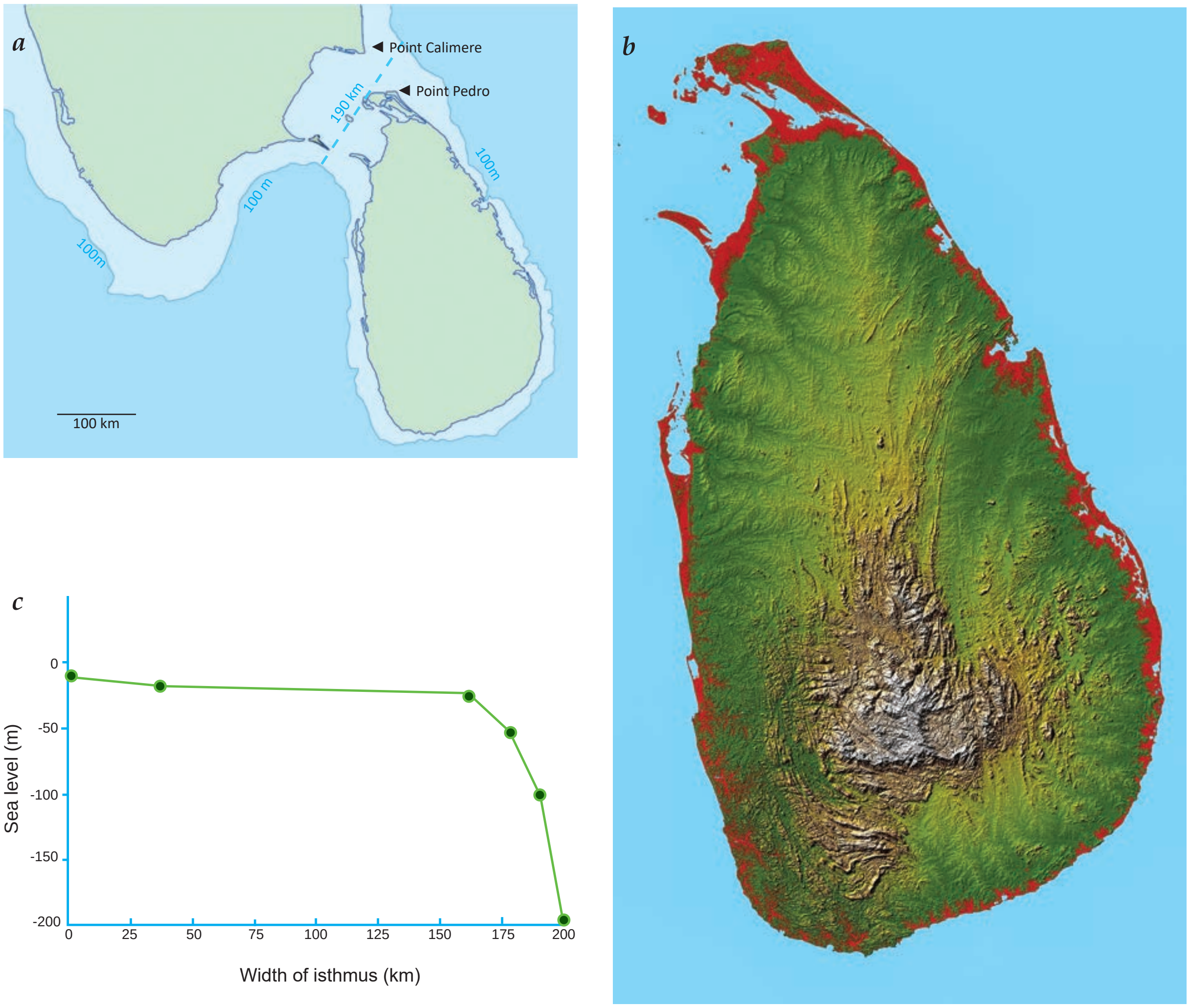
* Hirota *et al.* (2011) showed that when annual precipitation declines to around 2000 mm, tropical forest, rather than changing gradually to a mix of species better adapted to a drier climate, may tip suddenly from forest to savannah. In any event, as Lohman *et al.* (2011) argue in the case of the Sunda Shelf, even islands that now harbour rain forest may have been connected by savannah-like vegetation rather than forest during Pleistocene sea-level low-stands.

da islands and peninsula", they observed, "these changes were accompanied by a cool and arid climate, drastically different from the perhumid and relatively stable climate of the Miocene and early Pliocene. Isolation". The situation on the Palk Isthmus seems consistent with such a scenario.

Bose *et al.* (2016) speculated that the close phylogenetic relatedness of rainforest endemics between the southern Western Ghats and Sri Lanka was perhaps a result of these taxa, having persisted in Pleistocene refugia in the island, dispersing to the Western Ghats [implicitly via the Palk Isthmus] between the last interglacial and the Last Glacial Maximum, and undergoing parapatric speciation. Such an ecological model, however, is not consonant with the evidence of dispersal presented by the fauna (see 3.9.5, below) and exchange of evergreen flora between Sri Lanka and the Western Ghats by terrestrial dispersal probably pre-dates the Pleistocene and perhaps the Pliocene, too.



NASA/JPL/NGA

Figure 3.65. ***a,*** Bathymetry of the India–Sri Lanka region, based on UK Hydrographic Nautical Chart No. 828 *Cochin to Vishakhapatnam*. The 100 m isobath marks the approximate edge of the continental shelf. Sea levels fell more than 100 m on at least six occasions in the past 1 My (Figure 3.63a), during which times the Palk Isthmus was ~190 km wide at its narrowest point (dashed line). ***b,*** the low-lying coastal region of Sri Lanka < 10 m elevation (coloured red) extends more than 10 km inland at many places, including in the south-western wet zone 'floodplain'. This also highlights the areas of greatest risk of inundation with sea-level rise associated with climate change (Gopalakrishnan & Kumar, 2020). The extent of inundation that resulted from the 24-m sea-level high-stand 120 kya (see Figure 3.63c) was substantially greater. ***c,*** Approximate width of Palk Isthmus *vs* sea level based on present-day bathymetry, based on UK Hydrographic Nautical Chart No. 828 *Cochin to Vishakhapatnam*.

3.9.5 The Isthmus as a biodiversity corridor

Bossuyt *et al.* (2004) investigated the relationship between the mainland and insular representatives of an assortment of Sri Lankan and south Indian taxa: freshwater crabs, freshwater shrimps, cyprinid fishes, rhacophorid shrub frogs, caecilian amphibians and shield-tail snakes. Given that Sri Lanka and southern India had been repeatedly connected during prolonged and frequent sea-level low-stands throughout the Pleistocene, including one from ~40–7 kya, considerable faunal exchange was expected across the isthmus that would have spanned the now 25 km wide Palk Strait, especially among more vagile taxa (Kodandaramaiah, 2009). Such intermittent connectivity might have been expected to result in a complex pattern of repeated vicariance and dispersal events*, producing a species pump, as has been the case, for example, with the rhacophorid frogs on Borneo (Hertwig *et al.*, 2013), although for *Rhacophorus* in the Sunda region as a whole, it is *in situ* diversification, rather than dispersal, that has contributed most significantly to species richness and endemism (O'Connell *et al.*, 2018).

In the case of several freshwater-fish groups in the Sunda region, Sholihah *et al.* (2021a) showed that Pleistocene speciation events were associated more frequently with boundaries of paleoriver watersheds than island boundaries. Speciation through allopatry between islands connected and disconnected by sea-level fluctuations played a relatively minor role.

Nevertheless, falling sea levels during glacial maxima reduced the geographic separation between watersheds, possibly leading to the rivers draining into the Gulf of Mannar from opposite sides of the Palk Strait to coalesce, facilitating the exchange of freshwater organisms between India and Sri Lanka. The climate, and the vegetation of these watersheds of the Palk Isthmus, however, filtered the fish species that passed through them, explaining why so few rainforest-associated species—and vicariance-driven species-pairs—are shared between Sri Lanka and the mainland.

Bossuyt *et al.* (2004) discovered that while a few lineages showed evidence of migration between the mainland and Sri Lanka, most clades, even among the arguably more putatively vagile groups such as freshwater crabs and shield-tail snakes, exhibited remarkable philopatry. They showed that India-Sri Lanka sister-group relationships predated the Pleistocene, showing that Pleistocene sea level fluctuations did not play an important role in defining Sri Lanka's biodiversity. They concluded that:

> 'The inferred phylogenetic trees demonstrate that the overall limited biotic interchange has left both areas with an unexpectedly large number of endemics… The uniqueness of both sides of the Palk Strait is most noticeably illustrated by caecilians and shieldtail snakes: in both cases, all sampled island species represent endemic monophyletic groups. Finally, although the pattern of limited biotic exchange is less apparent in strictly aquatic groups, part of Sri Lanka's fish and shrimp species nevertheless form distinct clades. These observations jointly indicate that exchange between the mainland southern Indian and insular Sri Lankan faunas has been severely restricted, despite the recurrent existence of a broad (>100-km wide) land bridge during several episodes of sea level low stands.'

Bossuyt *et al.* (2004) found also that uropeltid

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* It has long been maintained that the distribution of species across Sundaland has been shaped by the alternation of dispersal opportunities when its shallow shelf emerged during periods of lowered sea level, followed by vicariance when sea level rose during interglacials (Lohman *et al.,* 2011*).* Recent findings on the geomorphology of the shelf suggest, however, that it subsided during the Pleistocene: it was never submerged between the Late Pliocene and *ca* 400 kya (Husson *et al.*, 2019). There was thus, until recently, no barrier to terrestrial dispersal between the major islands except perhaps the climate and vegetation of the intervening lowlands. The results of Sholihah *et al.* (2021a) for freshwater fishes is broadly consistent with this scenario. Cros *et al.* (2020) show that even in the case of songbirds (five species in Timaliidae, Pellorneidae and Pycnonotidae), gene flow between western Sundaland and Borneo generally ceased some time after 400 kya. One of the sampled species, *Pycnonotus plumosus*, however, showed a strong signature of continued gene flow between Borneo and western Sundaland through the Last Glacial Maximum. This was "the most dispersive species" among the birds included in the study. The Sri Lankan situation, however, appears to have been fundamentally different, mediated more by climate than by sea level during the Plio-Pleistocene.

snakes, freshwater crabs, caecilians and *Pseudophilautus* shrub-frogs each colonized Sri Lanka only once from the Indian mainland, going on subsequently to diversify on the island and, in the case of the crabs and shrub frogs, occasionally back-migrate to India (Beenaerts *et al.*, 2010, Meegaskumbura *et al.*, 2019).

While the exact causes of the limited dispersal of aquatic and other organisms between the rain forests of the southern Western Ghats and south-western Sri Lanka remain to be fully explored, they almost certainly relate to the inability of organisms that were adapted to a perhumid climate to disperse across the strongly seasonal savannah and thorn-forest environment of the Palk Isthmus (Ashton, 2014; Ali, 2018; Morley, 2018). Thus, the endemic diversifications on Sri Lanka resulted not from Pleistocene species-pumping, as in the case in the Sunda Islands (Hertwig *et al.*, 2013), but isolation caused by the vicariance barrier formed by an arid Palk Isthmus, which was subaerial for much of the past ~5 My.

Even today, the climate of Mannar is not only strongly seasonal but also more arid than almost anywhere else on the island. The Mannar Peninsula records barely 1200 mm of rainfall annually and has a dry period that lasts half the year, from April to September (Figure 2.6). Conditions on the Indian mainland, across the Palk Strait, are little different. For the Kala basin, Iresh (2020; pers. comm.) reported from meteorological time-series data acquired over the 1985–2019 period, minimum annual rainfall less than 700 mm at seven of 17 monitoring stations in some years. This suggests that episodes of extreme aridity occur in the region even now.

The ecological barrier posed by the isthmus is perhaps nowhere better illustrated than in the case of the Asian forest-scorpion genus *Srilankametrus* (Figure 3.66). The genus is known from five species endemic to Sri Lanka and two confined to Tamil Nadu (Southeast India) (Prendini & Loria, 2020: see Figure 3.8). The molecular phylogeny of Loria & Prendini (2020) included the four extant members of the Sri Lankan diversification, for which they estimated an early Miocene crown age (no Indian species were included in the analysis). Despite these species occurring in all Sri Lanka's climatic zones, including the more arid parts of the dry zone, none of them appears to have dispersed across the Palk Isthmus.


Tharindu Ranasinghe

Figure 3.66. *Srilankametrus indus*, one of the five species of this genus that are endemic to Sri Lanka.

The Palk Isthmus thus appears to have been, at least since the late Miocene, more an ecological bottleneck than a biodiversity corridor between India and Sri Lanka. The most recent evidence of humid forests in Southeast India, from the lignite deposits of Neyveli and Tiruvakkarai in Tamil Nadu, date to the Miocene or at latest, the early Pliocene (Mehrotra *et al.*, 2014). These are pre-dated by extensive Early Cretaceous shale deposits accumulated in depressions under anoxic conditions around Rameshwaram and Ramanathapuram in Tamil Nadu, resulting in the oil and gas fields immediately across the Palk Strait from Sri Lanka (Valdia, 2016: 490), but lacking on the island itself. Like north-western Sri Lanka, south-eastern India appears since then to have experienced so consistently an arid and strongly seasonal climate that even apparently vagile species occurring in the tropical dry broadleaf forests of southern India, such as the leopard cat (*Prionailurus bengalensis*), failed to make it across the isthmus and into Sri Lanka. Indeed, Mukherjee *et al.* (2010) show, from climate models, that Sri Lanka presents a habitat little different from the species' present environment in the southern Western Ghats.

The Palk Isthmus seems to have been too inhospitable—too arid?—to allow, among large birds, even the Great Indian Bustard (*Ardeotis nigriceps*), and among mammals the blackbuck (*Antilope cervicapra*), Nilgiri tahr (*Nilgiritragus hylocrius*), four-horned antelope (*Tetracerus quadricornis*), Nilgiri marten (*Martes gwatkinsii*) and the Nilgiri langur

(*Semnopithecus johnii*) to make the crossing to Sri Lanka. The ranges of all these species, according to Mukherjee (1974), formerly extended to the south-eastern extremity of the peninsula—the region adjacent to the present Palk Strait. While some of these are cold-adapted species, the isthmus itself was exposed primarily during glacial maxima and their associated climatic cooling (Flenley, 1998). In any event, cold-adapted plant species were able to make the crossing to populate the island's hills, the flora of which bears a striking similarity to that of the South Indian mountains.

Perhaps more remarkable is that several reptile genera occurring in the forests of the southern Indian Peninsula failed to cross into Sri Lanka, such as *Agasthyagama*, *Chalcides, Draco, Eublepharis, Ophiophagus, Rhabdops, Salea, Indotestudo, Scincella* and *Psammophis* (Figures 3.67, 3.68; Das, 1996; Srikanthan *et al.,* 2021). Correspondingly, Sri Lankan endemics such as *Ceratophora, Cophotis, Lyriocephalus* and *Otocryptis* failed to disperse to India.

While the Palk Isthmus during the Plio-Pleistocene did not—unless exceptionally—serve as a biotic corridor for rainforest species, it appears not to have done so even for many dry-adapted ones: as a result, Sri Lanka shows scant evidence of a fauna adapted to xeric conditions.

Bauer *et al.* (2010) and Lajmi & Karanth (2020) show the divergence between sister-species pairs of *Hemidactylus* geckoes between South India and Sri Lanka to date to the early Miocene. The former authors, however, doubted whether the aridification of the Palk Isthmus explains the apparent inability of these lizards to cross between Sri Lanka and the mainland: 'Although this may be true for frogs and other mesic adapted groups,' they observed, 'it does not apply to Sri Lankan *Hemidactylus* species, none of which are forest-restricted. Indeed, the endemic species *H. hunae* and *H. lankae* (Figure 3.69) are chiefly restricted to the dry zone and *H. depressus* and *H. parvimaculatus* are broadly distributed across the island, including the dry zone… the cladogenic patterns of the endemic Sri Lankan *Hemidactylus* reflect far older events in the history of South Asia.'

Lajmi *et al.* (2019) showed, for these geckos, that while the ancestors of *H. depressus* and *H. hunae* immigrated from India in the Early and Middle Miocene, respectively (their phylogeny recovered seven India–Sri Lanka dispersal events), only two dry-adapted species made non-human mediated crossings from India to Sri Lanka since the Miocene: *H. lankae* and *H. scabriceps*. Such dispersal events, however, were not necessarily dependent on a land bridge between India and Sri Lanka: they may have occurred also by rafting (see, for example, Siler *et al.*, 2012). This is especially the case given that the Palk Isthmus was inundated during much of the early Miocene (Epa *et al.*, 2012; Reuter *et al.,* 2021). Indeed, Lajmi *et al.* (2019) grant that the vicariant separation of the Sri Lankan and Indian lineages owing to Miocene marine transgressions could explain their evolution. In any event, as shown above, even some species adapted to a xeric environment were unable to disperse across the Isthmus during the Plio-Pleistocene.

The diversification of some 38 (nominal) species of *Cnemaspis* day-geckoes in Sri Lanka, although represented also in the dry zone, is concentrated in the wet zone (Manamendra-Arachchi *et al.*, 2007; Karunarathna *et al.*, 2019; Uetz *et al.,* 2021). The regional distribution of the genus is typical of wet-adapted taxa: Sri Lanka-South India, with a disjunction across central India, then reappearing in western Malesia. Agarwal *et al.* (2017) inferred from a molecular analysis that the Sri Lankan *Cnemaspis* diversification stemmed from at least two dispersal events from the mainland 28 (34–23) Mya and 17 (22–13) Mya, which results were replicated by Agarwal *et al.* (2020). These authors also estimated a divergence time of 7 (8–5) My between the diverse Sri Lankan clade and its sister group in Sumatra. Their limited sampling from Myanmar and Thailand, unfortunately, precludes a conclusion as to whether the Sumatran population derives from a long-distance oversea dispersal event or vicariance stemming from extinction in the intervening (terrestrial) stretch of India-Myanmar-Thailand. The close relationship between the Myanmarese, Sunda and Sri Lankan members of the *Cnemaspis kandiana* group recovered by Lee *et al.* (2019), however, hints at a long-distance overseas dispersal scenario*. Never-

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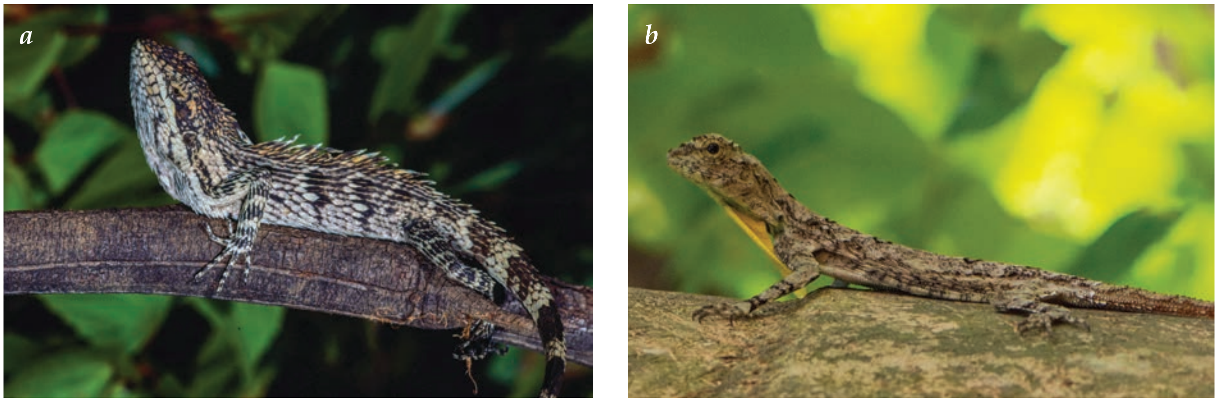
* Mudannayake *et al.* (2019) show that oceanic dispersal best explains also the distribution of *Cycas zeylanica* (Cycadaceae), a species restricted to the wet zone of Sri Lanka and the Andaman-Nicobar island group. The genus *Cyathea* too, exhibits a trans-oceanic disjunction between Asia and Madagascar (Nagalingum



Indraneil Das

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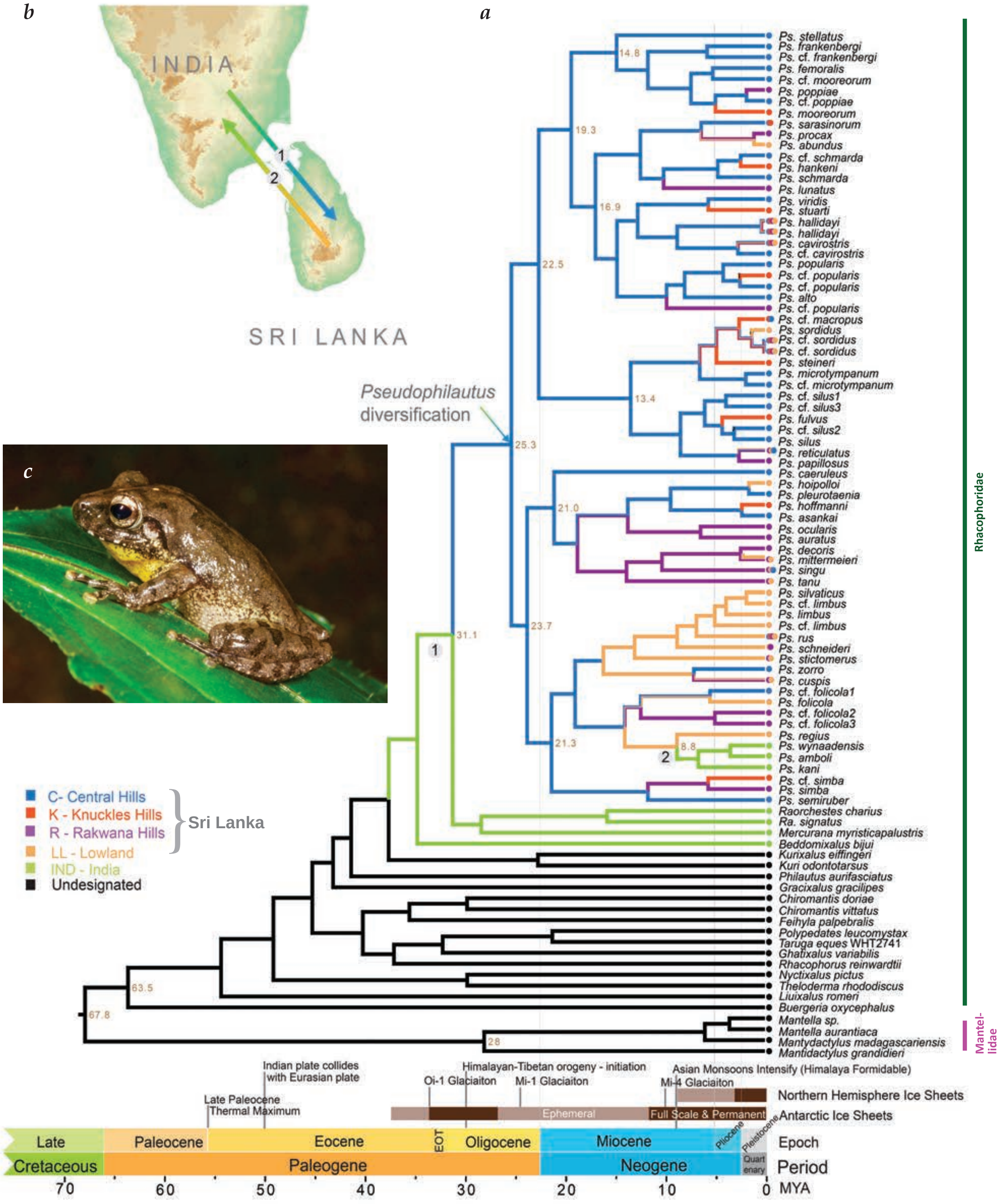
Figure 3.67. ***a,*** *Salea horsfieldii* (Agamidae): the genus occurs in the Western Ghats but is absent from Sri Lanka. ***b,*** The gliding lizard *Draco dussumieri*, which is restricted to the Western Ghats south of Goa and the Eastern Ghats of Andhra Pradesh. The genus is absent from Sri Lanka and the rest of Peninsular India, though recurring from Northeast India to the Sunda Islands and the Philippines.

Indraneil Das

Figure 3.68. *Indotestudo travancorica*, a Western Ghats testudine genus that is absent from Sri Lanka.

Ruchira Somaweera

Figure 3.69. *Hemidactylus hunae,* an endemic gecko restricted to Sri Lanka's dry zone. As observed by Bauer *et al.* (2010), even such arid-adapted geckos appear to have been unable to cross between Sri Lanka and India when the Palk Isthmus was subaerial during glacial maxima, a restriction reflected also in the *Cnemaspis* day-geckos (Agarwal *et al.*, 2017).



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theless, the substantial divergence times between the Sri Lankan and Indian clades suggests that even these diurnally active geckoes, some species of which are widely distributed in the dry zones of Sri Lanka and southern India, have been inhibited from utilizing the Palk Isthmus as a dispersal corridor during the Plio-Pleistocene.

The remarkable diversification on Sri Lanka of rhacophorid shrub frogs of the genus *Pseudophilautus* too, illuminates the limited utility of the Palk Isthmus as a biodiversity corridor. Seventy-six extant species of *Pseudophilautus* are recognized, with several more as yet undescribed and yet others suspected to have succumbed to extinction in the past century (Manamendra-Arachchi & Pethiyagoda, 2005; Meegaskumbura & Manamendra-Arachchi, 2005; Meegaskumbura *et al.*, 2019; Ellepola *et al.*, 2021). The diversification is monophyletic, stemming from a common ancestor that migrated from India in the Oligocene, ~31 Mya (Meegaskumbura *et al.*, 2019), and restricted to the island's wet zone except for a single species, *P. regius*, which occurs also in the dry zone. These authors showed that in the ~31 My since then, only a single back-migration to India has taken place, in the late Miocene, ~9 Mya*. Unsurprisingly, the resulting Indian diversification of *Pseudophilautus* is recovered as the sister-group of *P. regius* (Figure 3.70). Yet, although *P. regius* presently occurs in the Mannar Peninsula, which is among the most arid regions of contemporary Sri Lanka, it evidently failed to disperse across the isthmus for the entirety of the Plio-Pleistocene, presumably because this landscape was too arid. The timings of these India–Sri Lanka amphibian dispersals are consistent with those recovered for the Sunda Archipelago (O'Connell *et al.*, 2018) and the Philippines (Brown *et al.*, 2013), which too, involve connectivity between islands in shallow-shelf seas during sea-level regressions.

Figure 3.71. The endemic Sri Lankan green pit-viper *Craspedocephalus trigonocephalus*. The common ancestor of this species and the South Indian *C gramineus*, to which it has a sister-group relationship, crossed the Palk Isthmus ~9 Mya (Alencar *et al.*, 2016). Despite occurring also in Sri Lanka's dry zone, *C. trigonocephalus* has remained confined to Sri Lanka (see also Mallik *et al.*, 2021).

◀ **Figure 3.70.** Timing of diversification and dispersal of *Pseudophilautus*. ***a,*** Time-calibrated tree of Sri Lankan and Indian *Pseudophilautus* (numbers in brown are dating estimates in My); key events include (1) the common ancestor of *Pseudophilautus* migrating to Sri Lanka during the late Oligocene, a late-Oligocene-to-Pleistocene diversification on the island, and (2) the late Miocene back-migration to the mainland. ***b,*** Depiction of *Pseudophilautus* dispersal events between India and Sri Lanka. ***c,*** *Pseudophilautus regius*, the only member of this extensive endemic diversification that is wholly restricted to Sri Lanka's dry zone. Note the 67.8 Mya split between the Asian Rhacophoridae and the Madagascan Mantellidae. Adapted from Meegaskumbura *et al.* (2019), which contains the confidence intervals associated with timing events and an explanation of the geoclimatic context.

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et al., 2011), though whether this is a result of vicariance or dispersal remains to be determined.

* This date coincides with the dispersal to Sri Lanka of the common ancestor of the endemic Sri Lankan pit-viper *Craspedocephalus trigonocephalus* (Figure 3.71) and its South Indian sister group, *C. gramineus* (Alencar *et al.*, 2016). Although *C. trigonocephalus* occurs in both the wet zone and the dry zone, it is absent from the arid zone adjacent to the Palk Isthmus, which suggests that the isthmus served as a vicariance barrier over the past ~9 My. Given that *C. trigonocephalus* is the only member of the genus on the island, Ali & Vences (2019) cited this as an example of anagenesis or anacladogenesis *sensu* Stuessy *et al.* (1990), though not ruling out the former existence of a sister species that has since been extirpated.

Van Bocxlaer *et al.* (2009) estimated the origin of *Adenomus,* a genus of torrent toads endemic to Sri Lanka's wet zone, to have occurred between 22.4 ± 3.6 and 17.0 ± 2.9 Mya. Given that the Palk Isthmus was submerged for much of the time 17–13 Mya (Reuter *et al.*, 2021), this group must have dispersed to Sri Lanka in the mid-Miocene, while a rainforest corridor still persisted on the isthmus.

In the case of the microhylid frogs, which depend on small water bodies such as forest pools and phytotelmata for reproduction, Gorin *et al.* (2020) showed there to have been three immigration events across the Palk Isthmus in the late Miocene or early Pliocene, at 5.5 (95 % CI range 7.7–3.5), 6.6 (9.3– 3.7) and 6.9 (9.6–4.6) Mya. These mean ages occur at the last stage during which a late-Miocene humid corridor could have existed on the Isthmus. These authors also recovered a further vicariance event, between Indian and Sri Lankan populations of *Microhyla ornata,* 1.4 (2.4–0.7) Mya. This species, however, occurs in a variety of habitats that includes savannah, scrub and dry deciduous forest throughout South Asia.

Another group of interest in this respect is the diversification of the fan-throated agamid lizards of the genus *Sitana*, commonly associated with arid habitats in both India and Sri Lanka. The diversification of *Sitana* in the Indian Peninsula—some 15 species—took place in the mid-Miocene to Pliocene, presumably as the climate aridified. One of these species went on to colonize arid coastal areas in Sri Lanka, within which population Amarasinghe *et al.* (2015) recognized an incipient morphological diversification into two endemic species. Notwithstanding Amarasinghe *et al.* (2015) and Deepak *et al.* (2016), who had shown the Sri Lankan populations to be morphologically distinct from the Indian *S. ponticeriana*, the molecular analysis of Deepak & Karanth (2018) shows the Sri Lankan taxa to be genetically indistinguishable from *S. ponticeriana* (Figure 3.72), which occurs in south-eastern India including the western (Rameshwaram) end of the Palk Isthmus.

If indeed it exists, the Sri Lankan 'diversification' of *Sitana* could be the result of polymorphism or changes in plastic characters resulting from the adaptation of the founder population to the Sri Lankan environment (populations exposed to novel environments diverge rapidly because of the genetic assimilation of adaptive characters: Parsons & Robinson, 2006).

Nevertheless, what is perhaps most striking about the exchange of *Sitana* between India and Sri Lanka is the case of a species that failed to make the crossing. *Sitana visiri* occurs in sympatry (or at least parapatry) with *S. ponticeriana* in coastal sand dunes and grassland habitats in south-eastern India (Deepak *et al.*, 2016), proximal to the Palk Isthmus. The two species, adapted to the xeric conditions of the region, diverged in the Pliocene (Deepak & Karanth, 2018). Yet, only one of them (the common ancestor of *S. ponticeriana* and the Sri Lankan species) successfully dispersed to Sri Lanka despite repeated and prolonged terrestrial connections through the Pleistocene.

Pearson & Ghorpade (1989) observed a similar limitation also among tiger beetles (Cicindelidae), whose members shared between Sri Lanka and south India 'are grassland, scrub forest and riverine species. The frequent connections between the island and the mainland have apparently facilitated the dispersal of species in these habitats more than in moist forests'.

Few species illustrate the arid environment of the (now submerged) Palk Isthmus better than the tarantula *Poecilotheria hanumavilasumica* (Theraphosidae). Discovered only recently (Smith, 2004), the species was reported from a narrow range at the Indian end of the isthmus: the Island of Rameshwaram and the proximal mainland region around Mandapam (Siliwal *et al.,* 2008). The 'xeric isthmus' hypothesis that suggests itself from the examples we mention in this section would posit that the species would occur also on the Sri Lankan side of the isthmus. Through a survey of the Mannar region, Nanayakkara *et al.* (2015) demonstrated exactly that. They reported *P. hanumavilasumica,* an arboreal species, in hollows in the thorny shrub *Dichrostachys cinerea* in Mannar (Figure 3.73). Meanwhile, *P. hanumavilasumica* has not been reported from anywhere else in India or Sri Lanka: it appears to be adapted to the particularly arid conditions of the region of the Isthmus.

Even mammals that are adapted to life in dry forests, such as the now ubiquitous red muntjak (*Muntiacus muntjak*), appear to have crossed the Palk Isthmus to reach Sri Lanka not only just once, but as Martins *et al.* (2017) show, as long as 1.5

million years ago*. Chakraborty *et al.* (2007) show the divergence between the South Indian nonnet macaque, *Macaca radiata,* and the Sri Lankan toque macaque, *M. sinica*, both of which occur in also arid environments and which have a sister-group relationship, occurred as long as 1 Mya. This suggests there was little or no gene flow across the Palk Isthmus during that time.

A handful of taxa, however, appear to have made the crossing to Sri Lanka very recently. In a molecular analysis of the Sri Lankan and South Indian palm civets (*Paradoxurus hermaphroditus*), for example, Veron *et al.* (2015) found the mainland and insular populations to belong to the same haplogroup, leading them to suspect recent anthropogenic introduction. The same may be the case also with the hog deer (*Hyelaphus porcinus*), which occurs in the sub-Himalayan belt and again in southwest Sri Lanka, while absent from the peninsula of India: it does not appear in Pleistocene archaeological contexts in southern India (Chauhan, 2008; McCarthy & Dissanayake, 1994). Manamendra-Arachchi (2012) argued, however, that it may be represented in archaeological contexts in Sri Lanka.

In a study of bird distributions within India, and between India and Sri Lanka, Ramachandran *et al.* (2017) found the Sri Lankan bird community to be the most distinct from others in the mainland, including that of the southern Western Ghats. The avifauna of the southern western Ghats turned out to be more similar to those of distant regions within the Indian peninsula than to that of Sri Lanka. They attributed this to the marine barrier posed by the Palk Strait, though acknowledging that barriers such as the 'dry regions of south-eastern peninsular India and northern Sri Lanka add to the complexity of this biogeographic divide.'

This idea was tested also by Sreekar *et al.* (2020). Noting that Bossuyt *et al*. (2004) had suggested


Ruchira Somaweera

V. Deepak

Figure 3.72. ***a,*** *Sitana devakai* an agamid lizard occurring in Sri Lanka's north-western dry zone, which appears to be the insular vicar of the South Indian *S. poticeriana*; ***b,*** although present in arid habitats on the Indian side of the Palk Isthmus, *Sitana visiri* (Deepak *et al.*, 2016; Deepak & Karanth, 2018) appears never to have crossed the Palk Isthmus to Sri Lanka.


Ranil Nanayakkara

Figure 3.73. *Poecilotheria hanumavilasumica,* a tarantula known only from the extremities of the erstwhile Palk Isthmus, from around Rameshwaran Island in India, and Mannar Island in Sri Lanka. It appears to be specialized to the region's markedly xeric environment.

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* It is possible that the island's population of *M. muntjak* stems from multiple independent dispersals. The limited samples available to these authors may not have fully reflected the structure of the population.

that the Western Ghats and Sri Lanka should be treated as two distinct biogeographic units owing to the high degree of endemicity of the freshwater and reptile faunas on either side of the Palk Strait, they assessed how land use, climate and geographical barriers independently affect bird distributions in the region. They concluded that 'the Palk Strait is the most important driver of local community assembly in the biodiversity hotspot, surpassing the effects of changes in land use and climate.' While this may be true, it fails to acknowledge that the Palk Isthmus has been emergent and available as a dispersal corridor for much of the past 5 My. Had the climate of the isthmus been comparable to that of the lesser barriers to bird dispersal these authors tested, such as the relatively dry Palghat and Goa gaps (Ramachandran *et al.*, 2017), a greater similarity would be expeced between the avifaunas of Sri Lankan and Western Ghats. This, however, was not the case.

The Sri Lanka Junglefowl, *Gallus lafayettii* (Figure 3.74a), for example, is one of the few endemic vertebrates to occur in all its elevational and climatic regions of the island, including Mannar. Nevertheless, it appears to have been unable to traverse the Palk Isthmus to reach India, where its putative mainland vicar, *Gallus sonneratii* occurs, albeit not in the vicinity of Rameshwaram. Lawal *et al.* (2020) show *G. lafayettii* to have diverged from *G. sonneratii* ~1.8 Mya (95 % CI: ~1.9–1.5 Mya), and there is no evidence that either species made a subsequent crossing of the Palk Isthmus.

In other cases, birds widespread in India and whose ranges extend to the very south of the peninsula—such as the Spotted Owlet (*Athene brama;* Figure 3.74b)—have failed to become established in Sri Lanka. The yellow-throated bulbul (*Pycnonotus xantholaemus*) is another such case: it has a wide distribution in the dry zone of southern India but appears never to have dispersed to Sri Lanka.

Martynov & Palatov (2020) made a parallel observation in the case of a group of winged insects of Gondwanan antiquity in Sri Lanka: the ephemopteran family Teloganodidae. 'Presently, only the narrow Palk Strait separates Sri Lanka and India', they noted. 'Although mayflies have winged stages which are capable of aerial dispersal, the teloganodid fauna of the island shares no species with India or other countries of Indian subregion, which is in contrast to the vast number of other mayfly families (Sivaramakrishnan *et al.*, 2009). All species of Teloganodidae found in Sri Lanka are island endemics.'

Ajith Ratnayaka

Charles J Sharp

Figure 3.74. ***a,*** The Sri Lankan junglefowl, *Gallus lafayettii,* one of the island's few endemic vertebrates to occur in all elevational and climatic regions, including Mannar. It appears, however, to have been unable to utilize the Palk Ismus to reach India. ***b,*** The spotted owlet (*Athene brama*), has a range extending across the whole of continental South Asia, including southernmost peninsular India, but excluding Sri Lanka. The inability of such species to disperse across the Palk Isthmus, however, was likely due more to the unavailability of ecological niches than a climate-vegetation barrier.

The failure of such putatively vagile species to disperse between India and Sri Lanka is, however, not in every case owing to the climate of the Palk Isthmus having served as a barrier. Koparde *et al.* (2019) show, for example, that the absence of the Spotted Owlet from Sri Lanka may be a consequence of Quaternary climate change. In the case of the Bay-backed Shrike (*Lanius vittatus*), which


Lalith Ekanayake

Figure 3.75. Until large-scale deforestation of the island began in the late 19th century, Asian elephants (*Elephas maximus*) occurred throughout Sri Lanka, from sea level to the highest regions, such as Horton Plains (2100 m asl; Pethiyagoda, 2012). They frequently make short marine transits and have been observed even in the open ocean, more than a kilometre offshore. Despite their ability to inhabit even the most arid parts of Sri Lanka, they are genetically distinct from the South Indian population, with which a terrestrial connection existed until ~500 generations ago. The Isthmus may therefore have served as a barrier to gene flow between the Indian and Sri Lankan populations.


Sudath Nanayakkara

Figure 3.76. *Srilankamys ohiensis*, an endemic genus and species of rodent confined to Sri Lankan rain forests. Buzan *et al.* (2011) showed that its sister group comprises of a large group of Asian and Southeast Asian genera, from which it diverged 6.7 ± 0.74 Mya, before the climate of the Palk Isthmus aridified.

occurs throughout the Indian Peninsula but is absent from Sri Lanka, the sighting of occasional vagrants on the island suggests that these birds are capable of crossing the strait but are ecologically unadapted to residence in Sri Lanka (Ripley & Beehler, 1990; Warakagoda *et al.*, 2012).

In the Sunda Archipelago too, new terrestrial connections resulting from repeated Quaternary sea-level low-stands failed to provide for the unfettered dispersal of biotas—including species considered to be vagile—isolated during interglacials, such as gibbons (Hirai *et al.*, 2005), orangutans (Steiper, 2006) and elephants (Fernando *et al.*, 2003). The inability of the last-mentioned mammals to disperse to and from Borneo is especially surprising given that Asian elephants (*Elephas maximus*) utilize habitats ranging from sea level to elevations over 2000 m asl, and from xeric thorn scrub to rain forest. What is more, they are able to travel tens of kilometres in a day and even undertake short marine crossings. In the case of Sri Lanka, despite elephants occurring also in the most arid regions of the island, they retain a genetic signature suggestive of isolation (Figure 3.75; Jayewardene, 1994: 7; Fleischer *et al.*, 2001). For example, only 7 percent of Sri Lanka's bull elephants bear tusks, while 95 percent of those in South India are tusked (Sukumar, 1995; Fernando, 2000). The reason for this disparity has variously been attributed to selective hunting in Sri Lanka (Kurt *et al.*, 1995), founder effect, a recessive allele, or the greater impact of genetic drift on a smaller, insular Sri Lankan population (Fernando, 2000).

Until now, no rainforest-associated sister groups have been found to occur in Sri Lanka and India, respectively, with a divergence time post-dating the early Pliocene, *ca* 5 Mya (Figure 3.76). This datum, by itself, perhaps illustrates best how influential the climate of the Palk Isthmus has been in modulating the island's biodiversity.

3.9.6 Evidence from India: The Palghat Gap. The Palghat Gap[*] (Figure 3.77), a transverse ~30-km-wide east-west valley bisecting the Western Ghats 10.5–10.8°N, offers opportunities to assess the ability of wet-adapted taxa to cross a relatively arid barrier of extent comparable to the Palk Isthmus. With an annual rainfall of 2.1 m at Palakkad, however, the Palghat valley is, though among the driest regions of the southern Western Ghats, considerably wetter than the region of the Palk Isthmus (Ramesh & Pascal, 1991; Kumar, 1994).

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[*] Correctly the Palakkad Gap, but we follow the more frequent international usage.

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Figure 3.77. The Western Ghats are bisected by the Palghat Gap, a lowland plain, the climate and vegetation of which are strongly reminiscent of the dry zone of Sri Lanka. The Gap is about as wide as the former Palk Isthmus, and studies across many plant and animal taxa show it to have served as a barrier to biotic dispersal over the past several tens of millions of years.

The Gap, which appears to be the result of the upthrust of the Nilgiri Hills to the north, and the Annaimalai-Elaimalai Hills to the south, together with shearing and erosion (D'Cruz *et al.*, 2000; Valdia, 2011), is of uncertain age, though Gunnell & Radhakrishna (2001) considered it to date to the Late Cretaceous.

In a study of the ~30 species of the anuran genus *Nyctibatrachus* (Nyctibatrachidae), however, Van Bocxlaer *et al.* (2012) showed that frogs north and south of the Gap belong to separate clades deriving from an Eocene common ancestor. While only a single northern ancestor dispersed southwards across the Gap (in the Miocene), no representatives of the southern clade ever succeeded in making a northward crossing of the Gap.

Among freshwater fishes, John *et al.* (2013) showed that the populations of red-lined torpedo barbs of the cyprinid genus *Sahyadria* north and south of the Palghat Gap diverged in the Paleocene, ~57 Mya[*], while for the hillstream loach genus *Mesonoemacheilus,* the time-calibrated phylogeny of Anoop *et al.* (2018) showed species north and south of the gap to have diverged in the Miocene, with no dispersals across the Gap since then. The latter timing is reflected also in the distribution of the hillstream loach genus *Bhavania*, a Western Ghats endemic. Sidharthan *et al.* (2020) found the diversification south of the Gap to be the result of a north-south dispersal 11.2 (95 % HPD 15.8–7.6) Mya, the crown age of the clade, in the Tortonian Miocene.

An analysis of 67 lineages (putative species) of rhacophorid frogs of the genera *Raorchestes* and *Pseudophilautus* on either side of the Gap, however, recovered a substantially earlier initial diversification into north-of-Palghat and south-of-Palghat clades, dating to ~30 Mya (Vijayakumar *et al.*, 2016). Only six subsequent south-to-north and four north-to-south range expansions across the valley were detected. Among the latter were the Sri Lankan *Pseudophilautus* shrub frogs that back-migrated to India via the Palk Isthmus in the late Miocene (~8.8 Mya: Meegaskumbura *et al.*, 2019), going on to make a single crossing of the Palghat Gap shortly thereafter.

The action of the Gap as a biogeographic barrier, however, depended also on the intrinsic dispersal abilities of indiviudal taxa. Sudasinghe *et al.* (2021b) showed, for example, that the Gap had little effect on the north-south dispersal of species of *Dawkinsia*; indeed, it may have facilitated east-west dispersal in some species in this genus.

The Palghat Gap has caused a trenchant disjunction also in the flora of the Western Ghats: almost 87 percent of the region's flowering-plant species occur south of the Gap, with 37 percent of those in this southern sub-region being endemic to it (Kumar *et al.*, 2011; Bhagwat *et al.*, 2014). The Gap appears to have served as a biogeographical barrier to the dispersal also of many putatively vagile groups, including elephants (Vidya *et al.*, 2005) and montane birds (Robin *et al.*, 2010, 2015[†]), with divergences across it ranging from the Miocene to the Pleistocene.

It appears therefore, that the Gap is of considerable antiquity, though not yet dated through geological analysis. Nevertheless, as Bose *et al.* (2019) show, there is in any case a northward decline in phylogenetic and niche diversity along the

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[*] Which date perhaps pre-dates the entry of Cyprinidae to India and appears to be a gross over-estimate.

[†] Ramachandran *et al.* (2017) show however, that for birds as a whole, the Palghat Gap was not recovered as a major biogeographic division within the Western Ghats. Klaus *et al.* (2014) too, in a study of the freshwater crabs, showed that the Palghat Gap does not appear substantially to have affected historical dispersal patterns.

Western Ghats, explained by past climatic instability and current hydric stress. This scenario was supported, in the case of scolopendrid centipedes, also by Bharti *et al.* (2021), who showed a declining south-north gradient in phylogenetic diversity in the Western Ghats, with the Palghat Gap serving as a distinct barrier to dispersal.

Similarly deep divergences separate sister groups also in other pairs of terrestrially-connected habitats in the region: *e.g.*, the caecilians of the genus *Gegeneophis* occurring in the Eastern and Western Ghats of India, a distance of ~400 km, diverged some 35 Mya (Gower *et al.*, 2016), and the populations of the agamid lizard genus *Lyriocephalus* in the Knuckles Hills and Sinharaja Forest, Sri Lanka, separated by a distance of ~100 km of rain forest, diverged as long as 4.3 Mya (Schulte *et al.*, 2002; see also Biswas & Pawar, 2006). Biswas & Karanth (2021) provide an elegant review of the role of the Palghat and other gaps within the Western Ghats in shaping the region's biodiversity.

The relatively more seasonal climate of the Palghat Gap thus appears to have inhibited biotic dispersal between the moist forests of the Western Ghats north and south of it. It is unsurprising then, that the substantially more arid Palk Isthmus presented a trenchant barrier to India–Sri Lanka dispersals. The isthmus, which connected Sri Lanka to the mainland during successive Pleistocene sea-level low-stands, failed to serve as a corridor for biotas unadapted to its climate. As the case of *Sitana* above shows, it did not facilitate the immigration to Sri Lanka of even some arid-adapted species. It was, nevertheless, the only terrestrial biotic gateway to the country.

Even today, Sri Lanka's northern 'dry-zone' plain receives rather less than 1500 mm of highly seasonal rainfall annually and endures a dry season that spans four to six months, compared with the markedly aseasonal pattern of rainfall in the south-western wet zone (Figure 2.6). Within the dry zone, the region of Mannar, which lies on the erstwhile Palk Isthmus, is exceptionally arid. As with the Palghat Gap, it was the dry and strongly seasonal climate of the Palk Isthmus, rather than inundation during periods of high sea level, that served as the principal impediment to faunal and floral exchange between southern India and Sri Lanka.

3.9.7 The Toba Event and Late-Pleistocene aridity

The volcanic eruption at Toba, on Sumatra, ~74 kya emitted a large mass of ash and sulphur aerosols into the stratosphere, attenuating insolation, increasing albedo, and causing Earth's temperature to fall by 3–5°C for the next several centuries. During this time, glaciation had in any case led to increased aridification, as the dominance of C_4 savannah vegetation in the peninsula of India suggests (Farooqui *et al.,* 2010). With the amelioration of Pleistocene aridity in the Holocene, evergreen forests, which had been isolated in refugia in humid valleys or which existed only as riparian vegetation, expanded in the southern Western Ghats, beginning as recently as 7–4 kya (Bera & Farooqui, 2000; Farooqui *et al*., 2014). This included taxa associated with riparian vegetation or rainforests also in Sri Lanka, such as *Terminalia, Hopea, Mangifera, Drypetes, Mallotus, Calophyllum, Syzygium*, and *Schefflera* (Farooqui *et al*., 2010). This led Farooqui *et al*. (2014) to conclude that the Neogene rain forest flora recorded from the Varkala cliff in southern Kerala has persisted in the region since Marine Isotope Stage 6 (195–123 kya). They observed also that the abundance and diversity of the rainforest pollen assemblage during Marine Isotope Stage 5a (~80 kya) was comparable to the present-day flora of the southern Western Ghats, indicating that the precipitation pattern was similar to—or more intense than—that now prevailing in the region. The extent of evergreen forest during Marine Isotope Stage 5a,c and e, however, was greater than that prevailing at present, suggesting that this flora is even now in a state of refuge. They concluded also that monsoon circulation over southern India remained broadly in statis since the Middle Miocene Climate Optimum (~14 Mya) and the flora in the South-Western Ghats is 'a fossil ecosystem and a relic of the Tertiary period.' This was certainly true also of Sri Lanka's wet zone.

3.9.8 Palk Isthmus aridity: a counter-example.

A danger in constructing a biogeographic scenario retrospectively from selected examples, rather than prospectively by testing hypotheses, is that the examples could be cherry picked to fit the narrative. We do not wish, then, to convey the impression that all studies to date are consistent with an increasingly seasonal Palk Isthmus beginning in the early Pliocene, xeric for the whole of the Pleistocene. There is, in any event, a dearth of such studies. However, the cause of the Lorisiformes is worth discussing because it runs counter to the arguments we have made in section 3.9.5.

Tharindu Ranasinghe

Figure 3.78. *Loris tardigradus*, the endemic slender loris of Sri Lanka's wet zone.

The genus *Loris* (Figure 3.78) contains two species: *L. lydekkerianus*, distributed in the dry zones of southern India and Sri Lanka, and *L. tardigradus*, an endemic of Sri Lanka's wet zone (Pethiyagoda, 2012). *Nycticebus*, the sister group of *Loris*, is disjunct, ranging approximately from the north-eastern India to Southeast Asia and Sundaland. The time-calibrated phylogeny of Pozzi *et al*. (2015) dates the divergence of *Loris* and *Nycticebus* to the early Oligocene (~30 Mya). This is consistent with their distribution on either side of Chatterjee's partition[*]. For the two species of *Loris*, however, they recovered a divergence time of 2.0 (95% HPD 1.2–2.9) Mya, which implies that *L. lydekkerianus* dispersed across the Palk Isthmus within the last ~3 Mya, at which time xeric conditions prevailed. *Lorises* are generally arboreal, rarely descending to the ground. Yet, if during this interval the Isthmus supported the dry deciduous forests with which *L. lydekkerianius* is associated, we would expect many other South Indian species too, to have immigrated to Sri Lanka (section 3.9.5).

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[*] See section 3.6.1 for other examples.

SUPPLEMENT 4

Sri Lankan freshwater crabs

Freshwater crabs are among the best-studied groups of aquatic organisms in Sri Lanka. A total of 51 gecarcinucid species (all endemic) in seven genera (five endemic; Figure S4.1) are recognized from the island (Bahir *et al.*, 2005). The preponderant majority of species was discovered only recently, in the decade 1995–2005. The molecular phylogeny of Bossuyt *et al.* (2004) showed this diversification to be the sister group of *Gubernatoriana*, a genus endemic to the Western Ghats, with a divergence time interval of ~11.9–16.5 Mya, and with some members of a single clade (the lowland *Spiralothelphusa-Oziotelphusa* group) having back-migrated to India 6.1–8.4 Mya.

While 15 of the 51 species have extents of occurrence greater than 1000 km^2, 26 are considered 'micro-endemics', with ranges often less than 1 km^2 (Bahir *et al.*, 2005). Similar distributions are true also of the Western Ghats' Gecarcinucidae, of which Klaus *et al.* (2014) noted, 'None of the montane species has a widespread distribution that would comprise more than one mountain top, or 'sky island'… This tendency to localised or small (spatial)-scale endemism is expected for freshwater crabs (Jesse *et al.*, 2010), especially if the species have more semi-terrestrial to terrestrial habits'.

Beenaerts *et al.* (2010) presented a time-calibrated phylogeny of the Sri Lankan crabs, which showed the diversification to be younger than estimated by Bossuyt *et al.* (2004), deriving from a Late Miocene (~7.4 Mya) common ancestor.This was around the last time a perhumid climate (as indicated by dipterocarp forests) existed in the lowlands of south-eastern India, and hence the Palk Isthmus. These authors showed the diversification of freshwater crabs on Sri Lanka to have begun in the lowlands, followed by an early (5.5 Mya) divergence into three clades, each broadly restricted to a distinct elevational zone: lowland, < 270 m asl; 270–1060 m; and 910–2420 m.

Because most species are only semi-aquatic, their dispersal depends more on the availability of a moist substrate rather than on waterways. Of the 38 putative species in the phylogeny constructed by Beenaerts *et al.* (2010), 28 were each restricted to a single zone, with species-richness in the lowlands and uplands each being 29 percent, and that in the highlands 16 percent. Unlike in the case of freshwater fishes, crabs displayed no clade-level endemism within river basins, though the great majority of species is confined to the wet zone.

M. M. Bahir

M. M. Bahir

M. M. Bahir

Figure S4.1. Representatives of Sri Lanka's diverse freshwater-crab fauna. ***a,*** *Ceylonthelphusa savitriae,* a narrow-range endemic confined to Morningside (1060 m asl), at the eastern edge of the Sinharaja UNESCO World Heritage Site; ***b,*** *Perbrinckia sanguinea,* a species restricted to high elevations (~1200 m asl) in the Knuckles Hills; and *Oziotelphusa hippocastanum,* which is widely distributed across the island's eastern dry-zone lowlands (Bahir & Yeo, 2005).

SUPPLEMENT 5

The Perils of Intuitive Biogeography: A Sri Lankan story

J. C. Willis's theory of Age and Area

The availability of a georeferenced taxonomic 'database' by way of Henry Trimen's *A hand-book to the flora of Ceylon* (1893–1900) allowed John Christopher Willis (1868–1958, Figure S5.1), his successor as director of the Royal Botanic Gardens, Peradeniya, to undertake further investigations of the distribution of the island's flora. Adept at handling 'big data' in the age before electronic computers (see Pethiyagoda, 2007: 86), Willis soon set to work and became the first botanist to observe the high incidence of narrow-range endemism in the island (Willis, 1915; see also Figure 2.7 and Ashton & Gunatilleke, 1987: 275–277).

Willis was fascinated by endemism and especially the remarkable incidence of the 'micro-endemics' restricted to a single site such as a mountaintop (see Willis, 1906 for Ritigala; Willis, 1908 for hilltop floras generally; and Willis, 1911 for Namunukula). Were these relicts of species that had previously enjoyed wider distributions, he wondered, or had they evolved autochthonously, in situ?

He rejected the possibility that the ranges of such species might have been restricted by edaphic specialization, or by climate, rainfall, or an inherent inability to disperse. Noting that many micro-endemic species occur syntopically with non-endemic congeners, he hypothesized that the former were incipient species that had evolved recently, leading him to conclude that widespread species (and by extension, taxa) were evolutionarily older than ones with more restricted ranges*.

Figure S5.1. John Christopher Willis.

Willis hinted at this conclusion in a 1907 paper in the *Annals of the Royal Botanic Gardens, Peradeniya*, and might have let the matter rest had not Sinnott & Bailey (1914), in an early study of plant phylogeny, suggested that herbaceous plants were of more recent origin than woody ones. In a paper read to the Royal Society on 10 December 1914, they observed that 'There is a great preponderance of herbs in temperate regions and of woody plants in the tropics.' They concluded from this observation that 'herbaceous vegetation, most richly developed in the great land-mass of the north temperate zone, has spread thence over most of the globe', going on to add, 'The endemic plants in a flora are usually to be regarded as its most ancient element… endemic trees or shrubs are almost always very ancient.'

Willis (1915) proposed his theory, which soon came to be known as the Theory of Age and Area, not as a direct rebuttal of Sinnott and Bailey's (1914) hypothesis but as an original thesis based on his own analysis of Trimen's plant-distribution data. In his *Hand-book*, Trimen had not only mentioned which species were endemic to Sri Lanka

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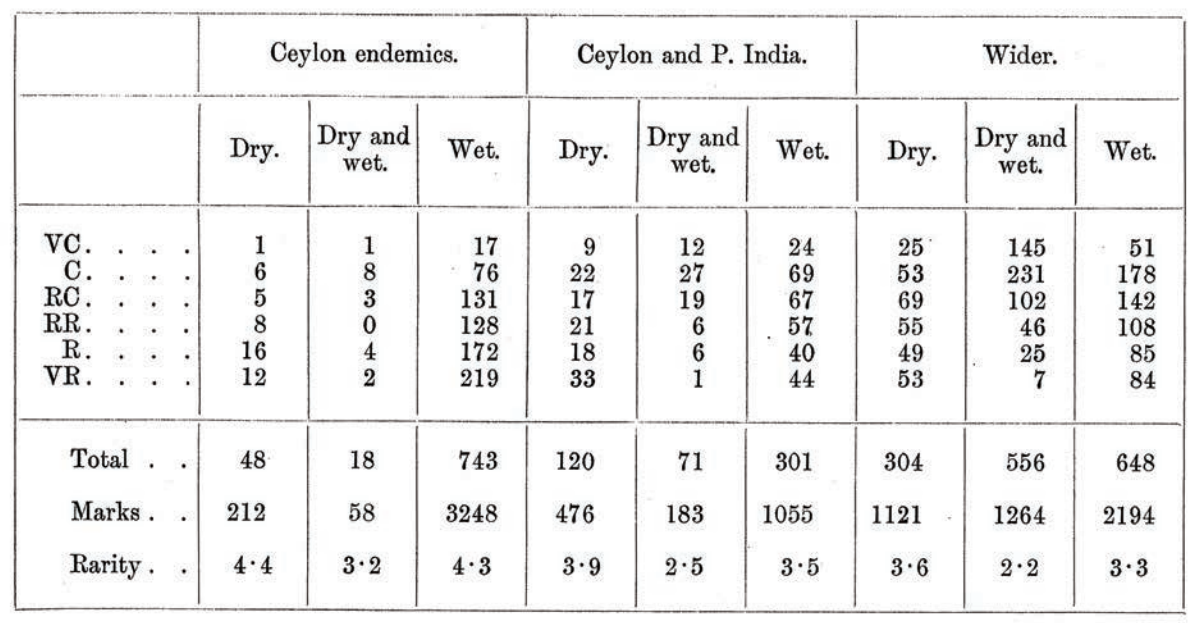
* Darwin, in his (1861) *On the origin of species*, had arrived at exactly the opposite conclusion: 'as the favoured forms increase in number, so, generally, will the less favoured decrease and become rare. Rarity, as geology tells us, is the precursor to extinction. We can see that any form which is represented by few individuals will run a good chance of utter extinction, during great fluctuations in the nature of the seasons, or from a temporary increase in the number of its enemies. But we may go further than this; for, as new forms are produced, unless we admit that specific forms can go on indefinitely increasing in number, many old forms must become extinct… I think it inevitably follows, that as new species in the course of time are formed through natural selection, others will become rarer and rarer, and finally extinct.'

but also provided an index of rarity, on a scale of 1–6. Willis was quick to observe in these data that 'The rarest plants in Ceylon are the local endemics, the next most rare those also common to Peninsular India, and the commonest those of wider distribution… From these interesting figures', he continued,

> 'one may conclude that the local endemic species have not been developed in any kind of advantageous response to local conditions. They are much rarer than those species which are also common to Peninsular India, and these again than those of wider distribution… The second conclusion drawn is that on the average, the commonness of a species depends upon its age from the time of its arrival in, or evolution in, the country. The commonness of any individual species will, of course, also depend upon its degree of adaptation to local conditions, and upon many things that can only be regarded as chance, such as the sudden appearance of new factors, like diseases, etc., in the problem. In other words, on the average, species are developed quite indifferently to local conditions, though it is possible that they may be developed because of these conditions.'

With this argument, Willis was seduced into the idea that wide-ranging species are more ancient than narrow-ranging ones. The theory, while accepting the process of evolution, rejected Darwin's proposition that the primary mechanism involved in speciation was natural selection (Figure S5.2). The accumulation of infinitesimally small variations to create distinctive 'Linnean' species, argued Willis, would take much longer than geological time allowed (Willis, 1907). 'Nearly seventy years ago,' he wrote, 'Lyell [1853] said, "Might not the births of new species, like the deaths of old ones, be sudden?" and it appears to me… one can hardly arrive at any other conclusion' (Willis, 1922).



	Ceylon endemics.			Ceylon and P. India.			Wider.		
	Dry.	Dry and wet.	Wet.	Dry.	Dry and wet.	Wet.	Dry.	Dry and wet.	Wet.
VC. . . .	1	1	17	9	12	24	25	145	51
C. . . .	6	8	76	22	27	69	53	231	178
RC. . . .	5	3	131	17	19	67	69	102	142
RR. . . .	8	0	128	21	6	57	55	46	108
R. . . .	16	4	172	18	6	40	49	25	85
VR. . . .	12	2	219	33	1	44	53	7	84
Total . .	48	18	743	120	71	301	304	556	648
Marks . .	212	58	3248	476	183	1055	1121	1264	2194
Rarity . .	4·4	3·2	4·3	3·9	2·5	3·5	3·6	2·2	3·3

THE ROYAL SOCIETY OF LONDON

Figure S5.2. Willis (1915) performed the earliest numerical analyses of the flora of Sri Lanka in relation to the floras of the Indian peninsula and regions farther afield (VC, very common; C, common; RC, rather common; RR, rather rare; R, rare; and VR, very rare). These showed, for example, that 'in the dry zone there are only 48 endemic species against 743 in the wet'. Willis's work was obscured, however, by fundamental flaws in his reasoning. Following his first polemic against natural selection (Willis, 1907), he went on to make numerous incorrect assumptions (*e.g.*, 'Natural selection requires that many forms shall modify in the same *direction*' [our emphasis]). Based on these, he argued that while evolution does occur, and that mutations do take place, the mechanism involved is not natural selection. He does not appear to have recognized that variation within species was key to the process of natural selection.

Willis did not restrict the single-step origin of new species: he claimed that 'a single mutation, usually very divergent from the parent form, may give rise, at one step (not gradually as under Darwinism) to a new form, of family, generic, specific or varietal rank' (Willis, 1949). Willis (1942) had given this process the moniker 'kaleidoscopic mutation', an allusion which suggested that with each turn of the spindle, a set of dramatically different shapes appears in the kaleidoscope, based, however, on a combination of fixed templates*.

An early supporter of the Age and Area theory was the Dutch botanist Hugo Marie de Vries (1848–1935) who, though noted for rediscovering (together with Carl Correns and Erich von Tschermak) Mendel's laws of heredity in 1900, challenged the gradual evolution of species posited by the Darwinian model. Instead, he proposed a Mutation Theory that held that new species arise through single mutations. De Vries (1916), having tested Willis's arithmetic, concluded,

> It is obvious that some general law must be underlying these phenomena… If the endemic species had originated by natural selection of infinitesimal steps, and in response to the local conditions, which are obviously the only conditions that matter when the species first appears, they must have been, from this very origin, better adapted to these conditions than their parent species. According to the theory of natural selection it would follow that they must surpass their forerunners in the struggle for life and soon spread to a higher degree of commonness. But… the reverse is true.

Opposition to Willis, however, was quick to galvanize, principally in the form of Henry Nicholas Ridley (1855–1956) who, in a devastating critique in *Annals of Botany* (1916), systematically demolished Willis's arguments. Given that Willis's original (1915) paper was based largely on the data in Trimen's *Hand-book*, Ridley questioned, for example, Trimen's 'degrees of rarity', correctly pointing out that because Trimen's sampling was biased towards the favourite locations of his collectors, consequent conclusions on abundance and distribution would necessarily be subject to sampling bias.

Willis, however, clung tenaciously to his thesis, digging himself deeper into the mire, rebutting his detractors' arguments by surrounding his hypothetical assertions with special conditions that made them impossible to falsify. In all, between 1915 and his death in 1958, he published some 18 papers and three books substantially on Age and Area.

Although kaleidoscopic mutation has, of course, been universally rejected, the determinants of rarity and the relationship between the extent of geographic range and evolutionary age continue to be important fields of inquiry. Even some of its severest critics grudgingly admitted that Age and Area held considerable intuitive appeal: its conclusions were almost as obvious and seductive as they were false.

Willis's theory is likely to be remembered, however, largely for the debate it caused and the research it precipitated: almost a hundred papers addressing the issue have been published since 1915 and the widespread use of the label 'Age and Area' in the ecological literature shows that it is an idea that lives on, though of course, in a different context.

Adapted from Pethiyagoda & Sudasinghe (2017).

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* Willis seems to have been unaware that St George Jackson Mivart, a fierce critic of Darwin, had gone down this road already. Mivart (1871: 139, 297) denied gradual change resulting from natural selection (based on fitness) from among the variation that occurs within species. Instead, he argued that selected individuals had benefited from 'jumps' in character-states, hence accelerating evolutionary processes.

4

Biogeography of Sri Lanka's freshwater fishes

When we change our focus from individual taxon histories to shared biotic area histories, we move historical biogeography beyond the dispersal versus vicariance debate to a period of discovery. — Parenti & Ebach, 2013.

4.1 The early phase

4.1.1 19th-century ichthyogeography. The affinity Sri Lanka's freshwater fishes have to the ichthyofauna of southern India is, at first glance, 'obvious': the two landmasses have broadly the same geological history and climate (Dissanayake & Chandrajith, 1999; Lal *et al.*, 2009; Teale *et al.*, 2011). Moreover, they have been connected by the Palk Isthmus for most of the past 25 My, during which period sea levels were substantially below those of the present day (Miller *et al.*, 2005; Figure 3.63).

The realisation that the southern hill ranges of India contain an extraordinary ichthyofauna, however, was slow in coming. While the cataloguing of global fish faunas during the 19th century by authors such as Georges Cuvier and Albert Günther had paved the way for broad patterns of distribution of freshwater fishes to be discerned, the distribution data available to these authors was often scant, with only a country name (*e.g.*, 'Ceylon') or location of the sender of the specimens (rather than the location at which they were collected) being recorded. This period was characterized by inventory-building, with little attention to the patterns of distribution of fishes.

The arrival in India of Francis Day, a British Army surgeon, paved the way for a new age of ichthyological exploration in the region. Day collected extensively throughout the subcontinent and was able, in his *Fishes of India* (1875–88), to record at a spatial resolution never before attempted, the distributions of 369 species of freshwater fishes from 'British India', including Sri Lanka.

From an analysis of these distributions, Day (1879) found that of the 73 genera of freshwater fishes he recognized from India, 62 extended to Burma and/or the Malay Archipelago, or both, whereas only 15 extended to the Palaearctic (broadly, Eurasia and Africa north of the 27th parallel). 'The ichthyology of India and Ceylon', he concluded, 'is far less Palaearctic than it is Malayan… We are unable to ascertain one single genus which is solely African and Indian, as all the African forms which extend to India are either likewise present in the Palaearctic region, or else in the Malay Archipelago, or in both… It would thus appear that the irruption of the majority of the freshwater forms common to Africa and India must have been by way of the Mediterraneo-Persic subregion.'

Day (1879: 563) then went on to contemplate the origin of Sri Lanka's freshwater-fish fauna:

> 'Here a great difficulty exists, as the fishes of that island still remain to be thoroughly worked out. Bleeker's *Cobitoïdes et de Cyprinoïdes de Ceylan* [Bleeker, 1865] unfortunately does not enumerate the localities whence his examples were obtained; consequently one is ignorant as to whether they came from the northern or southern districts, or from both. And this question is important when examining into the zoology of that island, the southern portion consisting of hill-tracts which Mr. Blanford classes with Malabar and the 'low country on the west coast of India

> from Cape Comorin to a little north of Bombay, and a range of hills near the same coast as far north probably as the Tapti river…' The northern portion of Ceylon, he considers, belongs to the Indian province or subregion…
>
> 'Some materials exist, however, for investigating this question, as we know of 41 species of freshwater fishes belonging to 29 genera inhabiting Ceylon. The genera consist of 9 Acanthopterygians, 6 Siluroids, 1 Scombresocid, 1 Cyprinodont, and 12 Cyprinoids, with one exception, all having representatives in Malabar, the single exception being the genus *Channa*, very closely allied to the ubiquitous Indian genus *Ophiocephalus* [*sic*], from which it is separated because it is deficient of ventral fins…
>
> 'The Malabar fish-fauna is intimately related to that of Ceylon and (but to a decreased extent) with that of the southern portion of the Coromandel Coast, as some species extend their range as far as the Kistna [Krishna River].'

'The freshwater fish-fauna of Ceylon would show a very slight connexion with Africa, and that only through the same genera being distributed throughout India and Malabar', Day (1879) concluded. Then, recognizing that the Sri Lankan freshwater fishes bore a close similarity to those of southwest India, he pointed to three striking instances in which fishes present in his 'Ceylonese subregion' occurred further afield while being absent elsewhere in India: 'Genus *Channa* is found in Ceylon and China[*], but absent from intermediate localities. *Polyacanthus signatus* [*Belontia signata*] has only been taken in Ceylon and Java[†]. Genus *Etroplus* through the Ceylonese subregion, and an allied genus in Madagascar.'

Finally, having reviewed the general conclusions of Wallace (1876) with regard to the zoogeography of the Oriental region, Day (1879) presciently concluded:

> 'In short, many zoologists consider that the Indian fauna was formerly very similar to the Malayan; that something occurred which acted injuriously on that fauna; while a communication occurring with Africa, and perhaps due to the Indian climate becoming more tropical, a development of African forms occurred, but that this commingling did not take place on the more elevated regions; that afterwards there was a large irruption of Malayan forms due to a connexion being formed between Burma and Eastern Bengal, and that they overran the Hindustan subregion… There must at a former period have existed a land communication between Malabar and Ceylon and the Malay Peninsula[‡].'

Indeed, Alfred Russel Wallace (1876) too, had arrived at the same conclusion. 'The island of Ceylon', he wrote, 'generally agrees in its productions with the Southern part of India… it has several birds which are allied to Malayan and not to Indian groups, and a fine butterfly of the genus *Hestia*, as well as several genera of beetles, which are purely Malayan…' (see Figure 3.54b).

While Wallace's (1876) conclusions were limited by the dearth of information on the distribution of Indian freshwater fishes, Blanford (1901), in his pioneering zoogeographic analysis of India, which followed the above-mentioned works of Day, had no such excuse. Nevertheless, he summarily dismissed the region's freshwater ichthyofauna: 'The freshwater fishes found in the Malabar tract, but not elsewhere in the Indian Peninsula,' he noted, 'are *Silurus*, two carps (*Homaloptera* and *Scaphiodon*), and *Sicydium*, one of the gobies. None of these is of importance.' Inexplicably, he neglected the survey and analysis of Day (1876a,b; 1879), who remarked particularly on the Malayan and African affinities of the fishes of this region.

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[*] At the time Day wrote this, only two species of snakeheads lacking pelvic fins were known: the Sri Lankan *Channa orientalis* and the Chinese *C. asiatica*. Seven more have since been described: *C. andrao, C. bleheri, C. brunnea, C. burmanica, C. hoaluensis, C. ninhbinhensis* and *C. nox*. Li *et al*. (2006) and Rüber *et al*. (2020), in their molecular phylogenetic analyses of snakeheads, showed that the loss of pelvic fins occurred independently at least three times in Channidae and is therefore of little value to systematics.

[†] *Belontia* occurs also in the perhumid southern region of the Malay Peninsula.

[‡] There was, of course, already such a 'land communication' via the Indian peninsula, Bengal and Myanmar, but the absence of many Western-Ghats and Sri Lankan taxa from there led Day, and later Deraniyagala (1952), to contemplate a more direct trans-oceanic connection.

4.1.2 Progress in the 20th Century. The freshwater-fish distribution patterns observed by Day (1879) and Günther (1880), and the questions they raised, have for the most part continued to bedevil Sri Lankan zoogeography to the present time. Sunder Lal Hora (1896–1955) was the first ichthyologist since Day to seek to reconstruct the historical biogeography of India. Hora (1952, 1953a) listed fifteen species of fishes in six families, which occur in peninsular India but are widely separated from conspecific populations farther east, suggesting that these fishes dispersed into India not much before the Pliocene and hence, too late for them to reach Sri Lanka. Hora postulated that they crossed into the peninsula of India during a pluvial phase, via the Garo and Khasi hills of Meghalaya and then the Satpura and other hill ranges that almost connect these to the northern Western Ghats. 'As a result of a detailed study of the genera and species inhabiting these regions', Hora (1937) concluded, 'I am definitely of the opinion that the freshwater fish fauna of India in the main originated in South-eastern Asia, most probably in Indo-China, and spread westwards by successive waves of migration to India'.

Hora, however, went on thereafter to advocate his Satpura Hypothesis (Hora, 1944, 1953b; since challenged, see Daniels, 2001), and work on the biogeographical relationships of the Indian and Sri Lankan freshwater fishes fell once more into neglect. Nevertheless, though the exact routes of dispersal of Southeast Asian lineages into India remain unknown, Hora's broad conclusion was correct: the preponderance of India's (and hence, Sri Lanka's) freshwater fishes have their origins in eastern Laurasia.

Paul E. P. Deraniyagala (1900–73), having compared many species of Sri Lankan freshwater fishes with their closest Indian relatives, considered that 'the island's various endemic genera, species and subspecies, apparently evolved during different epochs of separation—of varied duration—from the mainland (Deraniyagala, 1952: 1). 'Several Ceylon subspecies that are but feebly differentiated from their Indian counterparts probably date back to this last separation 5000 years ago… The affinities between Ceylon and the Malayan area are more noteworthy as they are not shared with India. They are the tendency for some Cyprinidae to suppress the perforated lateral line* and also the restriction of the genera *Belontia* Myers and *Channa* Gronov solely to Ceylon and the Malayan area.'

Deraniyagala (1955) elaborated further on this construction:

> 'The close similarity of the island's aquatic fauna to that of India indicates the recent derivation of the former from the latter. The advent of fresh water fishes and amphibians could only have been possible across a land connexion traversed by rivers and a study of the 54 species of Ceylon's strictly fresh water fishes reveals that there are 2 endemic genera [*Malpulutta* and *Horadandia*], 9 endemic species and 10 endemic subspecies, the remainder being indistinguishable apart from their Indian counterparts. This supports the view that most of these species have not been isolated sufficiently long to evolve differences from the parent stock. In other words, their isolation is relatively recent.'

Silas (1952a) too, had arrived at the same conclusion:

> 'The very great similarity of the freshwater fish fauna of Ceylon to that of peninsular India, especially to the 'Malabar' [Kerala] leads one to the inevitable conclusion that the island received its fish fauna from the mainland… Thus, as on the Indian Peninsula, the influx of the bulk of this fauna to Ceylon would date back to not earlier than the Pliocene [date argued in Silas, 1952b]. However, palaeontological evidence suggests that a small element of the present-day freshwater fish fauna of Ceylon could belong to the Early Eocene period.'

As noted in the previous chapter, Sri Lanka's paleontological record is, with three narrow exceptions, scant: a Miocene marine and estuarine bivalve and gastropod fauna at sites such as

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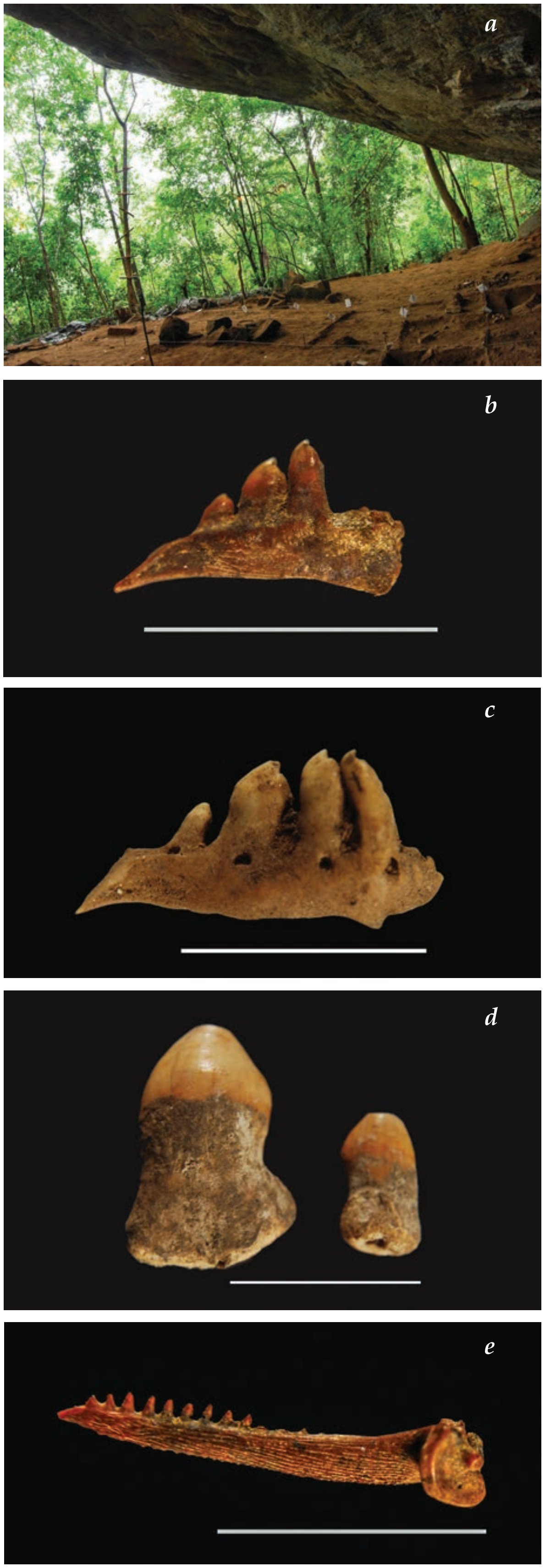
* Loss or reduction of the lateral line in small cyprinids is likely a consequence of reduction in body size (*e.g.*, *Rasboroides* spp., *Horadandia atukorali* and *Puntius titteya*): see list of miniature South and Southeast Asian cyprinids in Kottelat & Vidthyanon (1993); also Rüber *et al.* (2007).

Minihagalkanda on the south-eastern coastline of Yala National Park and Aruwakkalu on the north-western littoral (dated to the Burdigalian by Epa *et al.*, 2012; see Figure 3.62); mammals from the Pleistocene fluviatile alluvia in the south-western lowlands of Ratnapura (see Figure 3.57; also, Deraniyagala, P. E. P., 1955, for a comprehensive review); and 'open air' midden remains in caves occupied by humans in the Late Pleistocene (reviewed by Deraniyagala, S. U., 1992). Freshwater fishes such as carps and catfishes have been reported from this last group (Figure 4.1; Wedage *et al.*, 2019, 2020).

The vegetation and climate of the Western Ghats are in many ways similar to those of Sri Lanka's central hills (Subramaniam & Nayar, 1974; Valdia, 2016), and a close affinity has been identified also in their vertebrate faunas (Domrös, 1976; Ripley, 1980; Kortmulder *et al.*, 1990). The two ranges are separated by a distance of only ~400 km and are likely of similar age (Gunnell & Harbor, 2008; see also footnote * on p. 13). Wadia (1941) concluded that the deformation of the Tabbowa series dates the upwarp that produced the central massif to the early Cretaceous. But as shown in the previous chapter, and by Bossuyt *et al.* (2004), neither proximity nor ecological similarity resulted in a substantial sharing of the biotas of the two regions at least since the end of the Miocene. As concluded by Ali (2018), 'Presumably a filter has in the past impeded transfer to/from [Sri Lanka]. Importantly, the climate of the extensive lowland areas that abut the currently sundered causeway in northern Sri Lanka and southern India is Tropical Savannah'.

Owing, perhaps, to their perceived 'close similarity', the Sri Lankan and South Indian fish faunas did not come to be critically compared in the remainder of the 20th century. The biotas of shelf



Postgraduate Institute of Archaeology, University of Kelaniya.

Figure 4.1. Freshwater-fish bones excavated from a midden C^{14} dated to 14–8 kya beneath a rock shelter (the Pothgul Lena 'cave' at Alavala, ***a***) occupied by early modern humans. Pharyngeal teeth of ***b,*** *Dawkinsia filamentosa*; ***c,*** *Systomus sarana;* and ***d,*** *Tor khudree;* and ***e,*** pectoral spine of *Heteropneustes fossilis.* Other freshwater fishes represented include species of *Mystus* and *Clarias*. Though 40 km from the sea, the midden included also remains of the black-tip shark (*Carcharhinus limbatus*) and myliobatiform rays (Kelum Manamendra-Arachchi, pers. comm.). Scale bars: 1 cm.

Table 4.1. Genera of freshwater fishes occurring in the Western Ghats and/or Peninsular India (derived from Raghavan & Dahanukar, 2013; and Dayal *et al*., 2014) that are absent from Sri Lanka, indicating also whether the genus is monotypic, rheophilic, stygobitic, and endemic to the Indian Peninsula (PI). Families absent from Sri Lanka are indicated with an asterisk. We use a broad definition of rheophily: genera whose members exhibit anatomical adaptation to life in fast-flowing waters (Lujan & Conway, 2015), and those associated mostly with such habitats.

	Monotypic	Rheophilic	Stygobitic	Endmic to PI
Aenigmachannidae*				
Aenigmachanna	-	-	+	+
Ailiidae*				
Eutropiichthys	-	-	-	-
Proeutropiichthys	-	-	-	-
Silonia	-	-	-	-
Ambassidae				
Chanda	+	-	-	-
Parambassis	-	-	-	-
Amblycipitidae*				
Amblyceps	-	+	-	-
Badidae*				
Badis	-	-	-	-
Dario	-	-	-	-
Bagridae				
Batasio	-	-	-	-
Hemibagrus	-	?	-	-
Olyra	-	+	-	-
Rita	-	-	-	-
Sperata	-	-	-	-
Balitoridae*				
Balitora	-	+	-	-
Bhavania	-	+	-	+
Ghatsa	-	+	-	+
Travancoria	-	+	-	+
Botiidae *				
Botia	-	+	-	-
Clariidae				
Horaglanis	-	-	+	+
Cobitidae				
Pangio	-	-	-†	-
Cyprinidae				
Bangana	-	-	-	-
Cirrhinus	-	?	-	-
Eechathalakenda	+	-	-	+
Gymnostomus	-	?	-	-
Haludaria	-	-	-	+
Hypselobarbus	-	-	-	+
Lepidopygopsis	+	+	-	+
Kantaka	+	+	-	+
Neolissochilus	-	?	-	-
Nukta ‡	+	-	-	-
Oreichthys	-	?	-	-
Osteobrama	-	-	-	-
Osteochilichthys	-	+	-	+
Parapsilorhynchus	-	+	-	+
Rohtee	+	-	-	-
Sahyadria	-	-	-	+
Schismatorhynchos	-	-	-	-
Tariqilabeo	-	+	-	-
Thynnichthys	-	-	-	-
Waikhomia	-	-	-	+
Danionidae				
Betadevario	+	+	-	+
Cabdio	-	-	-	-
Chela	-	-	-	-
Danio	-	-	-	-
Neochela	+	-	-	+
Opsarius	-	+	-	-
Salmostoma	-	-	-	-
Horabagridae*				
Horabagrus	-	-	-	+
Pachypterus	-	-	-	-
Pseudeutropius	-	-	-	-
Kryptoglanidae*				
Kryptoglanis	+	-	+	+
Nandidae*				
Nandus	-	-	-	-
Nemacheilidae				
Indoreonectes	-	+	-	+
Mesonoemacheilus	-	+	-	+
Nemacheilus	-	+	-	-
Nemachilichthys	+	+	-	+
Notopteridae *				
Notopterus	-	-	-	-
Pangasiidae*				
Pangasius	-	-	-	-
Pristolepididae*				
Pristolepis	-	-	-	-
Psilorhynchidae*				
Psilorhynchus	-	+	-	-
Siluridae				
Pterocryptis	-	-	-	-
Sisoridae*				
Bagarius	-	+	-	-
Gagata	-	-	-	-
Glyptothorax	-	+	-	-
Pseudolaguvia	-	+	-	-
Synbranchidae				
Rakthamichthys	-	-	-	-

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† Although the genus *Pangio* is not stygobitic, a single species in the Indian peninsula, *P. bhujia,* an endemic of Kerala, is (Anoop *et al.*, 2019).

‡ Yang *et al.* (2012) subsumed *Nukta* in *Bangana.* We follow Kottelat (2017) in tentatively treating *Nukta* as a valid genus.

islands that have experienced regular contact with the mainland are, after all, expected to be closely related (Darlington, 1957; MacArthur & Wilson, 1967; Voris, 2000).

Indeed, such a relationship had long been posited also in the case of Sri Lanka. Wallace (1876), for example, observed:

> 'The Island of Ceylon is characterized by such striking peculiarities in its animal productions as to render necessary its separation from the peninsula of India as a sub-region; but it is found that most of these special features extend to the Neilgherries and the whole southern mountainous portion of India, and that the two must be united in any zoo-geographical province. The main features of this division are, –the appearance of numerous animals allied to forms only found again in the Himalayas or in the Malayan sub-region, the possession of several peculiar generic types, and an unusual number of peculiar species.'

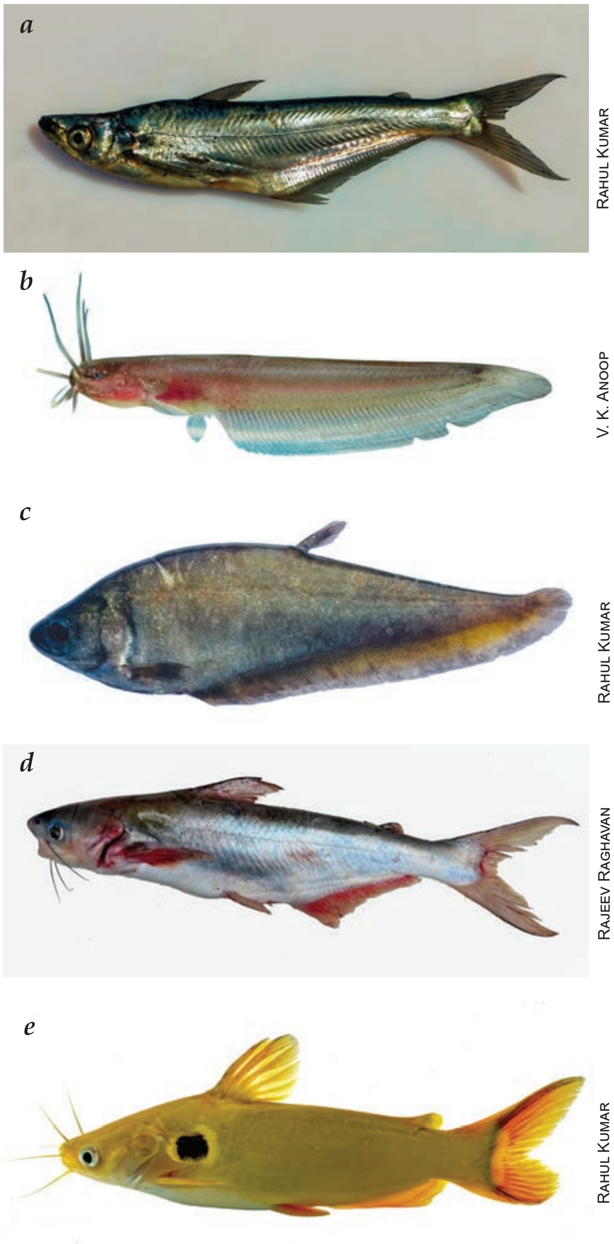
It was this 'province' that Myers *et al.* (2000) eventually recognized as the Western Ghats–Sri Lanka Biodiversity Hotspot, because it is composed of 'a community of species that fits together as a biogeographic unit'.

4.2 The regional context

It takes only the most cursory overview to see that compared with the richness and diversity of the freshwater fishes of the Indian Peninsula, Sri Lanka's ichthyofauna is markedly depauperate. The island is home to around 80 hololimnic fish species: the ones we treat here as 'freshwater fishes' (see Table 5.2). By contrast, almost 300 freshwater-fish species are recorded from the Western Ghats, to which about 200 species are endemic (Dahanukar *et al.*, 2004, 2011; Dayal *et al.*, 2014). Some 67 genera of freshwater fishes occurring in the Western Ghats or southern peninsular India are absent from Sri Lanka. No fewer than 14 families of freshwater fishes that occur in Peninsula India are absent from Sri Lanka (Table 4.1).

Both richness and diversity are highest towards the southern extremity of this mountain chain, south of the 30-km wide Palghat Gap (approximately 10.5–10.8°N; see Figures 3.7), which separates the Nilgiri Hills to the north from the Anaimalais to the south (Bhimachar, 1945). Freshwater-fish species richness in rivers south of the Palghat Gap, such as the Bharatapuzha, Chalakkudy, Manimala, Pamba and Periyar, is vastly greater than in those to the north, often exceeding 100 species per basin, with high basin-level endemism (Dahanukar *et al.*, 2011).

Of the freshwater fishes that occur in India south of the Palghat Gap, fourteen families are



Rahul Kumar

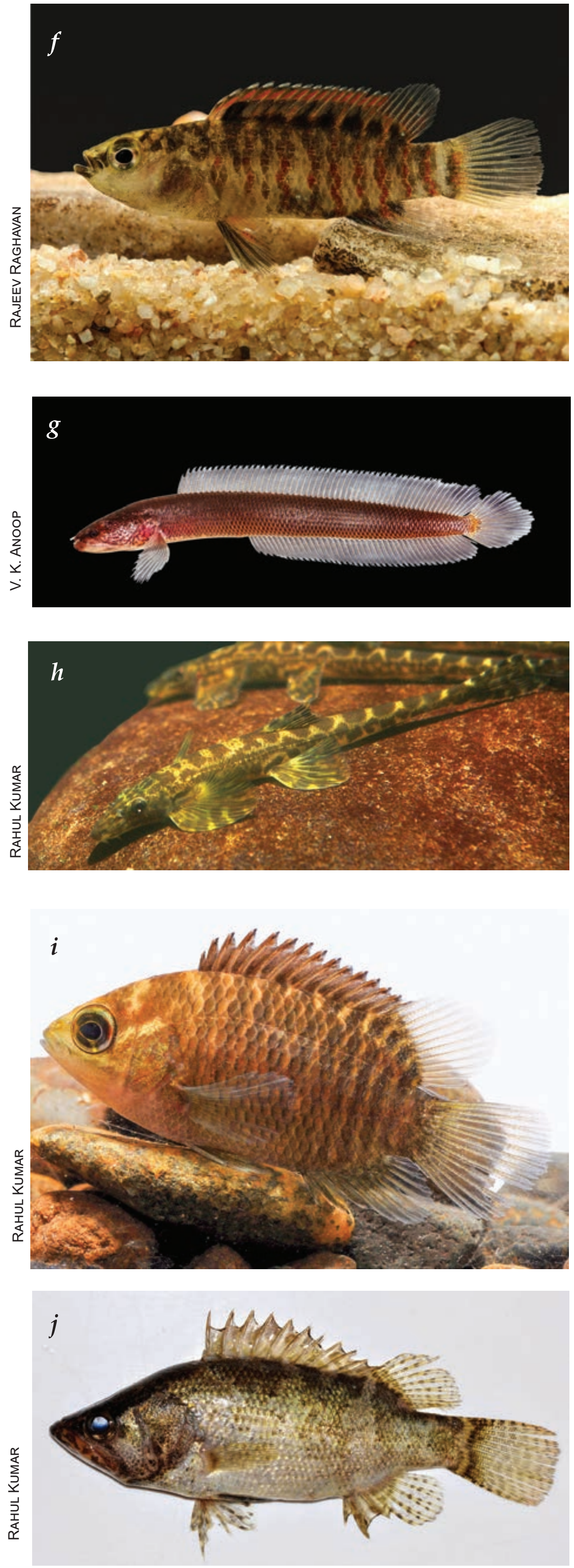
V. K. Anoop

Rahul Kumar

Rajeev Raghavan

Rahul Kumar

Figure 4.2. Caption on next page: ▶



◄ ▲ **Figure 4.2.** Representatives of the 14 freshwater fish families present in India south of the Palghat Gap but absent from Sri Lanka: ***a,*** *Silonia* (Ailiidae); ***b,*** *Kryptoglanis* (Kryptoglanidae); ***c,*** *Notopterus* (Notopteridae); ***d,*** *Pangasius* (Pangasiidae); ***e,*** *Horabagrus* (Horabagridae); ***f,*** *Badis* (Badidae); ***g,*** *Aenigmachanna* (Aenigmachannidae); ***h,*** *Travancoria* (Balitoridae); ***i,*** *Pristolepis* (Pristolepididae); ***j,*** *Nandus* (Nandidae); ***k,*** *Glyptothorax* (Sisoridae); ***l,*** *Amblyceps* (Amblycipitidae); ***m,*** *Botia* (Botiidae); and ***n,*** *Psilorhynchus* (Psilorhynchidae).

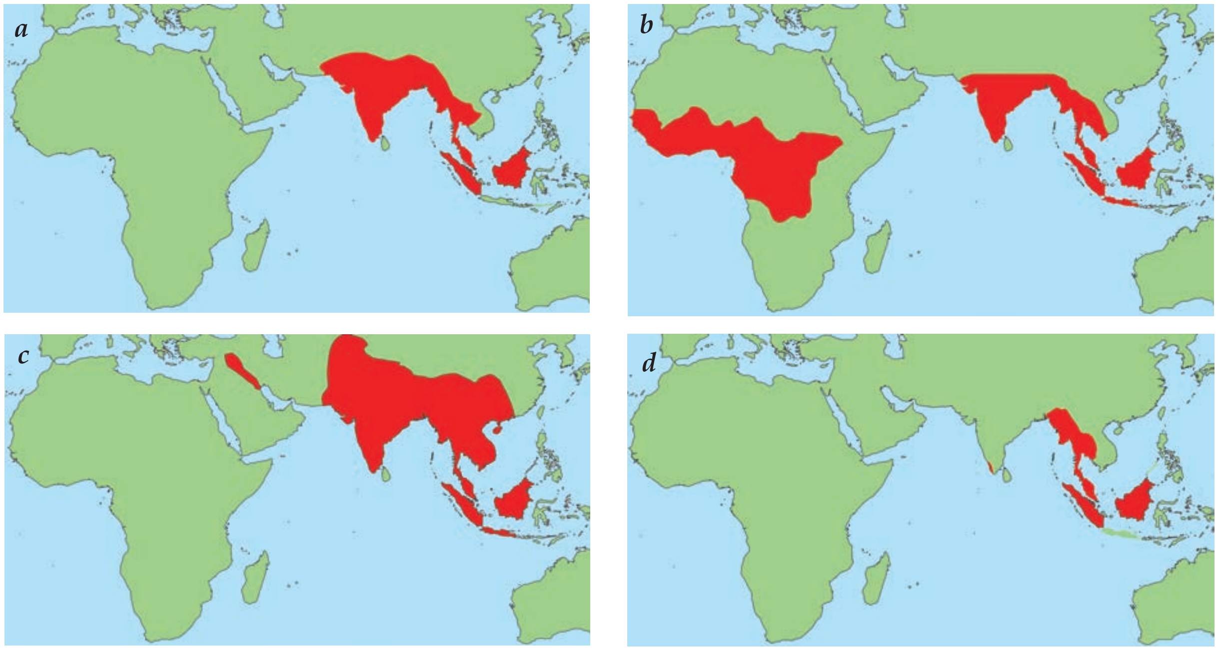


Figure 4.3. The approximate global distribution of some of the freshwater-fish families present in southern India and elsewhere but absent from Sri Lanka: ***a,*** Nandidae; ***b,*** Notopteridae; ***c,*** Sisoridae; ***d,*** Pristolepididae (adapted from Berra, 2007). Note the disjunct distribution of Pristolepididae between the Western Ghats and Southeast Asia, paralleling that of *Belontia* and the clade inclusive of *Malpulutta* and *Pseudosphromenus,* and that inclusive of *Rasboroides* and *Horadandia, vs* their Southeast Asian sister groups. Note that although all four families failed to cross the Palk Isthmus into Sri Lanka, they were able to disperse across the Sunda lowlands between the Malay Peninsula, Borneo and Sumatra.

absent from Sri Lanka: Aenigmachannidae, Ailiidae, Amblycipitidae, Badidae, Balitoridae, Botiidae, Horabagridae, Kryptoglanidae, Nandidae, Notopteridae, Pangasiidae, Pristolepididae, Psilorhynchidae and Sisoridae[*] (Figures 4.2, 4.3).

As explained in Chapter 5, the Malwathu and Kala drainages of north-western Sri Lanka appear to have been connected during the Plio-Pleistocene, via the Palk Isthmus, with the Tamiraparani and Vaigai rivers of south-eastern India (see Figure 5.1). The latter rivers, however, contain several genera absent from Sri Lanka, including *Bhavania, Cirrhinus, Hypselobarbus, Mesonoemacheilus, Salmostoma* and *Pachypterus* (Indra, 1992; Martin *et al.,* 2000; Rajgopal & Davidar, 2013). The Sisoridae, in particular, show a remarkable diversification in India (Jayaram, 1974) but it seems the Palk Isthmus could not facilitate their dispersal to Sri Lanka.

Sri Lanka's ichthyofauna is notable also for the absence of stygobitic fishes such as *Horaglanis* spp. (Clariidae), *Kryptoglanis shajii* (Kryptoglanidae), *Rakthamichthys roseni* (Synbranchidae), and the recently-discovered *Pangio bhujia* (Cobitidae) and two species of *Aenigmachanna* (Aenigmachannidae), which occur in the coastal plain of Kerala (Vincent & Thomas, 2011; Subhash Babu, 2012; Anoop *et al.,* 2019; Britz *et al.*, 2019, 2020a; Kumar *et al.*, 2019; Raghavan *et al.,* 2021). Especially surprising are the number of euryhaline taxa, such as *Carinotetraodon* (Tetraodontidae) and *Horabagrus* (Horabagridae) which, though common in west-flowing rivers and their estuaries in southern India, failed to disperse to Sri Lanka. Interestingly, Yamanoue *et al.* (2011) and Sathyajith *et al.,* (2019) showed that the putative sister groups of *Carinotetraodon travancoricus*, an endemic of south-western India, occur in Southeast Asia, from the Ganges eastwards.

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[*] Species-level similarity, however, is not addressed here because of the poor taxonomic state of many of the relevant groups of fishes. For example, of the 44 species of inland fishes Sumith *et al.* (2011) considered to be shared between Sri Lanka and the Western Ghats, 18 are victims of misidentification or erroneous taxonomy.

4.3 Gondwanan disjunctions

The wider relationships of the Sri Lankan and south Indian fishes too, have long attracted interest. Day (1879) and Günther (1880), for example, noticed the disjunction between the Sri Lankan and southern Indian cichlids (now in *Etroplus** and *Pseudetroplus*), and their sister group, *Paretroplus,* which is confined to Madagascar. '*Etroplus* inhabits Southern and Western India and Ceylon,' observed Günther (1880), 'and has its nearest ally in a Madagasse freshwater fish, *Paretroplus*. Considering that other African chromides have acclimatized themselves at the present day in saline water, we think it more probable that *Etroplus* should have found its way to India through the ocean than over the connecting land area; where, besides, it does not occur.'

There was, after all, no support in Günther's time for a terrestrial connection across the 3800 km span of ocean that separates Madagascar and Sri Lanka, although Sclater (1864), supported by Wallace (1876), had hypothesized a sunken subcontinent named Lemuria to account for the zoogeographical disjunctions between these two regions (see also Figures 3.27, 3.29). Blanford (1901) too, subscribed to the same idea: there was no other explanation for the numerous trans-oceanic biotic relationships that were by then being discovered.

A significant proportion of the Madagascan biota shows much closer affinities to lineages in India–Sri Lanka and Southeast Asia than to those in Africa (reviewed by Warren *et al.*, 2010; and Buerki *et al.*, 2013, 2014). Given that Madagascar and Africa are separated by just ~400 km of sea (~300 km if the Comoros are considered a stepping-stone), and that Madagascar and Sri Lanka-India are separated by a 3800-km expanse of Ocean, this is, at first glance, surprising.

Wallace (1876) was so struck by this tantalizing connection that he wrote: 'In our discussion of the origin of the Ethiopian fauna, we have supposed that a close connection once existed between Madagascar and Ceylon. This was during a very early tertiary epoch; and if, long after it had ceased and the fauna of Ceylon and South India had assumed somewhat more of their present character, we suppose the approximation or union of Ceylon and Malaya to have taken place, we shall perhaps be able to account for most of the special affinities they present…'

When he came to consider the geographic relationships of the Sri Lankan freshwater fishes, Hora (1937) too, was at a loss to explain how cichlids got from Madagascar to India.

'It is generally believed that the land connection between India and Africa disappeared somewhere about the transition period between the Cretaceous and the Tertiary', he wrote. 'It is during the obscure interval between the Cretaceous and the Tertiary that nearly all the modern types of bony fishes originated…'. Eduard Suess's (1885) *Das Antlitz der Erde*, in which he postulated a former 'Gondwäna-Land', which fragmented into Africa, Madagascar, the Mascarenes, Sri Lanka and India; and Alfred Wegener's (1912) *Die Entstehung der Kontinente*, which laid the groundwork for the theory of plate tectonics, were even then, in the absence of evidence of a causative mechanism, receiving scant attention.

Little light has been shed since then, on the origins of India's freshwater fishes. Jayaram (1977), for example, proposed numerous African and Asian biogeographic connections, but without evidence, and based on a taxonomy that has since undergone substantial revision. He regarded, for instance, Bagridae, Schibeidae, Clariidae and Cyprinidae to 'represent the true Indian components and comprise some autochthonous forms' on Gondwanan India. More recent work, however, suggests Asian origins for these groups (Sullivan *et al.*, 2006; Chen *et al.*, 2013; Kappas *et al.*, 2016; Murray, 2020). Fishes that can be shown definitely to have rafted to Asia on India since its rifting from Madagascar ~90 Mya are almost non-existent. The most compelling exception appears to be the Aenigmachannidae, a family recently reported from the Western Ghats, and which signals a Gondwanan origin, albeit ambiguously (Britz *et al.*, 2020).

Among freshwater fishes, the disjunct 'Gondwanan' distribution of the cichlid subfamily Etroplinae—and indeed, the Aplocheilidae, which occur only in Madagascar, Seychelles and southern Asia—are, at first glance, consistent with

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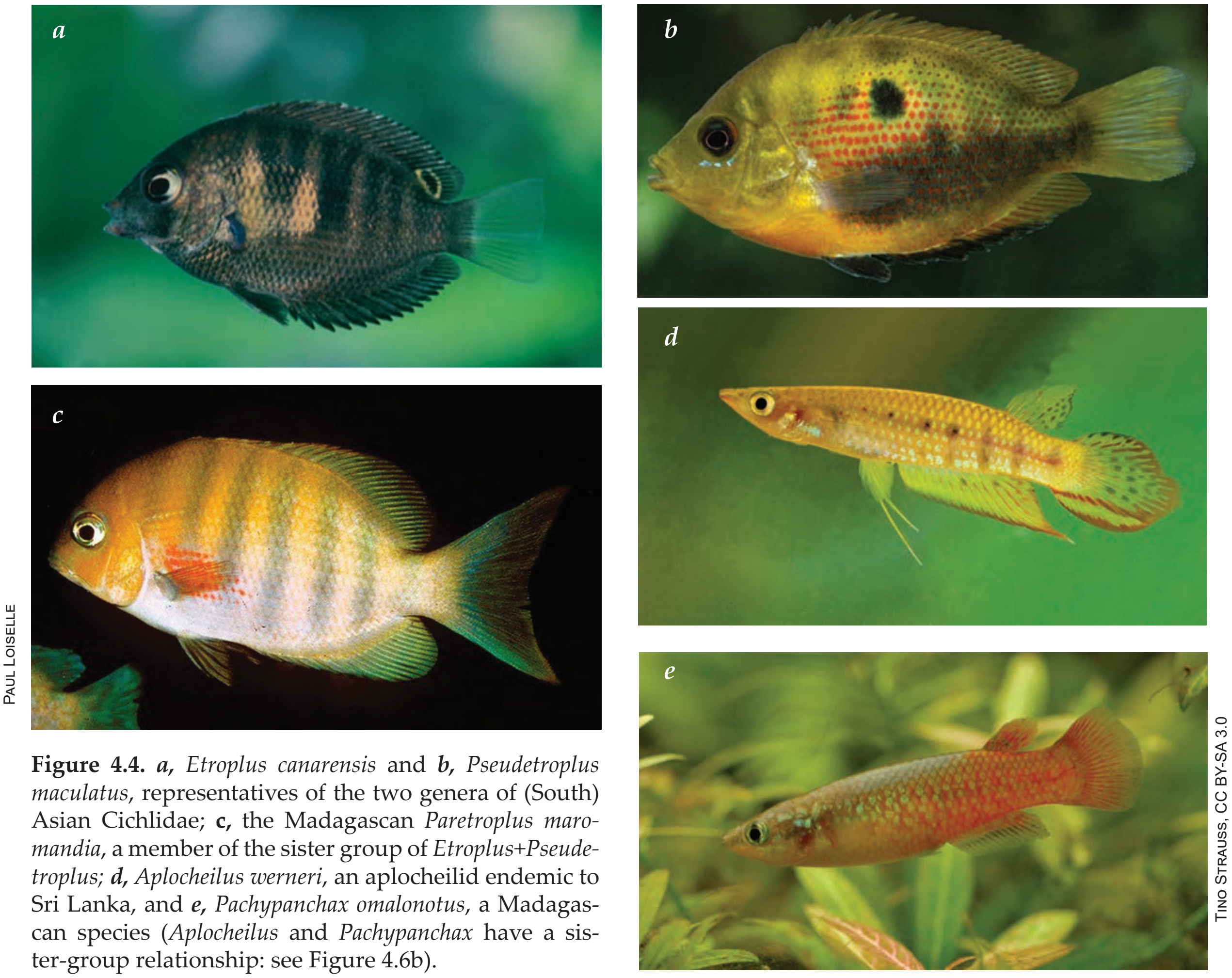
* Both genera were combined in *Etroplus* until Pethiyagoda *et al.* (2014b) retained *E. suratensis* and *E. canarensis* in *Etroplus*, while allocating the former '*E.*' *maculatus* to *Pseudetroplus.*



Paul Loiselle

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Figure 4.4. ***a,*** *Etroplus canarensis* and ***b,*** *Pseudetroplus maculatus*, representatives of the two genera of (South) Asian Cichlidae; **c,** the Madagascan *Paretroplus maromandia*, a member of the sister group of *Etroplus+Pseudetroplus;* ***d,*** *Aplocheilus werneri*, an aplocheilid endemic to Sri Lanka, and ***e,*** *Pachypanchax omalonotus*, a Madagascan species (*Aplocheilus* and *Pachypanchax* have a sister-group relationship: see Figure 4.6b).

Gondwanan vicariance. That, view, however, has not gone unchallenged.

4.3.1 Etroplinae. Although the etropline Cichlidae and the Aplocheilidae (Figure 4.4) are predominantly inhabitants of freshwaters, representatives of both occur also in the brackish waters of estuaries, mangroves and coastal swamps. While there are no marine species, extant or fossil, in either the Aplocheilidae or Cichlidae, some degree of salinity tolerance is evidently a secondarily derived condition in some species in both families, given their present occurrence in brackish-water habitats. This gives rise to doubt as to whether the observed 'Gondwanan' distributions of Aplocheilidae and Etroplinae are the result of vicariance or of dispersal (Lundberg, 1993; see Figures 4.5, 4.6). *Aplocheilus panchax*, for example, was shown by Beck *et al.* (2017) to have colonized the coastal regions of South and Southeast Asia as recently as the Plio-Pleistocene, going on even to cross Wallace's line to reach Sulawesi as recently as 30 kya.

Sparks (2004) had shown South Asian '*Etroplus*' (*i.e., Pseudetroplus* and *Etroplus*) to comprise a monophyletic clade that is sister to Madagascan *Paretroplus*, with their distribution explained by Gondwanan vicariance. The vicariance hypothesis posits that the South Asian representatives of these fishes drifted north on the Indian plate after it separated from Madagascar ~90 Mya (Storey *et al.*, 1995). This model is supported, for example, by the ~87 Mya (106–69 Mya) divergence time obtained for the Asian and Madagascan cichlid lineages according to the molecular clock employed by Azuma *et al.* (2008), arguably consistent with the rifting of India from Madagascar. The chrono-phylogeny of Matschiner *et al.* (2020), based on whole-genome sequences, however, shows the crown age of Cichlidae to substantially post-date the rifting of India and Madagascar, leaving oceanic dispersal as the only tenable hypothesis that explains the distribution of this family.

4.3.2 Aplocheilidae. The Aplocheilidae are known from two genera. The first, *Aplocheilus*, is represented by three species in Sri Lanka and five in India, including one (*A. panchax*) that inhabits coastal brackish and fresh waters from the Bay of Bengal to Sulawesi. The other is *Pachypanchax*, with six species restricted to Madagascar and a single species endemic to the Seychelles, which separated from India in the early Paleocene (Davies, 1968; McKenzie & Sclater, 1973).

Murphy & Collier (1997) and Pohl *et al.* (2015) showed in their phylogenies that a sister-group relationship exists between *Aplocheilus* and *Pachypanchax*. The topology of their phylogeny was broadly consistent with the sequence of Gondwanan fragmentation. The time-calibrated phylogeny of Costa (2013) shows the Asian *Aplocheilus* to have diverged from the Madagascar-Seychelles *Pachypanchax* ~84 Mya, coincident with the fragmentation of the Mascarene basin.

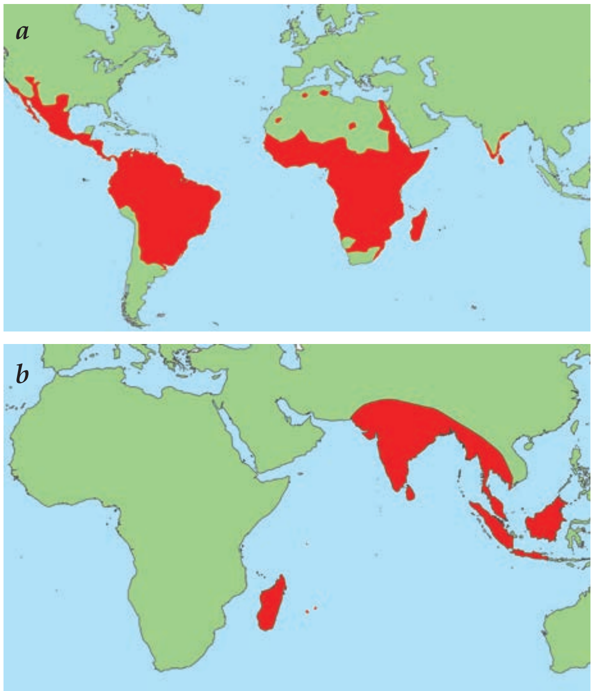

Figure 4.5. Approximate global distribution of ***a,*** Cichlidae (the Etroplinae are confined to Sri Lanka-India and Madagascar); ***b,*** Aplocheilidae (adapted from Berra, 2007).

4.4 Vicariance

The invocation of Gondwanan vicariance to explain the distributions of Aplocheilidae and Etroplinae, however, has had its critics (*e.g.*, Murray, 2001; Briggs, 2003b). Most time-calibrated phylogenies recover these groups as sister to all other Aplocheiloidei and Cichlidae, respectively. In a vicariance scenario, this would suggest that Cichlids evolved prior to rifting of Africa from East Gondwana—Madagascar, India, Antarctica, Australia—170 Mya (Chatterjee *et al.*, 2013; Figure 4.6a).

Such an ancient divergence time, however, is not supported by the fossil record: there is no evidence that ancestral cichlids had evolved by then (Murray, 2001). The oldest known fossils of Cichlidae and Aplocheiloidei date only to the Tertiary (*i.e.*, more recent than ~66 Mya), by which time the Indian plate was separated from Madagascar by a vast expanse of ocean. To support the allegedly re-

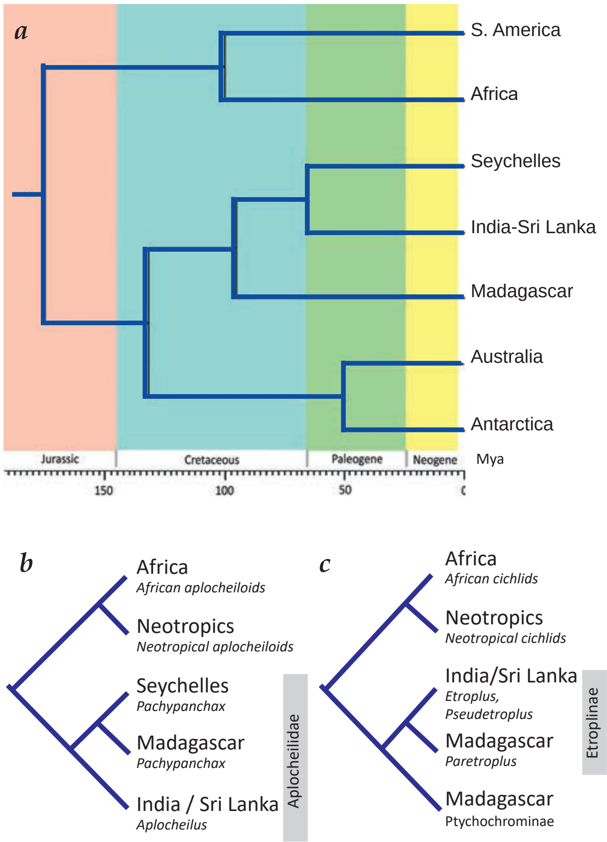

Figure 4.6. ***a,*** The sequence of fragmentation of Gondwanaland (adapted from Klaus *et al.*, 2011); and taxon-area cladograms of ***b,*** aplocheilid, and ***c,*** cichlid relationships, respectively (adapted from Sparks & Smith, 2004).

cent arrival of cichlids in Sri Lanka, Murray (2001) cited also Smith *et al.*'s (1994) *Atlas of Mesozoic and Cenozoic coastlines*, which erroneously shows Sri Lanka to have been below sea level in the Tertiary and until the Pliocene (approximately 66–5 Mya)*.

The time-calibrated phylogeny of Friedman *et al.* (2013) too, suggests cichlids evolved during the Paleocene (~65–57 Mya), substantially postdating the rifting of India from Madagascar. Friedman *et al.* (2013) estimate the divergence of the Madagascan and South Asian Etroplinae at 36.0 (42.2–30.3) Mya, well after India-Asia contact was complete.

More recently, a phylogenomic study by Ronco *et al.* (2020) estimated the crown age of cichlids to be 87.3 Mya (95 % HPD: 96.9–77.9 Mya), with Etroplinae diverging from the remaining cichlids at 76.2 Mya (86.6–66.3 Mya). In this scenario too, the split between Madagascan and South Asian Etroplinae must have occurred well after the India-Madagascar split ~90 Mya.

Briggs (2003a,b) had already questioned the Mesozoic breakup of Gondwana as the causative mechanism for the Asian distribution of Cichlidae and Aplocheiloidei, arguing that the fossil record, some contradictory molecular results, and other lines of evidence suggest a more recent dispersal. 'The aplocheiloid and cichlid fishes belong to the secondary freshwater fish category', he wrote. 'This means that at least some of the species can enter salt water.' Tolerance of saltwater, Briggs implied, allowed the ancestors of these fishes to disperse across the Indian Ocean, spanning gaps of thousands of kilometres. Although *Etroplus* and *Pseudetroplus*—and indeed, some tilapiine cichlids—sometimes venture into inshore marine environments (pers. obs.), it remains unknown whether they can complete their life cycle in saltwater. Chandrasekar *et al.* (2014), for example, found that adult *E. suratensis* did not survive in seawater of more than 35‰ salinity. However, we have reviewed credible photographic evidence of *Etroplus suratensis*, even accompanied by their young, from nearshore marine waters including harbours and reefs in Southeast Asia, where scattered feral populations occur. Rahul Kumar (pers. comm.) reports occasionally observing *E. suratensis* in the sea off Kollam, in Kerala State, India, syntopically with chaetodontids and scombrids.

This adds credibility to the increasing body of evidence that the dispersal of cichlid fishes across the Atlantic and Indian Oceans may have involved marine dispersal, especially considering the near-basal position Etroplinae seem to occupy in the phylogenies of Azuma *et al.* (2008) and Matschiner *et al.* (2020) (see also Matschiner *et al.*, 2017, 2019).

4.5 Land bridges and stepping-stones

A late Cretaceous connection between Madagascar and Sri Lanka has been invoked since van Steenis (1962) postulated† a since-submerged isthmus between the two islands. Greatly-lowered Oligocene sea levels (Haq *et al.*, 1988; Hutchison, 1989) were supposed to have resulted in significant portions of the Chagos-Laccadive Plateau and the then contiguous Mascarene Plateau and Seychelles Bank emerging above sea level, providing 'stepping stones' for biotic dispersal between Asia and Madagascar (Schatz, 1996; Warren *et al.*, 2010; see also Figures 3.27, 3.29).

Critics of the stepping-stone hypothesis, however, while pointing out that long-distance marine dispersal would nevertheless be called for, invoke alternative scenarios to explain the observed distributions. Hay *et al.* (1999) and Noonan & Chippindale (2006) argued, for example, that India and Madagascar may have been connected via Antarctica until the Late Cretaceous by the Kerguelen Plateau (Figure 3.29), a scenario Ali & Aitchison (2008) and Ali & Krause (2011) considered unlikely‡. The initial northward drift of the India-Seychelles plate was rapid (up to 21 cm·y^{-1}: Acton, 1999), quickly widening the oceanic gap between it and Madagascar (Bossuyt & Milinkovitch, 2001). Further, the separation of India-Seychelles from Madagascar was initiated by a mantle plume that generated large quantities of basaltic magma, po-

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* A misconstruction carried forward also into Morley *et al.* (2018: fig. 5). The reconstructions of *deeptimemaps.com*, for example, show Sri Lanka to have been emergent throughout the Cenozoic.

† 'There must have been an isthmian connection between Madagascar and Ceylon over the Seychelles-Comoros bank ('Lemuria')': van Steenis, 1962.

‡ More recently, Kappas *et al.* (2016) invoked 'dispersal from Africa… through shallow epicontinental Tethyan sea corridors to Asia' to explain Late Cretaceous connectivity between African and Asian catfishes ~82 (95 % HPD 92–73) Mya.

tentially an additional obstacle to biotic exchange (Storey *et al.*, 1995; Kumar *et al.*, 2001).

Nevertheless, proponents of dispersal have argued for land bridges and 'stepping-stone' island-chains, since submerged, to explain these disjunct distributions. Morgan (1981: fig. 2a) suggested that a system of successively-formed ridges and plateaus may have existed between Madagascar and India by way of the Maldive Archipelago (60–55 Mya), the Chagos Ridge (48 Mya) and the Mascarene Plateau (40 Mya).

Explaining the distribution of gecarcinucoid land crabs, Klaus *et al.* (2006) followed van Steenis (1962) in positing that these ridges and their adjacent continental shelves formed a land bridge between Africa, Madagascar and India that was nearly contiguous during Oligocene (*ca* 34–23 Mya) sea level low-stands, arguing that these 'Lemurian stepping stones' (Schatz, 1996) had facilitated also the dispersal of several plant taxa between Malesia and Africa-Madagascar via India–Sri Lanka. Buerki *et al.* (2013) too, thought it possible that Oligocene glaciation may have caused a drastic drop in sea level, leading to the emergence of ephemeral islands that could have acted as steppingstones for biotic dispersal between Madagascar and India-Laurasia. In this model, the fall in eustatic sea level, of as much as 250 m during the mid-Oligocene (Hutchison, 1989), caused shallower regions of the Indian Ocean to become emergent (Figure 3.27).

There is, however, a paucity of evidence; knowledge of the actual nature, extent and timing of connectivity between Madagascar, Africa, India and Laurasia in the Cretaceous and early Paleogene remains incomplete.

4.6 Oceanic dispersal

The oceanic dispersal of aplocheilids and etroplines appears unlikely at first glance, given that these fishes failed to cross even the relatively narrow Mozambique Channel that separates Madagascar from Africa. 'If dispersal is invoked to explain these disjunct distributions,' argued Sparks & Smith (2004), 'one must account for the presence of sister-group pairs on widely separated Gondwanan landmasses, and their concurrent absence from Africa and all intervening Indian Ocean islands of more recent (*e.g.*, volcanic Mascarenes) origin'. Sparks & Smith (2004) argued also that the distributions of the Aplocheilidae and Etroplinae are broadly consistent with the sequence of Gondwanan fragmentation (Figure 4.6).

In a review of all previous studies of this question, Matschiner (2019), while rejecting land bridges postdating the Madagascar-India split, invoked the high salinity tolerance of the Etroplinae to conclude that cichlids arrived in South Asia by oceanic dispersal. He supported this conclusion also with the argument that while Indian and African cichlids share the same *Enterogyrus* endoparasites, which have high salinity tolerance (Pariselle *et al.*, 2013; Vanhove *et al.*, 2016), they host different ectoparasites, which have low tolerance of salinity. Vanhove *et al.* (2016) suggested that these differences may be a consequence of prolonged exposure to high salinity during oceanic dispersal. Nevertheless, the fact that not one of the more than 1500 extant species of cichlids is a marine inhabitant weighs against this hypothesis. The fundamental problem for biogeographers is, if the crown group of cichlids evolved only in the Paleocene (*ca* 65–57 Mya), by which time India had been separated from Madagascar for more than 23 My, how did the ancestral etroplines get from Madagascar to India–Sri Lanka?

While this question remains to be answered definitively, Matschiner *et al.* (2020) offer a hypothesis that might explain the global distirbution of Cichlidae: 'An alternative hypothesis that is consistent with a young age of cichlids is the 'Independent colonization' scenario, according to which cichlids on all four landmasses [Asia, Africa, Madagascar and South America] independently evolved from a common marine ancestor that has since either gone extinct or remained undiscovered. This must have occurred before 45 Ma because the presence of freshwater cichlids by that time is well documented in the fossil record.'

As of now, the marine dispersal hypothesis appears to be the only one standing. It has been invoked to explain also the southern-hemisphere distribution of the freshwater-fish family Galaxiidae (Burridge *et al.*, 2012) which, like the Cichlidae, shows a topography suggestive of Gondwanan vicariance. A similar problem arises also in explaining how the ancestor of the Madagascan mantellid frogs—which are phylogenetically nested convincingly within an Asian clade—made the same transoceanic leap ~65 Mya (Meegaskumbura *et al.*, 2019; see Figure 3.70). Yuan *et al.* (2018) posited an island arc between India and Madagascar, and between India and Southeast Asia, to bridge the gaps. If, however, the split between Asian and Madagascan etroplines occurred as recently as ~36.0 (42.2–30.3) Mya as Friedman *et al.* (2013) estimate, marine dispersal will be the only plausible explanation for how the ancestor of *Etroplus* and *Pseudetroplus* reached Sri Lanka-India.

Thus, exactly how and when cichlids reached South Asia remains an open question. As observed by Parenti (2019) of the biogeography of fishes in general, '[The] modern biogeographical distributions of fishes reflect just remnants of once more complex and widespread distributions; they are incomplete spatial records, just as the fossil record is an incomplete temporal record. The ages of lineages known from fossils are underestimated and can only get older with new fossil discoveries.'

4.7 Ehiravini

The fresh and brackish-water clupeid tribe Ehiravini too, of which the genus *Ehirava* is restricted to Sri Lanka and southern India (Figure 4.7), shows a disjunct distribution that seems to call for a combination of vicariance and dispersal explanations. In addition to *Ehirava*, the Asian Ehiravini include *Dayella* (south-western India), *Clupeichthys* (Southeast Asia) and *Corica* (India, Thailand, Borneo), while *Sauvagella* and its sister group *Spratellomorpha* are restricted to Madagascar (Grande, 1985; Stiassny, 2002). A further genus, *Gilchristella*, is confined to South Africa. Given, however, that the clupeids (herrings and sardines) are preponderantly a marine family, the biogeography of Ehiravini has not attracted as much interest—or controversy—as has that of Cichlidae.

4.8 Freshwater-fish disjunctions: Southeast Asia

4.8.1 *Rasboroides-Horadandia.* As noted in the previous chapter, contact and biotic exchange between the Indian plate and the Sunda region may have commenced as early as 57 Mya. Cypriniformes had by then evolved and diversified in Asia (Chen *et al.*, 2013; Murray, 2020).

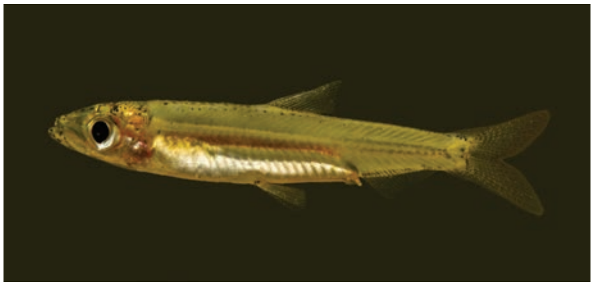

Figure 4.7. *Ehirava fluviatilis*, a clupeid common in Sri Lanka's estuaries and dry-zone reservoirs (Amarasinghe *et al.*, 2002). It is confined to Sri Lanka and South India, where it co-occurs with *Dayella malabarica*: the two species are similar and often confused (Whitehead, 1972).

Rasboroides (Figure 4.8), known from two species endemic to rain forests in the south-western lowlands of Sri Lanka, is the sister-group of *Horadandia*, a genus restricted to Sri Lanka and southernmost India (Sudasinghe *et al.*, 2018a). The morphological study of Liao *et al.* (2011)* too, recovered *Horadandia* as the sister group of *Rasboroides*, the pair comprising the sister group of the Southeast Asian *Trigonostigma* (Figure 4.8c), though this relationship was not supported by their strict-consensus tree.

In their molecular phylogeny of Danioninae based on both nuclear and mitochondrial DNA, however, Tang *et al.* (2010) recovered *Rasboroides* as the sister group of all Rasborini combined, excluding *Amblypharyngodon.* This implied that the morphological affinity between *Rasboroides* and *Trigonostigma* is the result of convergence rather than phylogenetic propinquity. The molecular analysis of Rüber *et al.* (2007), though failing to recover a sister-group relationship between *Horadandia* and *Trigonostigma,* dated their most recent common ancestor to about the time of the Oligocene-Miocene boundary. The relationships of *Rasboroides* and *Horadandia,* were more recently investigated in the mitogenomic study of Sholihah *et al.*, (2021b). They recovered *Amblypharyngodon* as sister to all Rasborinae, with *Horadandia* + *Rasboroides* as sister to all remaining Rasborinae. The split between *Horadandia* + *Rasboroides* and the remaining Rasborinae was timed by these authors to the late Eocene (~40 Mya); these fishes, therefore, descend from the earliest Asia-to-India+Sri Lanka freshwater-fish—or far that matter, vertebrate—dispersal

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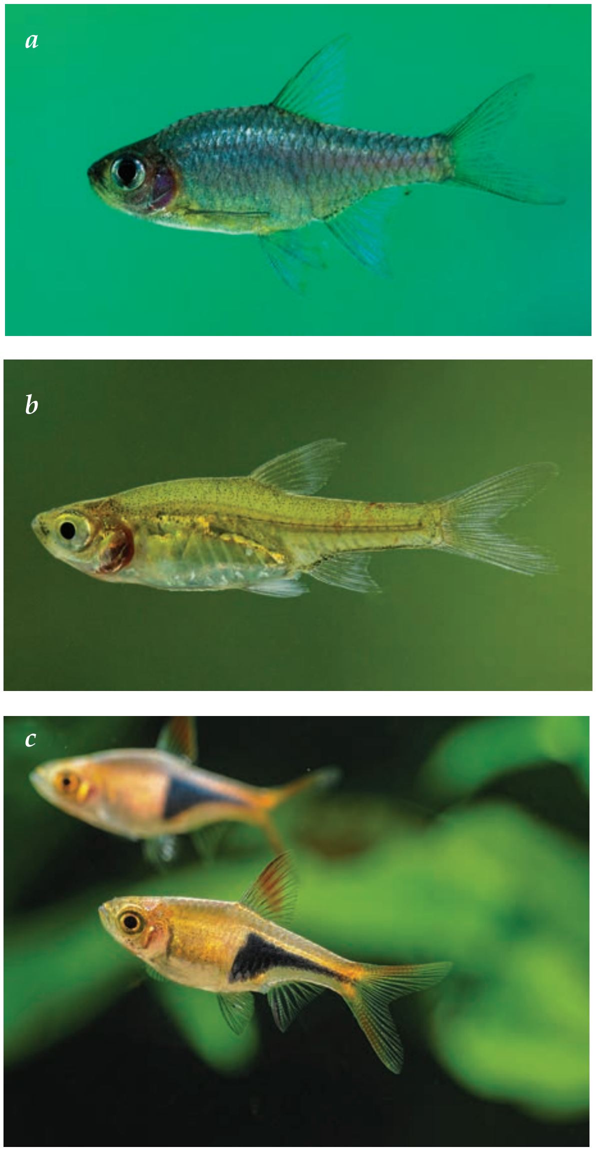
* Liao *et al.* (2011) reported *Rasboroides* and *Horadandia* to be the only rasborin genera to possess a frontoparietal fontanelle.



Tan Heok Hui

Figure 4.8. ***a,*** The genus *Rasboroides* (here, *R. pallidus*) is endemic to Sri Lanka and known from two species, which are the sister group of ***b,*** *Horadandia*, a genus confined to Sri Lanka and southern peninsular India. ***c,*** based on convergent morphology, *Trigonostigma* exhibits a sister-group relationship with *Rasboroides*+*Horadandia* in some maximum-parsimony trees (Liao *et al.*, 2011). The mitogenomic phylogeny of Sholihah *et al.* (2021b), however, recovered *Rasboroides* + *Horadandia* as the sister group of the Southeast Asian Rasborinae, with a divergence dating to around 40 Mya, in the late Eocene. They dated the split between *Rasboroides* and *Horadandia*, however, to the early Miocene.

known at this time. It was also at about this time that, in the second half of the Eocene (Miller *et al.*, 2011), sea level fell close to the present level, leading potentially to the first Cenozoic emergence of the Palk Isthmus.

The perhumid east-west corridor with less than four dry months, conducive to the exchange of rainforest-adapted taxa, which persisted between India and South-East Asia across the Ganges Valley from the middle Eocene to the Oligocene (Ashton, 2014: 391) ceased to exist some time prior to ~23 Mya (Ashton, 2014:412), with the exchange of freshwater fishes peaking at around 35 Mya and declining strongly since 15 Mya (Klaus *et al.*, 2016; see Figure 3.43b). Thus, by the Miocene, Chatterjee's partition (see 3.6.1) had begun to attenuate the dispersal of rainforest biotas between India and Southeast Asia. Such 'rain forest' lineages were subsequently extirpated on much of India, probably by increasing rainfall seasonality and Late Miocene aridification (Guleria, 1992; Rust *et al.*, 2010; Shukla *et al.*, 2013), but persisted within refugia in southwest Sri Lanka.

The sea level drop of up to 250 m below present at the Rupellian–Chattian boundary 28 Mya (Haq *et al.*, 1988; Hutchison, 1989) provided for a wide subaerial isthmus between Sri Lanka and southern India which, at the time, exhibited a perhumid climate (Morley, 2018). This facilitated the dispersal to Sri Lanka, perhaps for the first time, of rainforest-associated taxa, including *Pseudophilautus* shrub frogs (Meegaskumbura *et al.*, 2019) and among fishes, *Systomus* and *Belontia*, possibly together with ancestral *Malpulutta* and *Rasboroides*[*] (Rüber *et al.*, 2006; Sudasinghe *et al.*, 2020c). The isthmus was once again inundated during the Burdigalian Miocene, at latest (Epa *et al.*, 2012; Reuter *et al.*, 2021). By the beginning of the Pliocene, moist dipterocarp forests, which had persisted across India since the Eocene, were withdrawing to refugia in Sri Lanka's wet zone and the Western Ghats (Guleria, 1992; Rust *et al.*, 2010; Shukla *et al.*, 2013) as the climate of the south-eastern region of the peninsula and the north-western region of Sri

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[*] Sholihah *et al.* (2021) recovered a late Eocene split between *Rasboroides* + *Horandandia* and the Southeast Asian Rasborinae, which is consistent with this scenario. In their phylogeny, the *Rasboroides*-*Horandandia* split occurred at around the Oligocene-Miocene boundary.

Lanka became progressively more seasonal and arid, as it remains even today.

Thus, even though greatly lowered sea levels gave rise to a ~200-km-wide isthmus connecting India and Sri Lanka for much of the Plio-Pleistocene (Anonymous, 1977; Miller *et al.*, 2005; Figure 3.65), this appears to have served more as a filter* than a corridor for the dispersal of taxa adapted to rainforest environments (Bossuyt *et al.*, 2004; Sudasinghe *et al.*, 2020c; Reuter *et al.*, 2021). So it was, that the exchange of rainforest-adapted taxa between India and Sri Lanka ended prior to the Pliocene. The town of Mannar, which lies on the Sri Lankan side of the erstwhile Palk Isthmus, today receives a monthly average rainfall of less than 50 mm for more than half the year, whereas the island's perhumid south-west has no months with an average rainfall of less than 100 mm (Somasekaram *et al.*, 1988; see Figure 2.6).

4.8.2 *Belontia-Malpulutta.* The genus *Belontia*, with a species in Sri Lanka (*B. signata*) and another in the perhumid Sunda region (*B. hasselti*) (Figure 4.9), is altogether absent in the intervening area (India, Bangladesh and Myanmar). In their molecular phylogeny of the Anabantoidei, Rüber *et al.* (2006) estimated an Oligocene split between the two species (Figure 4.10), supported also by Wu *et al.* (2019). Interestingly, these analyses suggest also that *Malpulutta* + *Pseudosphromenus* (confined to Sri Lanka–South India; Figure 4.9) too, diverged from its Southeast Asian sister group *Macropodus* in the early Oligocene.

A handful of similar examples occurs also in the southern Western Ghats, such as *Channa diplogramma*, the uncannily similar sibling species of which, *C. micropeltes*, occurs only in the Malay Peninsula. Benziger *et al.* (2011) recovered a Miocene divergence between the two species (95 % HPD 21.8–9.5 Mya), consistent with the late-Miocene split estimated by Rüber *et al.* (2020). The distribution of the genus *Psilorhynchus* too, shows a similar disjunction, with some 20 species distributed in the Ganges-Brahmaputra river system and eastwards, with a single representative (*P. tenura)* restricted to the central Western Ghats (Arunachalam & Muralidharan, 2008). The Western Ghats lineage diverged from its northern sister group ~18 (95 % HPD: 26.3–11.2) Mya, in the early to mid-Miocene (Conway *et al.*, 2015).

The most credible biogeographic scenario that explains the disjunct distribution of the Sri Lankan and Southeast Asian *Belontia*, and between *Malpulutta* + *Pseudosphromenus* (restricted to south India and Sri Lanka) and the remaining Macropodusinae in Southeast Asia (*Betta, Macropodus, Parosphromenus* and *Trichopsis*), is an extensive former distribution between the two regions followed by an extirpation across the Indian Peninsula. In the case of those fishes associated with shaded rainforest streams and perennial wetlands, such an extirpation could have been caused by widespread aridification which, as already discussed, is inferred to have occurred in the Indian peninsula at the end of the Miocene.

It is noteworthy that *Rasboroides* is more dependent on a perhumid climate than *Belontia* and *Malpulutta,* which in turn occur in regions of higher rainfall than *Horadandia* and *Pseudosphromenus.* All three osphronemids have been recorded from the Deduru basin, in Sri Lanka's intermediate zone, between the dry zone and wet zone (see Figures 2.6, 2.11), which experiences a more seasonal weather pattern compared to the wet zone, to which *Rasboroides* is confined.

The divergence-time of ~28 (95 % HPD: 33–22) Mya between *Belontia signata* and its Southeast

Figure 4.9. ► ***a,*** *Belontia signata*, a Sri Lankan endemic; ***b,*** *Belontia hasselti*—the genus *Belontia* is confined to the perhumid Sunda region and Sri Lanka's wet zone (it is absent from India, Myanmar and Thailand). The Sri Lankan and Southeast Asian lineages were estimated by Rüber *et al.* (2006) to have diverged in the Oligocene. ***c,*** *Malpulutta kretseri*, a genus and species endemic to Sri Lanka's wet zone. ***d,*** *Pseudosphromenus cupanus*, confined to Sri Lanka and southern India. *Malpulutta* and *Pseudosphromenus* have a sister-group relationship, and together are the sister group of ***e,*** the Southeast Asian genus *Macropodus* (here *M. opercularis*). See Figure 4.10 for divergence times.

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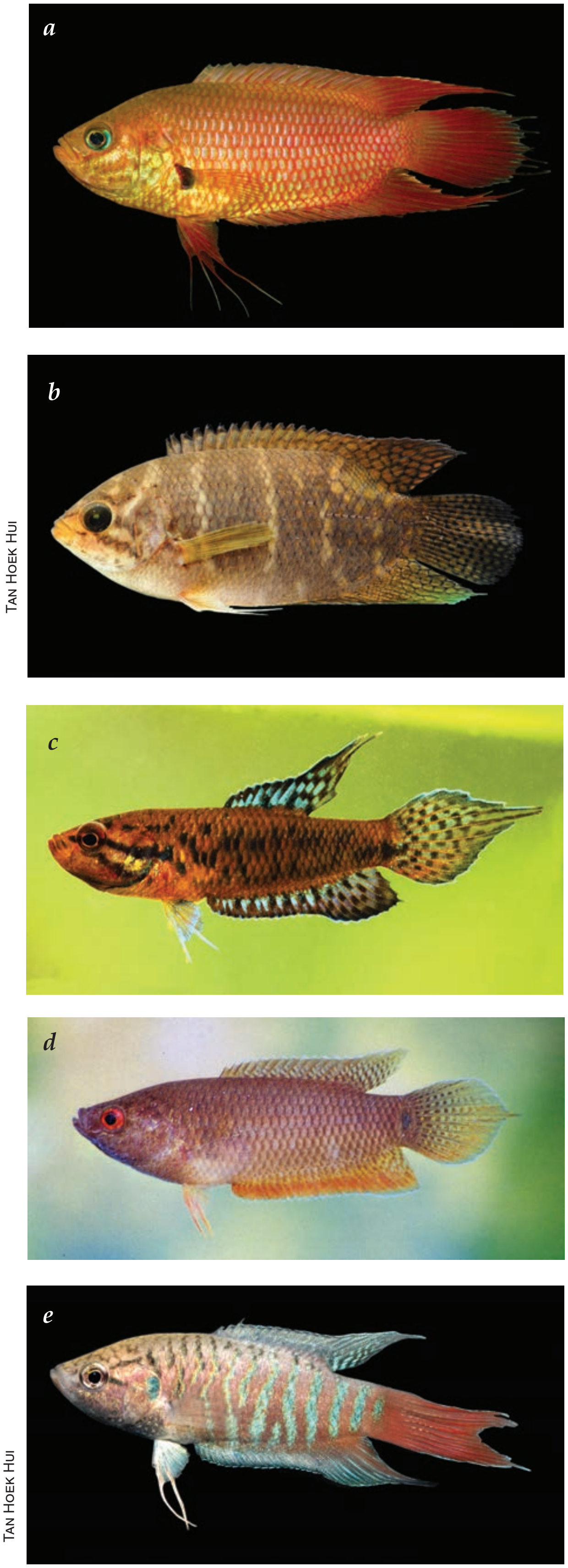
* Based on entirely different datasets, Sudasinghe *et al.* (2020c) and Reuter *et al.* (2021) converged on the idea that the Palk Isthmus served more as a 'filter' than as a conduit for biodiversity between India and Sri Lanka. 'Thus, even though greatly lowered sea levels gave rise to a ~200-km-wide isthmus connecting India and Sri Lanka for much of the Plio-Pleistocene (Anonymous, 1977; Miller *et al.*, 2005), this appears to have served more as a filter than a corridor for the dispersal of taxa adapted to perhumid forests': Sudasinghe *et al.* (2020c).



Asian sister-species, *B. hasseltii* (Rüber *et al.*, 2006; Figure 4.10) suggests, however, that their disjunctions occurred in the mid-Oligocene, first as a result of the biotic separation caused by the Chatterjee Partition, followed by an extirpation on India by the early Pliocene.

Aridification and increasing seasonality in India, except for the southern Western Ghats, is also the most plausible explanation for the large number of disjunct lineages occurring in the Western Ghats on the one side, and the eastern Himalaya and/or Southeast Asia on the other, which are absent from the intervening expanse of the Deccan (see 3.6.1). As articulated also by Gunnell (in Gunnell & Radhakrishna, 2001: 939), 'The high biodiversity and rate of endemism in the Southern Ghats does therefore not vindicate this region as being a centre of radiation within the Peninsula, but rather reflects its primary status as a particularly long-standing ecological refugium.' This applies equally to Sri Lanka's south-western wet zone quadrant. Lying within the intertropical convergence zone and benefiting also from orographic rainfall, Sri Lanka and the southern Western Ghats were able to serve as refugia for rainforest-adapted taxa, even if the climate of the latter was somewhat more seasonal than that of perhumid south-western Sri Lanka.

4.8.3 *Systomus.* The genus *Systomus*, which includes some 17 putatively valid species, ranges from Sri Lanka through India and the Malay Peninsula to Java. Pethiyagoda *et al.* (2012) showed *Systomus* to be monophyletic. While confirming this result, Yang *et al.* (2015), Ren & Mayden (2016) and Sudasinghe *et al.* (2020c) showed it to be also the sister group of the Afrotropical small barbs (hereafter, ASBs), a diversification of some 220 species. Several of the ASBs resemble *Systomus* in possessing both rostral and maxillary barbels and a last unbranched dorsal-fin ray that is stiff and posteriorly serrated, with some species exhibiting also a black lateral stripe (Figure 4.11) as exhibited by the Sri Lankan *S. pleurotaenia*.

Sudasinghe *et al.* (2020c) showed that four species of *Systomus* occur in Sri Lanka: *S. sarana*, a species widely distributed in the island and also across the Indian Peninsula, and three endemics, *S. asoka*, *S. pleurotaenia* and *S. martenstyni*.

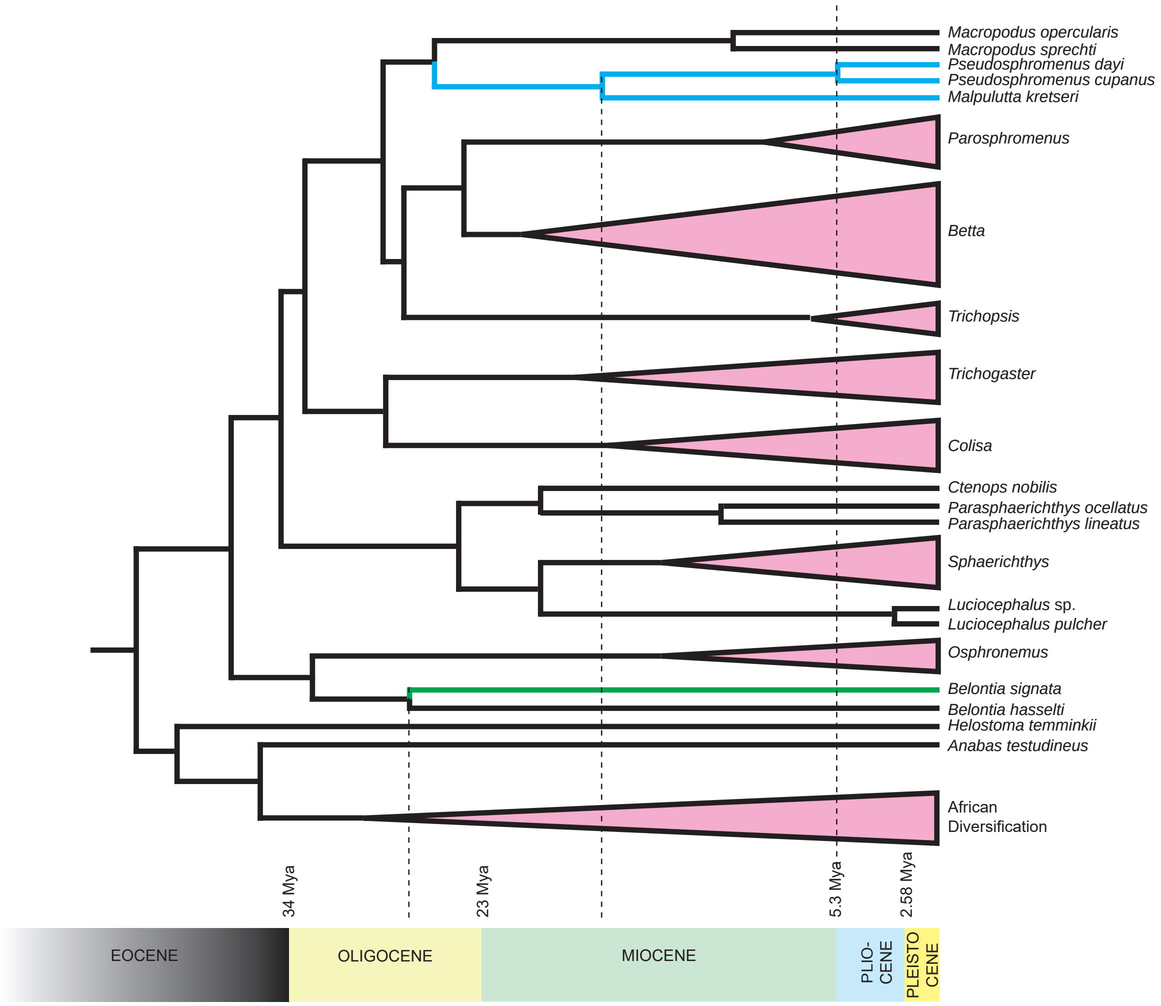


Figure 4.10. Chronogram of anabantoid diversification, based on Rüber *et al.* (2006, figure 7), showing the Oligocene divergence of the Sri Lanka-South Indian *Pseudosphromenus+Malpulutta* clade (blue) and the Sri Lankan *Belontia signata* (green) from their Southeast Asian sister-groups. For calibration intervals see Rüber *et al.* (2006: table 4 and figure 7).

The phylogeny constructed from the concatenated dataset of Sudasinghe *et al.* (2020c) suggests that the basal split between *Systomus* and the ASBs occurred 30 (95 % HPD 35.2–25.4) Mya[*], in the mid-Oligocene (see Figure 5.23). This is broadly consistent with the timings derived by Lavoué (2020) and Ren & Mayden (2016), who dated this split to between 30.5–23.0 Mya and 30.5–22.1 Mya (95 % HPD intervals), respectively. The collision of the Arabian and Eurasian plates, leading to the progressive opening of a terrestrial route between Eurasia and Africa across Arabia between the Late Eocene and mid-Miocene (Allen & Armstrong, 2008; Bialik *et al.*, 2019), intensified biotic exchange between Asia and Africa by the Burdigalian (Lavoué, 2020; McLoughlin, 2001; Sil *et al.*, 2020; Wu *et al.*, 2019). This supplied the first opportunities for Cyprinidae, which originated in Southeast Asia (Chen *et al.*, 2013), to disperse into Africa.

The Oligocene witnessed sea levels up to 250 m below present (Haq *et al.*, 1988; Hutchison, 1989), providing for a wide subaerial isthmus between Sri Lanka and southern India which, at the time, experienced a perhumid climate (Morley, 2018). This provided perhaps the first opportunity for dispersal to Sri Lanka of rainforest-associated taxa, and this window may have lasted, even if

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[*] The 95 % confidence intervals for this split, of 30.5–23.0 Mya (Lavoué *et al.*, 2020) and 30.5–22.1 Mya (Ren & Mayden, 2016), while somewhat later than that estimated by Sudasinghe *et al.* (2020c), nevertheless suggest a late-Oligocene divergence.

Johannes Pfleiderer

Figure 4.11. Members of the smiliogastrine clade that includes the Asian genus *Systomus* and the Afrotropical Small Barbs (ASBs). ***a–c,*** members of the endemic Sri Lankan diversification, which dates to the early Miocene: ***a,*** *Systomus asoka*, a species known only from two small, disjunct populations within the Kelani basin; ***b,*** *S. martenstyni*, which occurs only in streams draining the Knuckles Hills; and ***c,*** *S. pleurotaenia*, which has a wide distribution in the elevation range 20–480 m asl in the wet-zone's rivers and larger streams, from the Attanagalu to the Nilwala basins, inclusive. ***d,*** *Enteromius holotaenia* (image laterally inverted), an ASB with a wide distribution in tropical West Africa. *Enteromius* are a genus within the clade that forms the sister-group of *Systomus*. Like *S. pleurotaenia*, *E. holotaenia* too, exhibits a black midlateral band, possesses both rostral and maxillary barbels, and has a posteriorly serrated last unbranched dorsal-fin ray (Cutler *et al.*, 2019). Many ASBs lack all or some of these characters: see Armbruster *et al.* (2016) for a discussion of convergence *vs* shared evolutionary history in ASBs.

intermittently, until the Palk Isthmus underwent a protracted inundation during the Burdigalian Miocene (~20–16 Mya; Epa *et al.*, 2012; Reuter *et al.*, 2021). Such a scenario is consistent with the divergence times available for the dispersal to Sri Lanka of the most recent common ancestors of *Rasboroides-Horadandia, Belontia signata-B. hasseltii, Malpulutta-Pseudosphromenus,* the endemic diversification of *Systomus*, and the *Pseudophilautus* shrub frogs (Sudasinghe *et al.*, 2020c; Rüber *et al.*, 2006, 2007; Meegaskumbura *et al.*, 2019).

India-Sri Lanka dispersal continued through the Miocene, whenever the Palk Isthmus was emergent, but was increasingly inhibited as the climate of India grew more arid and seasonal through the Plio-Pleistocene (Guleria, 1992; Rust *et al.*, 2010; Shukla *et al.*, 2013). There is no evidence of fishes associated with a perhumid climate dispersing between India and Sri Lanka since then, though the Pliocene witnessed the immigration of a modest number of lineages associated with high rainfall (*e.g.*, see *Devario, Laubuka,* discussed in 5.4.2 and 5.4.4, below).

Thus, even though greatly lowered sea levels gave rise to a ~200-km wide isthmus connecting India and Sri Lanka for much of the Plio-Pleistocene (Anonymous, 1977; Miller *et al.*, 2005), this may have served more as a filter than a corridor for the dispersal of taxa associated with rain forests (Sudasinghe *et al.*, 2020c). Species adapted to life in the ephemeral rivers, ponds and swamps of floodplains, however, were able to disperse across the two landmasses whenever climate allowed.

The four Sri Lankan species of *Systomus* derive from at least two dispersal events. The earliest of these, dated to the early Miocene, involved the common ancestor of the endemics *S. asoka, S. pleurotaenia* and *S. martenstyni*, all of which are associated with regions of high rainfall and low seasonality. The subsequent events involved *S.*

sarana, a generalist species ubiquitous in the lowlands of Sri Lanka and Peninsular India. It occurs abundantly in the lowland floodplains of both the dry and the wet zones, as well as the lower regions of the central hills.

Of the subclade of *Systomus* that is endemic to Sri Lanka, two species are restricted to the island's southwestern wet zone (Figure 4.11). *Systomus asoka* occurs only in the Kelani basin, in the vicinity of Deraniyagala and Kitulgala. The second species, *S. pleurotaenia* ranges from the Attanagalu basin in the island's west to the Nilwala basin in the south. Both are habitat specialists and occur primarily in relatively large, deep, well-oxygenated streams and rivers traversing rain forests. The third species among the endemics is *S. martenstyni*, which is restricted to a part of the Mahaweli basin, principally to streams and rivers draining the Knuckles hills.

The crown age of the endemic subclade of *Systomus* associated with rain forests in Sri Lanka was estimated by Sudasinghe *et al.* (2020c) as 21.1 (95 % HPD: 26.3–15.7) Mya. Consistent with the dispersal model hypothesized above, it appears that having entered Sri Lanka via the Malwathu-Kala river system in the early Miocene, before the rise in sea level during the Burdigalian, an ancestral population went on to colonize the Knuckles Hills, as evidenced by *S. martenstyni*. Another population dispersed southwards, to colonize the foothill streams of the western wet zone (leading to *S. asoka* and *S. pleurotaenia*).

The central hills appear to have served as a barrier to dispersal between the Knuckles and south-western species. The Mahaweli and Kelani drain east to the Bay of Bengal and west to the Laccadive Sea, respectively. While they share a common boundary along a 600–2000 m-high, 40-km-long ridge between the Ginigathena and Horton Plains, the highest elevation at which the species of *Sytomus* occur is lower: *S. martenstyni*, 560 m; *S. pleurotaenia*, 380 m; and *S. asoka*, 70 m.

Although *S. martenstyni* and *S. asoka* resemble each other superficially (*cf.* Figure 4.11a,b), Sudasinghe *et al.* (2020c) showed the latter to be the sister species of *S. pleurotaenia*, which has a markedly different appearance (Figure 4.11c). Additionally, they dated the most recent common ancestor of *S. pleurotaenia* and *S. asoka* to 16.0 Mya (95 % HPD: 21.6–11.1 Mya). Based on groups investigated so far, these species of *Systomus* appear to represent the oldest diversification of freshwater fishes in Sri Lanka.

4.9 Plio-Pleistocene dispersal

The Pleistocene saw brief sea-level transgressions of up to 24 m above present levels (see Figure 3.63), inundating Sri Lanka's wet-zone floodplain, further isolating its rivers and reducing gene flow between them. The populations of freshwater-fish species shared between rivers show evidence of this isolation, *e.g.*, by exhibiting unique haplotypes. But the broad picture shows the island's fishes to comprise three distinct groups, with little evidence of 'Pleistocene species-pumping':

(1) relictual lineages deriving from the Eocene–Miocene dispersal, via India, of the rainforest-adapted Southeast Asian ancestors of *Malpulutta + Pseudosphromenus, Rasboroides + Horadandia, Belontia* and lineages such as the endemic diversification of *Systomus* and, perhaps, some clades presently in *Puntius*, such as *P. titteya.*

(2) a Plio-pleistocene dispersal of species adapted to life in open waters in southern India, giving rise to endemic diversifications, *e.g.*, in *Pethia, Devario, Laubuka* and *Rasbora.*

(3) a sharing of fishes associated with the dry zone floodplains of southeast India and Sri Lanka during the late Pleistocene or even the early Holocene, so long as the Palk Isthmus remained subaerial (*e.g.*, *Amblypharyngodon grandisquamis, Devario malabaricus, Esomus thermoicos, Lepidocephalichthys thermalis, Puntius dorsalis, P. chola, Rasbora dandia, R. microcephala, Mystus nanus, Channa kelaartii,* and *C. striata;* see 5.2).

The paucity of molecular studies in India, and the near absence of such studies focusing on the fishes of the south-eastern segment of the Indian peninsula, however, handicap the further analysis of the hypotheses at (2) and (3), above. Nevertheless, some progress has been possible, based on sampling largely within Sri Lanka in the context of available sequences from India.

SUPPLEMENT 6

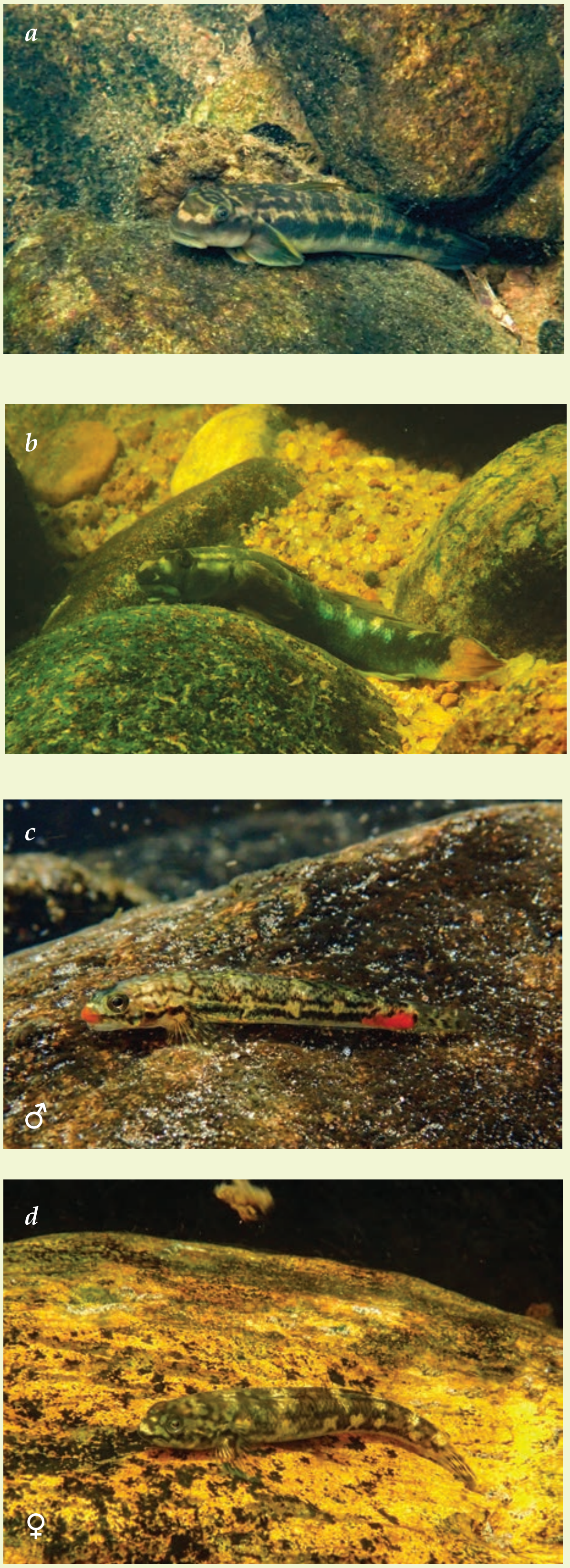
Gobies

It was not without misgivings that we elected to omit gobies (Figure S6.1) and anguillid eels from the checklist of freshwater fishes in Tables 5.1 and 5.2. This was necessary because these fishes are amphidromous and hence, capable of marine dispersal. Sri Lanka's freshwater-goby inventory, while exceeding that of the Western Ghats, is comparable to that of oceanic islands such as Madagascar, the Mascarenes and Seychelles (Máiz-Tomé *et al*., 2018).

Sicydiinae represent about half the goby species recorded from freshwaters above the tidal influence in Sri Lanka: *Sicyopterus griseus, Sicyopterus lagocephalus, Sicyopus jonklaasi* (Figure 4.12a–d), and *Stiphodon martenstyni*. The latter two species are considered endemic to Sri Lanka, and *Sicyopterus griseus* has been recorded from west-draining rivers in Kerala and southern Karnataka, India (Abraham *et al*., 2011), while *Sicyopterus lagocephalus*, the most widely distributed sicydiine, ranges from the Comoros Islands and Madagascar, across the tropical Indian Ocean, as far east as French Polynesia and as far north as southern Japan (Keith *et al*., 2015). *Stiphodon martenstyni* is known only from a single specimen, its holotype, collected at Atweltota in the Kalu basin in January 1981, together with *Sicyopus jonklaasi* (Watson, 1998). It has not been recorded since.

The island's sicydiines are usually reported only from the wet zone, from the Kelani to the Nilwala rivers, in the elevation range 25–270 m asl. However, we also recorded a single specimen each of *Sicyopterus griseus* and *Sicyopus jonklaasi* from the Deduru and Ma basins, respectively. Within the wet zone region, these fishes have a patchy distribution, occurring as small populations mainly in the cool, clear waters of foothill streams with a rock or pebble substrate (see Figure 2.16 a,b).

Sicydiinae appear to have evolved only as recently as the late Miocene (Keith *et al*., 2011; Taillebois *et al*., 2014), after speciose groups such as Cypriniformes had colonized India and Sri Lanka (Chapter 5). Keith *et al*. (2015) report that all sicydiines live their adult lives in freshwater, where they also reproduce. The larvae hatch in freshwa-



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ter and migrate to the sea, where they disperse by drift, finally metamorphosing several months later, upon reaching a suitable estuary, from where they ascend and colonize rivers once more.

Another goby, *Schismatogobius deraniyagalai* (Gobionellinae) (Figure 4.12e–f), occurs in foothill streams, though usually associated with sand substrates (Figure 2.17 a–c). This species too, has been shown to be amphidromous, with a reproductive cycle that may be similar to that of sicydiine gobies (Hans Horsthemke, pers. comm., in Pethiyagoda, 1991). It occurs also in rivers draining westward to the Arabian Sea in Karnataka, India (Arunachalam *et al*., 2014). The genus itself is distributed from Sri Lanka to Samoa, with *S. deraniyagalai* being the only species hitherto recorded from the western Indian Ocean (Keith *et al*., 2017).

The remaining species of gobies in Sri Lanka are ubiquitous in lowland streams and reservoirs in all climatic zones: *Awaous melanocephalus* (Gobionellinae) (Figure 4.12g), *Glossogobius giuris* and *G. celebius** (Gobiinae) (Figure 4.12f; Doug Hoese, pers. comm., states there appear to be other species of *Glossgobius* too, in Sri Lanka).

Glossogobius giuris has a wide distribution in countries bordering the tropical Indian Ocean, from South Africa and Madagascar, across India, Malaysia to China and northern Australia (Hoese & Hammer, 2021). *Glossogobius celebius* ranges from Sri Lanka to northern Papua (Hoese & Allen, 2011). The maximum elevation at which we recorded *Glossogobius* in Sri Lanka was 500 m asl.

The highest elevations from which we have recorded *Awaous melanocephalus* is 310 m asl. The species itself occurs from Sri Lanka and India across Southeast Asia to southern Japan. Both *Glossogobius* and *Awaous* are known to be amphidromous: they breed in freshwater but have marine larval and post-larval stages (Hoese & Allen, 2011; Yamasaki *et al*., 2011).

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* Hoese & Allen (2011) report specimens collected from a ‘Tributary of Giri Ganga [= Gin River], Hiniduma District’, well upstream of the tidal influence.

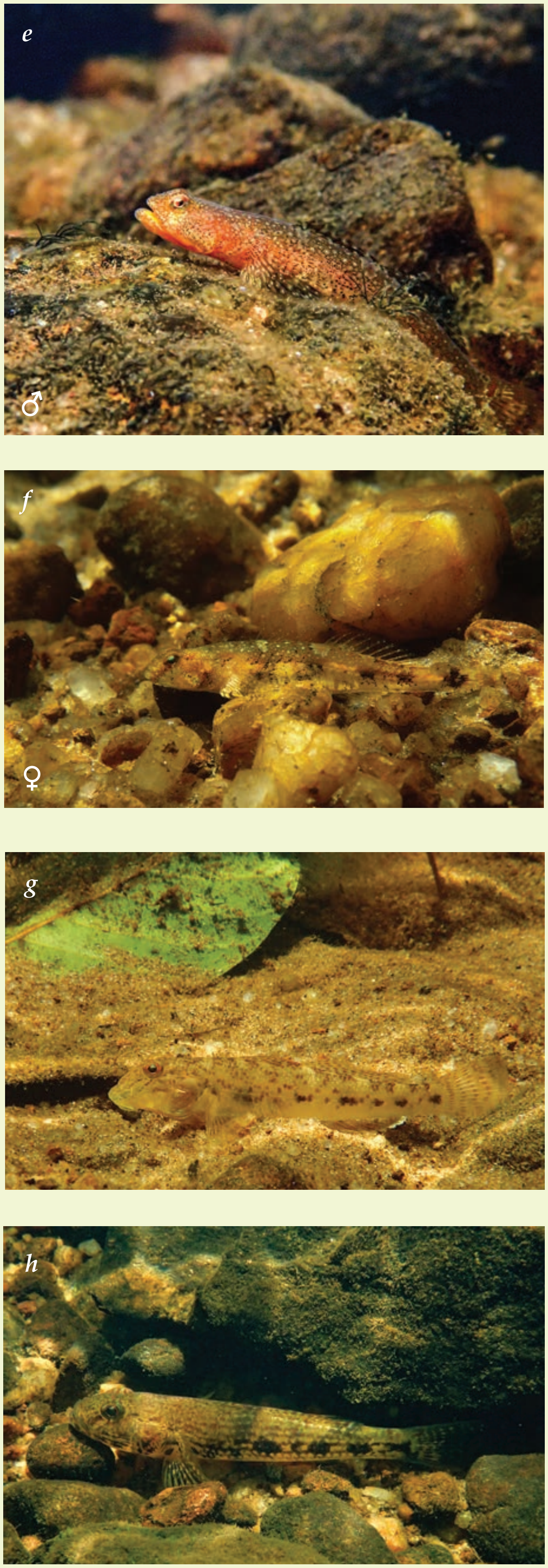

Figure S6.1. Sri Lankan freshwater gobies. ***a***, *Sicyopterus griseus*[1]; ***b***, *Sicyopterus lagocephalus*[2]; ***c***, ***d***, *Sicyopus jonklaasi*, male[3] and female[2], respectively; ***e***, ***f***, *Schismatogobius deraniyagalai*[1], male and female, respectively; ***g***, *Awaous melanocephalus*[1]; and ***g***, *Glossogobius* sp[1]. Superscripts indicate locations: 1, Pahiyangala, Kalu basin; 2, Gilimale, Kalu basin; 3, Athwelthota, Kalu basin.

5

Distribution and phylogeography

5.1 Routes of dispersal into Sri Lanka

As explained in the previous chapter, the only route by which freshwater fishes could disperse from India to Sri Lanka was via the Palk Isthmus, whenever it was exposed as a result of depressed sea level. Even when these conditions were met, it was additionally necessary that the climate of the isthmus was such that it supported the habitats—*e.g.*, rivers, substrates, wetlands, uplands, shade—required by the diverse assemblage of fishes which inhabited the aquatic ecosystems of southern India.

The topography of Sri Lanka's paleodrainages remains largely unknown. The rivers that now drain towards the erstwhile Isthmus are the Malwathu and the Kala (Figure 5.1). Based on geomorphological evidence, Deraniyagala (1958) posited that these two rivers had been confluent at least until the Pleistocene, forming a unified paleodrainage that was confluent also with the Mahaweli, or the part of it that drains the northern slopes of the Knuckles Hills.

The Kala and Malwathu rivers each discharges more than 500×10^6 m^{3}y^{-1} of water toward the now-submerged Palk Isthmus even now (Somasekaram *et al.*, 1988). On the Indian side, the Vaigai and Tamiraparani Rivers have their headwaters in mountain streams above 800 m elevation (Ramkumar *et al.*, 2019). If these Sri Lankan and Indian drainages coalesced on the Palk Isthmus, as the model of Ramasamy & Saravanavel (2019) suggests, they would have provided hydrological connectivity between the southernmost ranges of the Western Ghats and the northernmost hill streams of the Knuckles (Figure 5.1).

There was thus an early (Pliocene?) hydrological connection between the Knuckles Hills of Sri Lanka and the South Indian Vaigai-Tamiraparani system. In the course of the Pleistocene, however, the Knuckles came to drain almost exclusively to the Mahaweli, eastwards into the Bay of Bengal, while the Malwathu-Kala system derived its headwaters from low hills (< 870 m asl: Iresh, 2020) that border the northern Knuckles foothills and drained west, towards the Palk Isthmus. What is more, before reaching the Isthmus (or now, the sea) both these rivers traverse the lowlands of the island's first peneplain. The end-year rainy season sees vast areas of their deltas inundated and transformed into a floodplain, providing a mechanism for inter-basin dispersal of fishes.

The submarine topography of Palk Bay suggests that Adam's Bridge, the chain of shoals and sandbanks that now extends from the Mannar Peninsula of north-western Sri Lanka to the Rameshwaram Peninsula of south-eastern India, was a range of low hills during phases of lowered sea level. These hills fringed the southern littoral of

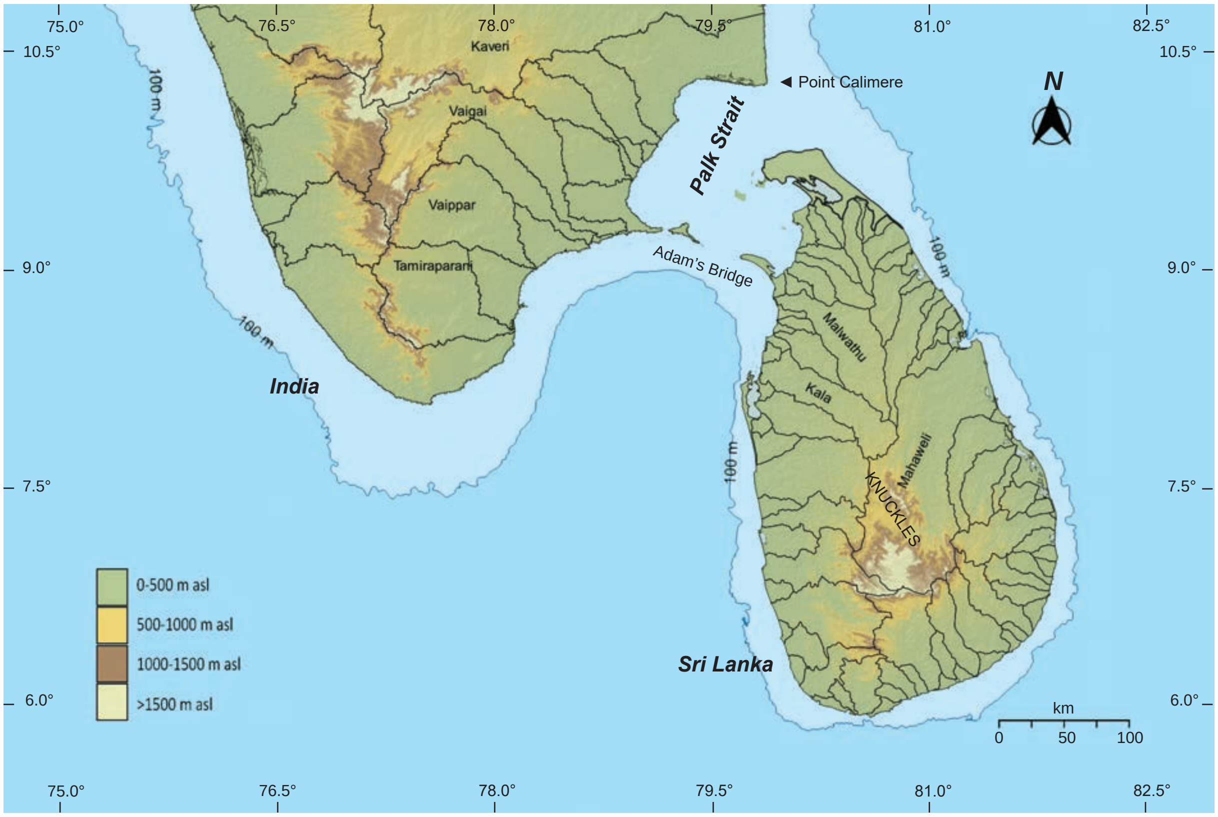

Figure 5.1. The principal eastern drainages of southernmost India: Cauvery (Kaveri), Tamiraparani and Vaigai, showing also the principal north-eastern rivers of Sri Lanka, the Malwathu and Kala rivers. Ramasamy & Saravanavel (2019) chart the now-submerged courses of the Tamiraparani and Vaigai Rivers during the Pleistsocene sea-level low-stands. The Malwathu and Kala rivers too, flowed into the same basin, and the former, especially, was likely confluent with the Tamiraparani during periods when the isthmus was emergent. There is evidence that the Knuckles Hills drained at least in part to the Malwathu-Kala during the Plio-Pleistocene, providing hydrological connectivity with southeast India. At times when the Palk Isthmus was emergent, Adam's Bridge was a chain of low hills bordering the southern littoral of the isthmus, into which the Cauvery, Vaigai and Tamiraparani rivers of India debouched. The hydrology of the northern palaeodrainages of the isthmus, however, remains unknown.

the isthmus. To their northeast was a vast plain that extended beyond the line connecting Point Calimere to Point Pedro, Sri Lanka's northernmost point (Figure 5.1). The sea in this region is shallow, rarely more than 10 m deep (Anonymous, 1977; George & Kumar, 2019), suggestive of a topography much like Sri Lanka's northern dry zone plain. Although the river systems of this plain are unknown, present-day topography suggests that India's Cauvery River too, may have drained into this plain. Such arid regions are able to support relatively high levels of biodiversity if they are topographically heterogeneous or have regions of high elevation (Šmíd *et al.*, 2021). The Palk Isthmus had neither, and was, hence, perhaps less able to support a biota even as rich as the dry zones of northern Sri Lanka and southern India during much of the Plio-Pleistocene.

Compared to the dry zone (rainfall < 1.8 m·y^{-1}), the south-western wet zone (rainfall > 2.5 m·y^{-1}) is substantially more topographically complex (see Figures 2.1, 2.6). While its rivers too, enter the sea via a coastal floodplain, this is much less wide. Further, most endemic fishes are confined to the wet zone, and associated with hard-substrate clearwater streams draining rain forests on the slopes of foothills. These species show limited ability to disperse between adjacent basins via the floodplain (see case studies at 5.4). Endemics adapted to life in slow-flowing streams in the lowlands (*e.g.*, *Puntius titteya, Mystus ankutta*), however, show a greater propensity to disperse between basins. Very few of Sri Lanka's endemic fishes (*e.g.*, the synbranchid *Ophichthys desilvai*) are confined to the swampy, lentic habitats of the floodplain.

5.2 Sri Lankan ichthyogeography: a brief review

The origin, speciation and distribution of freshwater fishes within Sri Lanka was first studied by Silas (1952a), who identified three 'ecological zones': (1) sluggish waters, (2) fluviatile or lacustrine waters and (3) torrential waters. Pethiyagoda (1991: 31) showed these zones to be of limited value in explaining the distribution of freshwater fishes in the island, and they are not further discussed here.

Senanayake (1980) was the first to attempt an investigation of the patterns of distribution of freshwater fishes within Sri Lanka based on a survey. He overlaid distribution data on the island's ichthyofauna not just on its river basins but also its broad topography, the three plains of erosion or 'peneplains' as conceived by Adams (1929) and Wadia (1943). These occupy the following approximate elevation ranges: (1) 0–125 m; (2) 125–750 m; and (3) 750–2500 m. A few peaks and valleys within each peneplain, however, transgress these limits.

Based on this analysis, Senanayake (1980) proposed three 'ichthyofaunal provinces': the South-western Province, the Dry Zone Province, and the Mahaweli Drainage Province, in addition to a Montane Zone (Figure 5.2). He showed each of these regions to contain distinct ichthyofaunal elements within a background of shared species. Notwithstanding the revisions in taxonomy that Sri Lanka's freshwater fishes have undergone in the past four decades, resulting in changes to the list of species considered endemic to the island, Senanayake's provinces continue to retain their identity. The wet zone, dry zone and Mahaweli basin each do have species confined to them. The ichthyofauna of the Montane Zone, however, is notably depauperate (discussed in sections 5.4.2 and 5.4.3, below).

But the sampling that has taken place since has resulted in the availability of distribution data at a much finer spatial scale. The taxonomy and systematics of the fishes too, have undergone substantial revision, providing for improved biogeographical analysis. The results presented in this chapter are based on the collection of the Wildlife Heritage Trust, now at the National Museum of Colombo, and records derived from fieldwork by Sudasinghe *et al*. 2014–2019, encompassing the island's major climatic, vegetational and hydrological units. We report on this dataset, summarized in Tables 5.1 and 5.2, and in section 5.3, below.

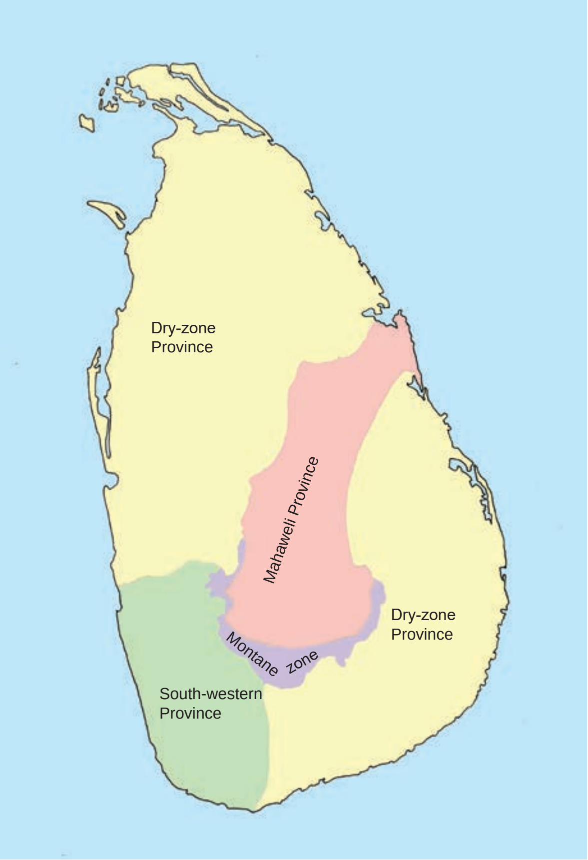

Figure 5.2. The ichthyological provinces, each of which hosts a distinct assemblage of fishes, identified by Senanayake (1980).

Senanayake's (1980) dataset is, nevertheless, of substantial value. Consider, for example, his observations on the freshwater fishes of the Jaffna Peninsula. This 'peninsula' is in effect an island separated from the mainland by a shallow lagoon (Figure 2.1). It is now connected to the Sri Lankan mainland by two causeways. Although Jaffna lies within the dry zone (its climate is arid by even the xeric standards of the dry zone: Figure 2.6) the Peninsula is unusual in that it lacks perennial streams, rivers or natural surface-water bodies: the only permanent surface waters are saline lagoons. Its freshwater fishes appear to depend largely on estuaries as drought refugia. Although small bodies of standing freshwater appear as temporary ponds and channels during the rainy months (October–December: Figure 2.6), the entire peninsula often loses its surface water in the course of the long dry season, during which the local people depend on water extracted from aquifers. The only bodies of open, inland water are the lagoons and a handful of villus (see section 2.6.4), the salinity of which varies according to rainfall.

Nevertheless, Senanayake (1980) recorded 15 species of indigenous freshwater fishes from the Jaffna peninsula. Perhaps more importantly, he also sampled fishes on Velanai ('Kayts'), an islet separated from Jaffna by some two kilometres of shallow sea. Freshwater fishes he recorded from there included *Amblypharyngodon grandisquamis, Puntius vittatus, Rasbora dandia, Systomus sarana, Anabas testudineus, Pseudetroplus maculatus, Oryzias* sp. and *Mystus gulio*.

Jaffna and Velanai serve as examples of what conditions on the Palk Isthmus may have been like at the end of the Pleistocene: a xeric landscape that could nevertheless support freshwater fishes associated with an ephemeral hydrology. Piet (1998b) pointed out that some of these fishes are adapted to surviving in drying pool beds, for example, by lubricating their gills with mucus to prevent collapse.

Senanayake was followed by Pethiyagoda (1991: 17), who provided an analysis of Sri Lanka's inland fishes according to their presence or absence in: (1) foothills and above; (2) lowland fluviatile regions; (3) lowland swamps and reservoirs; (4) brackish water (lagoons and estuaries); (5) wet zone; (6) dry zone; (7) Kelani basin; (8) Kalu basin; (9) Gin basin; (10): Nilwala basin; (11) Mahaweli basin; (12) 0–100m elevation; (13) 100–600 m; (14) 600–1000m; (15) > 1000 m. He showed that in all the river basins mentioned, the highest number of freshwater-fish species occurs in the 0–100 m elevation range, though in the case of endemics, a plurality occurs between the 100 and 600 m contours. Diversity then declines progressively in the 600–1000 m and >1000 m elevation ranges. This is broadly consistent with the findings of Senanayake (1980). Pethiyagoda (1991) also found (his table 2.6) that the inland fish faunas of the wet zone drainages (Kelani, Kalu, Gin and Nilwala) were much more similar to one another than any of them was to the Mahaweli, inferring from this that the central hills had served as a barrier to dispersal between the Knuckles (Mahaweli) and the south-western drainages[*]. However, he also drew attention to the Knuckles as an important centre of endemism within Senanayake's (1980) Mahaweli province, concluding: 'Thus, the Knuckles range lays a better and more clearly defined claim to recognition as an ichthyofaunal province than does the Mahaweli basin in its entirety. While the wet zone of the Mahaweli basin has a rainfall of < 3000 mm·y^{-1} the Knuckles are much wetter (> 4000 mm·y^{-1}) and compare well in terms of habitats with the southwestern province. The Knuckles therefore deserves recognition at least as a 'land island' biotope of special interest, if not an ichthyofaunal province (see also Wijewansa, 1988).'

5.3 Distribution of fishes within the island

Table 5.1 lists the 78 putatively hololimnic[†] fish species in Sri Lanka, together with the river basins from which they have been recorded. 'Absence data' in Table 5.1 should not be interpreted to mean that the species does not occur in a given basin, though this is probably the case for the larger basins that have benefited from greater sampling effort: Kelani, Kalu, Bentara, Gin, Nilwala, Mahaweli and Attanagalu.

These data allow several inferences to be made with regard to the spatial distribution of diversity and endemism. Consistent with the results of Senanayake (1980) and Pethiyagoda (1991), the present data too (Table 5.2), show that the wet zone contains the larger number of species (70), followed by the intermediate (46) and dry (36) zones. The last has only a single species, *Labeo lankae*, confined to it. Further, the discovery of two endemic species (*Rasbora adisi* and *Laubuka hema*)

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[*] Some species, such as *Belontia signata*, *Clarias brachysoma* and *Channa orientalis* (see section 5.4.9, below) however, were able to disperse at least once across this barrier.

[†] Species which obligatorily complete their life cycle in freshwaters. See Table 5.3 for a list of other fishes that occur in freshwaters, some of which too, are able to complete their life cycle in freshwater though they are evidently capable of marine dispersal as well.

Table 5.1. Distribution of the 78 species of fishes that obligatorily complete their life cycle in freshwaters in Sri Lanka, based on the collections of the WHT collection in the National Museum of Sri Lanka and the survey of Sudasinghe *et al.*, 2014–2019. Species endemic to Sri Lanka are preceded by an asterisk. For location of river basins, see Figure 2.11. Symbols: + (recorded); - (not recorded); ? (not yet recorded but likely to occur: included in totals); □ (introduced population: not included in totals); ● (confined to a single basin).

	Kelani	Bolgoda	Kalu	Bentara	Madu	Gin	Polwatta	Nilwala	Kirama	Urubokka	Walawe	Malala	Kirindi	Menik	Kumbukkan	Wila	Karanda	Ambalam	Gal	Andella	Magalavatavan	Mundeni	Maduru	Mahaweli	Pankulam	Yan	Mee	Ma	Kanakarayan	Mandekal	Parangi	Malwathu	Kal	Kala	Mi	Deduru	Karambalan	Maha	Attanagalu
	1	2	3	4	5	9	11	12	14	16	18	20	22	26	31	35	37	43	44	45	51	52	54	60	64	67	68	69	81	84	88	90	91	93	95	99	100	102	103
Cobitidae																																							
* *Lepidocephalichthys jonklaasi*	?	-	+	?	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lepidocephalichthys thermalis	+	+	+	+	+	+	?	+	+	?	+	?	+	+	+	+	?	?	+	?	+	+	?	+	+	?	?	?	?	+	+	+	?	+	+	+	+	+	+
Nemacheilidae																																							
* *Paracanthocobitis urophthalma*	+	-	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
* *Schistura notostigma*	+	-	+	+	+	+	+	+	?	+	+	-	?	+	+	-	-	-	+	-	-	-	?	+	-	-	-	-	-	-	-	-	-	-	-	?	-	+	+
* *Schistura madhavai*	-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Schistura scripta*	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinidae																																							
* *Amblypharyngodon grandisquamis*	+	+	+	?	+	?	?	+	?	?	+	?	+	+	+	+	?	?	+	?	?	+	+	+	+	+	?	+	+	?	+	+	+	+	+	+	+	?	+
Dawkinsia filamentosa	+	+	+	+	+	+	?	+	?	?	+	+	+	+	+	+	?	?	+	?	+	+	+	+	?	+	?	+	+	?	+	+	?	+	+	+	?	+	+
* *Dawkinsia srilankensis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Devario malabaricus	+	+	+	+	+	+	?	?	?	?	+	?	+	+	+	?	?	?	+	?	+	+	+	+	?	?	?	?	+	?	+	+	+	+	+	+	?	+	+
* *Devario memorialis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	-
* *Devario micronema*	+	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Devario monticola*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Devario pathirana*	-	-	-	-	-	-	-	●	-	-	□	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Esomus thermoicos	+	+	+	?	?	+	?	+	?	?	+	+	+	+	+	+	?	?	+	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
* *Garra ceylonensis*	+	-	+	+	-	+	-	+	+	-	+	-	+	+	+	+	-	-	+	-	-	+	+	+	-	-	-	-	-	-	+	+	-	+	-	+	-	+	+
* *Horadandia atukorali*	+	+	+	?	+	?	?	?	?	?	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	?	+	+	+	?	?	+
* *Labeo fisheri*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Labeo heladiva*	+	?	+	?	?	?	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	?	+	+	?	?	?	?	?	?	+	+	?	+	?	?	?	+	+
* *Labeo lankae*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	-	-	-	-
* *Laubuka hema*[¶]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Laubuka lankensis*	-	-	-	-	-	-	-	-	-	-	+	?	?	+	+	+	?	?	+	?	+	+	?	+	?	?	?	?	?	?	+	+	?	+	+	+	?	?	-
* *Laubuka varuna*	+	-	+	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
* *Pethia bandula*	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Pethia cumingii*	-	-	+	+	-	+	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Pethia melanomaculata*	-	-	-	-	-	-	-	-	-	-	?	?	?	?	+	+	?	?	+	?	?	+	?	+	?	?	?	?	?	?	?	+	?	+	?	?	-	-	-
* *Pethia nigrofasciata*	+	-	+	+	-	+	-	+	+	?	+	-	-	-	-	-	-	-	-	-	-	-	-	□	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
* *Pethia reval*	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	□	-	-	-	-	-	-	-	-	-	-	-	+	?	+	+
Puntius bimaculatus	+	+	+	+	?	+	?	+	?	+	+	?	+	+	+	+	?	?	+	?	+	+	+	+	?	?	?	?	?	?	?	+	?	+	+	+	?	+	+
Puntius thermalis	+	+	+	?	+	+	?	+	?	?	+	+	+	+	+	+	?	?	+	?	?	+	+	+	?	+	?	+	+	?	+	+	+	+	+	+	+	?	+

Continued …

Table 5.1 continued.

	Kelani	Bolgoda	Kalu	Bentara	Madu	Gin	Polwatta	Nilwala	Kirama	Urubokka	Walawe	Malala	Kirindi	Menik	Kumbukkan	Wila	Karanda	Ambalam	Gal	Andella	Magalavatavan	Mundeni	Maduru	Mahaweli	Pankulam	Yan	Mee	Ma	Kanakarayan	Mandekal	Parangi	Malwathu	Kal	Kala	Mi	Deduru	Karambalan	Maha	Attanagalu
	1	2	3	4	5	9	11	12	14	16	18	20	22	26	31	35	37	43	44	45	51	52	54	60	64	67	68	69	81	84	88	90	91	93	95	99	100	102	103
Puntius dorsalis	+	+	+	+	+	+	?	+	?	?	+	+	+	+	+	+	+	?	+	?	+	+	+	+	+	+	?	+	+	?	+	+	+	+	+	+	+	+	+
* *Puntius kamalika*	+	+	+	+	?	+	?	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	?	?	?	?	?	?	+
* *Puntius kelumi*	+	-	+	+	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
* *Puntius titteya*	+	+	+	+	-	+	-	+	-	-	□	-	-	-	-	-	-	-	-	-	-	-	-	□	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Puntius vittatus	+	+	+	+	+	+	?	+	?	?	?	?	?	?	?	+	+	?	?	+	?	+	+	+	?	+	+	+	?	+	+	+	+	+	+	+	+	?	+
* *Rasbora adisi*	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	?	?	+	?	+	+	+	+	+	+	?	+	-	-	-	-	-	-	-	-	-	-	-
* *Rasbora armitagei*	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rasbora dandia	+	+	+	+	+	+	?	+	?	+	+	?	+	+	+	?	?	?	+	?	?	+	?	+	?	?	?	?	?	?	+	+	?	+	+	+	?	?	+
Rasbora microcephala	+	+	+	+	+	+	?	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+	?	+	+
* *Rasbora naggsi*	-	-	+	-	-	+	-	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Rasbora wilpita*	?	-	+	+	-	+	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Rasboroides pallidus*	-	-	+	+	-	+	-	+	-	-	□	-	-	-	-	-	-	-	-	-	-	-	-	□	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Rasboroides vaterifloris*	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Systomus asoka*	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Systomus martenstyni*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Systomus pleurotaenia*	+	-	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Systomus sarana	+	+	+	+	+	+	?	+	+	?	+	+	+	+	+	+	?	?	+	?	+	+	+	+	+	?	?	+	+	?	+	+	+	+	?	+	?	?	+
Tor khudree	+	-	+	+	-	+	-	+	-	-	+	-	+	?	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	?
Bagridae																																							
* *Mystus ankutta*	+	-	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
* *Mystus nanus*	+	+	+	+	+	+	?	+	?	?	+	?	+	+	+	+	?	?	+	?	?	+	?	+	+	?	?	+	+	?	+	+	+	+	+	+	+	?	+
* *Mystus zeylanicus*	+	+	+	?	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	?	?	?	?	+	?	?	?	?	?	?	?	+	?	+	+	+	?	+	+
Siluridae																																							
* *Ompok argestes*	+	+	+	+	?	+	?	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	?	?	+
* *Ompok ceylonensis*	-	-	-	-	-	-	-	-	-	-	+	?	+	+	+	?	?	?	+	?	?	+	?	+	?	?	?	?	?	?	?	+	?	+	-	-	-	-	-
Wallago attu	+	-	?	-	-	?	-	?	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	+	-	?	-	-	-	-	-	+	-	?	-	?	?	+	+
Heteropneustidae																																							
Heteropneustes fossilis	+	+	+	+	+	+	?	+	?	?	?	?	+	?	?	+	?	?	?	?	?	+	?	+	?	?	?	?	+	?	?	+	?	+	+	+	+	?	+
Clariidae																																							
* *Clarias brachysoma*	+	+	+	+	?	+	?	+	-	-	?	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Aplocheilidae																																							
* *Aplocheilus dayi*	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Aplocheilus parvus	+	+	+	+	+	+	?	?	?	?	?	?	?	?	+	?	+	+	?	+	?	+	?	+	?	+	?	?	?	+	?	+	?	+	+	+	+	+	+
* *Aplocheilus werneri*	-	-	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Continued …

Table 5.1 continued.

	Kelani 1	Bolgoda 2	Kalu 3	Bentara 4	Madu 5	Gin 9	Polwatta 11	Nilwala 12	Kirama 14	Urubokka 16	Walawe 18	Malala 20	Kirindi 22	Menik 26	Kumbukkan 31	Wila 35	Karanda 37	Ambalam 43	Gal 44	Andella 45	Magalavatavan 51	Mundeni 52	Maduru 54	Mahaweli 60	Pankulam 64	Yan 67	Mee 68	Ma 69	Kanakarayan 81	Mandekal 84	Parangi 88	Malwathu 90	Kal 91	Kala 93	Mi 95	Deduru 99	Karambalan 100	Maha 102	Attanagalu 103
Syngnathidae																																							
Lophocampus ocellatus	+	?	?	?	?	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Synbranchidae																																							
* *Ophichthys desilvai*	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Ophisternon bengalense	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Mastacembelidae																																							
* *Macrognathus pentophthalmos*	?	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mastacembelus armatus	+	?	+	+	?	+	?	+	?	?	?	?	?	?	?	?	?	?	+	?	?	+	+	+	?	?	?	?	?	?	?	+	?	+	+	+	?	+	+
Cichlidae																																							
Etroplus suratensis	+	+	+	?	?	+	?	+	?	+	?	?	?	?	?	?	+	?	?	?	?	?	+	+	+	+	?	+	?	?	?	+	?	+	+	+	+	?	+
Pseudetroplus maculatus	?	+	?	?	?	+	?	?	?	?	?	?	?	?	+	+	+	?	?	?	?	+	+	+	?	+	+	?	+	+	+	+	?	+	+	+	?	?	+
Anabantidae																																							
Anabas testudineus	+	+	+	?	?	+	?	+	?	?	?	?	?	?	?	+	?	?	?	?	?	+	?	+	?	?	?	?	?	?	?	+	?	+	+	+	+	?	+
Osphronemidae																																							
* *Belontia signata*	+	-	+	+	-	+	-	+	+	-	+	-	?	?	?	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	?	+
* *Malpulutta kretseri*	?	-	+	+	-	+	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-
Pseudosphromenus cupanus	+	+	+	+	+	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	+	?	?	?	?	?	+	?	+	?	+	+	?	?	?	+
Channidae																																							
* *Channa ara*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
* *Channa* cf. *ara*[†]	+	-	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Channa kelaartii	+	+	+	+	+	+	?	+	?	?	+	?	+	+	+	+	?	?	+	?	+	+	?	+	?	?	?	?	?	?	?	+	?	?	?	+	?	+	+
Channa marulius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	-	-	-	-
* *Channa orientalis*	+	+	+	+	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Channa punctata	+	+	+	+	+	+	?	+	?	?	+	?	+	?	?	?	?	?	?	?	?	+	?	+	?	?	?	?	?	?	?	+	?	+	+	?	?	?	+
Channa striata	+	+	?	+	+	?	?	+	?	?	?	?	+	?	?	?	?	?	?	?	+	+	+	+	?	+	?	+	+	?	+	+	?	+	?	+	+	?	+
Total species[‡]	49		50	40		48		41																41															43
Total endemics[‡]	26		30	23		26		24																20															21

Notes

† The morphologically distinct but genetically ambiguous wet zone form given this label by Sudasinghe *et al.*, 2020b.

‡ Totals are given only for the seven most densely sampled basins.

¶ Our data shows this species to be confined to the Gal basin except for a single specimen recorded from Mahaweli, which appear to be the result of an upland river capture event between the Mahaweli and Gal basins.

Table 5.2. Freshwater fishes of Sri Lanka, showing association with climatic zone (DZ, dry zone, rainfall < 1.8 $m \cdot y^{-1}$; IZ, intermediate zone, rainfall 1.8–2.5 $m \cdot y^{-1}$; WZ, wet zone, rainfall > 2.5 $m \cdot y^{-1}$), and the minimum and maximum elevation (metres above sea level, rounded to the nearest 5 m) at which the species was recorded by the present authors. Symbols: + recorded; - not recorded; ? not recorded but likely to occur. Endemics are indicated by an asterisk, with species whose distribution in Sri Lanka suggests that they are likely to occur also in south-eastern India marked §. Footnotes are at bottom of next page.

	IZ	DZ	WZ	MIN	MAX
Cobitidae					
* *Lepidocephalichthys jonklaasi*	-	-	+	20	95
Lepidocephalichthys thermalis	+	+	+	5	1045
Nemacheilidae					
* *Paracanthocobitis urophthalma*	-	-	+	15	285
* *Schistura madhavai*	-	-	+	775	1055
* *Schistura notostigma*	+	-	+	15	1450
* *Schistura scripta*	-	-	+	80	80
Cyprinidae					
* *Amblypharyngodon grandisquamis*§	+	+	+	5	465
Dawkinsia filamentosa	+	+	+	5	575
* *Dawkinsia srilankensis*	+	-	+	80	460
Devario malabaricus	+	+	+	5	1285
* *Devario memorialis*	-	-	+	235	265
* *Devario micronema*	-	-	+	25	495
* *Devario pathirana*	-	-	+	30	315
* *Devario monticola*	-	-	+	1380	1580
Esomus thermoicos	+	+	+	5	295
* *Garra ceylonensis*	+	+	+	15	1575
* *Horadandia atukorali*§	+	+	+	0	85
* *Labeo fisheri*	+	-	+	80	495
* *Labeo heladiva*§	+	+	+	5	105
* *Labeo lankae*§	-	+	-	5	95
* *Laubuka hema*	+	-	-	115	295
* *Laubuka lankensis*§	+	+	-	5	480
* *Laubuka varuna*	-	-	+	5	60
* *Pethia bandula*	-	-	+	170	170
* *Pethia cumingii*	-	-	+	15	190
* *Pethia melanomaculata*§	+	+	-	25	295
* *Pethia nigrofasciata*[1]	-	-	+	15	520
* *Pethia reval*[2]	+	-	+	10	125
Puntius bimaculatus	+	+	+	5	1230
Puntius thermalis	+	+	+	5	185
Puntius dorsalis	+	+	+	0	765
* *Puntius kamalika*	?	+	+	5	65
* *Puntius kelumi*	-	-	+	15	380
* *Puntius titteya*[3]	-	-	+	10	870
Puntius vittatus	+	+	+	0	600
* *Rasbora adisi*	+	+	-	25	765
* *Rasbora armitagei*	-	-	+	295	310
Rasbora dandia	+	+	+	0	1210
Rasbora microcephala	+	+	+	5	235
* *Rasbora naggsi*	+	-	+	85	650
* *Rasbora wilpita*	-	-	+	45	115
* *Rasboroides pallidus*[4]	-	-	+	10	185
* *Rasboroides vaterifloris*	-	-	+	35	115
* *Systomus asoka*	-	-	+	65	110
* *Systomus martenstyni*	+	-	+	80	460
* *Systomus pleurotaenia*	-	-	+	20	380
Systomus sarana	+	+	+	5	680
Tor khudree	+	-	+	30	830
Bagridae					
* *Mystus ankutta*	-	-	+	15	285
* *Mystus nanus*§	+	+	+	5	460
* *Mystus zeylanicus*§	+	+	+	5	480
Siluridae					
* *Ompok argestes*	+	-	+	5	145
* *Ompok ceylonensis*§	+	+	-	0	480
Wallago attu	+	+	+	15	60
Heteropneustidae					
Heteropneustes fossilis	+	+	+	5	195
Clariidae					
* *Clarias brachysoma*	+	-	+	5	605
Aplocheilidae					
* *Aplocheilus dayi*	-	-	+	0	870
Aplocheilus parvus	+	+	+	0	495
* *Aplocheilus werneri*	-	-	+	5	120
Syngnathidae					
Lophocampus ocellatus	-	-	+	40	120
Synbranchidae					
* *Ophichthys desilvai*[5]	+	-	+	5	10
Ophisternon bengalense	+	+	+	0	10
Mastacembelidae					
Mastacembelus armatus	+	+	+	5	875
* *Macrognathus pentophthalmos*§[6]	?	+	?	5	5
Cichlidae					
Etroplus suratensis	+	+	+	0	195
Pseudetroplus maculatus	+	+	+	0	150
Anabantidae					
Anabas testudineus	+	+	+	0	150
Osphronemidae					
* *Belontia signata*	+	-	+	5	1065
* *Malpulutta kretseri*[7]	?	-	+	5	120
Pseudosphromenus cupanus	+	+	+	0	380
Channidae					
* *Channa ara*	+	+	+	80	460
Channa marulius	?	+	-	35	95
* *Channa* cf. *ara*[8]	-	-	+	5	60
Channa kelaartii	+	+	+	5	765
* *Channa orientalis*	-	-	+	5	1315
Channa punctata	+	+	+	5	150
Channa striata	+	+	+	5	150

in the relatively less-well explored eastern intermediate zone give this region too, new importance. Two endemic species otherwise restricted to the wet zone occur in the western intermediate zone (*Pethia reval* and *Ompok argestes*), in addition to one species otherwise restricted to the dry zone (*Pethia melanomaculata*).

Although the only contemporary record of *Macrognathus pentophthalmos* we have is from the dry zone of the Mahaweli basin, the species has a historical distribution that spans several basins in the south-western wet zone (Willey, 1910; Deraniyagala, 1932b; Pethiyagoda *et al*., 2008b). It appears to be either very rare or insusceptible to the sampling methods we have used.

The categorization of species as endemic in Tables 5.2 and 5.3, however, should be treated with caution. Before concluding that a species is endemic, it is necessary that its taxonomy be up to date and some effort made to establish its presence in the eastward-draining river basins of southern India. Almost all Sri Lankan species, however, are deficient with respect to one or both of these criteria. Putatively endemic species that occur widely in the dry zone, in particular, have a high likelihood of having conspecific or only recently diverged populations in south-eastern India. These include *Amblypharyngodon grandisquamis, Horadandia atukorali, Labeo heladiva, Labeo lankae, Laubuka lankensis, Pethia melanomaculata, Mystus nanus, M. zeylanicus, Ompok ceylonensis* and possibly, *Macrognathus pentophthalmos*. None of these has been shown to have a sister-group relationship to any other Sri Lankan species, which supports their being relatively recent dispersants from India. Several other species previously considered

Table 5.3. Species that commonly occur in freshwater in Sri Lanka but are known or inferred to have a marine life-history phase, or be capable of marine dispersal, as referenced. Species with populations known to breed and complete their life cycle in freshwater are marked with an asterisk (*). Those associated purely with rainforest streams are marked §.

Anguillidae
Anguilla bicolor [Aoyama, 2009]
Anguilla bengalensis [Aoyama, 2009]
Clupeidae
*Ehirava fluviatilis** [Newrkla & Duncan, 1984]
Muraenidae
Gymnothorax polyuranodon [Ebner *et al.*, 2011]
Syngnathidae
*Lophocampus ocellatus**§ [Dawson, 1985; Pethiyagoda, 1991]
Bagridae
Mystus gulio [pers. obs.]
Zenarchopteridae
Zenarchopterus dispar [?]
Hemiramphidae
*Hyporhamphus limbatus** [Kumara & Amarasinghe, 2008]
Belonidae
*Xenentodon cancila**§ [Foster, 1973]
Adrianichthyidae
Oryzias spp.* [pers. obs.]
Kuhliidae
Kuhlia marginata [Feutry *et al.*, 2013]
Gobiidae
Awaous melanocephalus [Yamasaki, 2007]
Glossogobius giuris [Hoese & Allen, 2011]
Glossogobius celebius [Hoese & Allen, 2011]
Schismatogobius deraniyagalai§ [Keith *et al.*, 2017]
Sicyopterus griseus§ [Keith *et al.*, 2015]
Sicyopterus lagocephalus§ [Keith *et al.*, 2015]
Sicyopus jonklaasi§ [Keith *et al.*, 2015]
Stiphodon martenstyni§ [Keith *et al.*, 2015]

Notes to Table 5.2

1 Several translocated populations exist. The highest elevation at which *P. nigrofasciata* was recorded was 1010 m asl, at Suriyakanda; the second highest was from the Belihul River at Pambahinna (590 m), also in the Walawe basin, though this may be a naturally-occurring population. The population translocated to the Mahaweli occurs in the range 480–660 m asl.

2 The population translocated to the Mahaweli basin occurs in the elevation range 480–660 m asl.

3 The population translocated to the Mahaweli basin occurs at around 795 m asl, and that in the Walawe is at 775–1010 m asl.

4 The population translocated to the Mahaweli basin occurs at 600–660 m asl, and that in the Walawe is at 1000–1010 m asl.

5 Although recorded by us only from the wet zone, the type locality reported by Bailey & Gans (1998), from secondary sources, is in the intermediate zone.

6 No voucher-supported records since 1927. Pethiyagoda *et al.* (2008) examined specimens in NMSL collected in 1926–27 from Kalutara (Kalu Basin) and Kelaniya (Kelani basin).

7 Although we recorded this species only from the wet zone, the type locality, Dandagamuwa (Deduru basin), is in the intermediate zone (Deraniyagala, 1927).

8 The morphologically distinct but genetically ambiguous wet zone form given this label by Sudasinghe *et al.*, 2020b.

to be endemic to Sri Lanka have been shown to occur also in India: *e.g., Esomus thermoicos* (Sudasinghe *et al.*, 2019b), *Channa kelaartii* (Sudasinghe *et al.*, 2020f), and *Dawkinsia filamentosa* (as *D. singhala*: Katwate *et al.*, 2020).

The gross distribution of Sri Lanka's freshwater fishes is summarized in Table 5.2, while Table 5.4 presents, for genera, data on endemicity, regional distribution and related data.

As seen from Table 5.2, twelve species (eight of them endemics) are confined to the lowlands < 100 m asl, while 54 are confined to elevations < 500 m asl. Only four species are confined to the mid-hill region between 100 and 500 m asl, each to a single basin (*Devario memorialis, Laubuka hema, Pethia bandula,* and *Rasbora armitagei*). Only ten species have ranges extending into mountain streams above 1000 m asl; five of these are endemics that more commonly occur in the foothills (*Channa orientalis, Devario monticola, Garra ceylonensis, Schistura madhavai,* and *S. notostigma*), the other five being the ubiquitous *Lepidocephalichthys thermalis, Devario malabaricus, Puntius bimaculatus* and *Rasbora dandia*. Only two species are confined to elevations above 500 m asl: *Schistura madhavai* and *Devario monticola*, both narrow-range endemics.

The basins with the greatest species richness is the Kalu (50 species, of which 30, are endemic), followed by the Kelani and Gin (49 and 48 species each, 25 and 26 endemics, respectively). Species-richness and endemism in the other three major wet-zone basins too, is high: Bentara and Nilwala (40 and 41 species, 23 and 24 endemic, respectively, in each). The island's largest basin, the Mahaweli, which drains a major part of the central mountains and almost the entirety of the Knuckles, however, has only 41 species (22 endemic). Five species are restricted to it, however, substantially more than is the case for the major western wet-zone drainages: Kelani (2), Kalu (1), Gin (1), Nilwala (1), Walawe (1) and Maha (1).

5.4 Phylogeography

Fishes dispersing to Sri Lanka through the Palk Isthmus in the island's northwest necessarily entered via the Malwathu-Kala drainage. Hence, these drainages would be expected to contain the phylogenetically basal populations for most wet-zone species. However, it is also possible that im-

Table 5.4. Genera of freshwater fishes occurring in Sri Lanka, showing: 1, endemicity; 2, restriction to Sri Lanka and peninsular India; 3, rheophilic adaptations; and 4, subterranean habitat (■), monotypy (●), and disjunct distribution between Sri Lanka and Southeast Asia (♦).

	1	2	3	4
Cobitidae				
Lepidocephalichthys	-	-	-	-
Nemacheilidae				
Paracanthocobitis	-	-	-	-
Schistura	-	-	+	-
Cyprinidae				
Amblypharyngodon	-	-	-	-
Dawkinsia	-	+	-	-
Devario	-	-	+	-
Esomus	-	-	-	-
Garra	-	-	+	-
Horadandia	-	+	-	-
Labeo	-	-	+	-
Laubuka	-	-	-	-
Pethia	-	-	-	-
Puntius	-	-	-	-
Rasbora	-	-	-	-
Rasboroides	+	-	-	-
Systomus	-	-	-	-
Tor	-	-	+	-
Bagridae				
Mystus	-	-	-	-
Siluridae				
Ompok	-	-	-	-
Wallago	-	-	-	-
Heteropneustidae				
Heteropneustes	-	-	-	-
Clariidae				
Clarias	-	-	-	-
Aplocheilidae				
Aplocheilus	-	-	-	-
Synbranchidae				
Ophichthys	-	-	-	■
Ophisternon	-	-	-	-
Mastacembelidae				
Mastacembelus	-	-	-	-
Macrognathus	-	-	-	-
Cichlidae				
Etroplus	-	+	-	-
Pseudetroplus	-	+	-	-
Anabantidae				
Anabas	-	-	-	-
Osphronemidae				
Belontia	-	-	-	♦
Malpulutta	+	-	-	●
Pseudosphromenus	-	+	-	-
Channidae				
Channa	-	-	-	-

Table 5.5. Genetic diversity of Sri Lankan freshwater fishes mentioned in the chapter. Number of sequences (N), number of haplotypes (h), polymorphic sites (S), parsimony-informative sites (P), nucleotide diversity (π), and haplotype diversity (Hd). *, **, and *** represent statistical significance at $0.10 > p > 0.05$, $p < 0.05$, and $p < 0.02$, respectively. Endemic species are in bold. LK indicates that only the Sri Lankan populations was sampled; RF, rainforest. Climatic zones: DZ, dry zone, rainfall < 1.8 $m\cdot y^{-1}$; IZ, intermediate zone, rainfall 1.8–2.5 $m\cdot y^{-1}$; WZ, wet zone, rainfall > 2.5 $m\cdot y^{-1}$.

Species	Habitat	Marker	N	h	S	P	π	Hd	Tajima's D test	Fu & Li's test
Dawkinsia filamentosa (LK)	Generalist: WZ, IZ, DZ	*cytb*	15	7	9	5	0.00228	0.857	-0.39518	-0.52867
		cox1	15	4	3	1	0.00082	0.467	-1.31654	-1.30356
Devario malabaricus (LK)	Generalist: WZ, IZ, DZ	*cytb*	28	11	22	8	0.00333	0.772	-1.28627	-2.31170
		cox1	28	10	9	4	0.00182	0.751	-1.49242	-1.73597
Devario micronema	RF associate: WZ	*cytb*	13	8	27	20	0.00777	0.885	-0.31266	0.24742
		cox1	14	7	10	8	0.00454	0.879	-0.31502	0.39137
Garra ceylonensis	Rheophilic: WZ, IZ, DZ	*cytb*	92	40	164	130	0.02540	0.961	-0.64274	-0.47986
		cox1	48	21	67	50	0.02061	0.948	-0.49558	-0.34909
Laubuka varuna	RF associate: WZ	*cytb*	19	13	29	26	0.02021	0959	0.92739	1.22107
		cox1	16	8	25	22	0.01511	0.900	0.97575	1.01016
Laubuka lankensis	IZ, DZ	*cytb*	41	17	40	34	0.02105	0.900	0.65412	0.68738
		cox1	39	14	17	12	0.00726	0.866	0.34340	-0.34433
Rasbora wilpita	RF associate: WZ	*cytb*	13	4	8	8	0.00600	0.808	1.44302	1.58604
		cox1	18	3	7	7	0.00416	0.621	1.02030	1.41513
Rasbora dandia (LK)	Generalist: WZ, IZ, DZ	*cytb*	26	8	11	5	0.00317	0.883	-1.16657	-1.58447
		cox1	26	6	6	2	0.00146	0.628	-1.21644	-1.87009
Rasbora microcephala (LK)	Generalist: WZ, IZ, DZ	*cytb*	14	5	4	0	0.00097	0.505	-1.79759 *	-2.44883 **
		cox1	15	4	4	0	0.0085	0.371	-1.81594 *	-2.51825 **
Rasbora naggsi	WZ, IZ	*cytb*	13	3	2	1	0.00115	0.564	-0.12688	-0.38456
		cox1	12	2	3	3	0.00193	0.409	0.77220	1.15369
Rasbora adisi	IZ, DZ	*cytb*	13	2	1	0	0.00026	0.154	-1.14915	-1.48111
		cox1	13	3	2	1	0.00071	0.410	-0.90920	-0.60889
Systomus sarana (LK)	Generalist: WZ, IZ, DZ	*cytb*	22	10	83	79	0.03241	0.883	2.00125 ***	1.93860 **
		cox1	38	9	32	29	0.02424	0.804	1.81753 ***	1.59664 ***
Systomus pleurotaenia	RF associate: WZ	*cytb*	13	7	94	92	0.03425	0.872	0.95279	1.61374 *
		cox1	13	6	48	48	0.02912	0.859	0.85832	1.63893 *
Pethia melanomaculata	IZ, DZ	*cytb*	12	7	9	7	0.00287	0.864	0.17135	0.50750
Pethia nigrofasciata	RF associate: WZ	*cytb*	39	23	64	49	0.01163	0.970	-0.66449	-0.20228
Pethia cumingii	RF associate: WZ	*cytb*	15	9	20	16	0.00691	0.914	0.87622	0.78798
Pethia reval	WZ, IZ	*cytb*	33	12	33	28	0.01078	0.877	1.63098	1.12476
Channa orientalis	WZ	*cox1*	31	15	70	56	0.04268	0.869	0.71131	0.50838
Channa kelaartii (LK)	Generalist: WZ, IZ, DZ	*cox1*	11	5	10	3	0.00455	0.764	-0.72042	-1.25839

migrants across the isthmus were adapted to xeric conditions and, having entered Sri Lanka, dispersed into the southern wet zone, where they diversified through ecological speciation (Gillespie *et al.*, 2020). With the possible exception of *Ompok argestes-O. ceylonensis* (which putative sister-group relationship has not yet been tested in a molecular analysis), the sister-group relationships which would then be expected between the dry and wet zones do not, however, seem to exist. This could be because of the extinction of dry-zone vicars as a result of Pleistocene aridification. Nevertheless, the present dry zone ichthyofauna appears to be almost entirely shared with India.

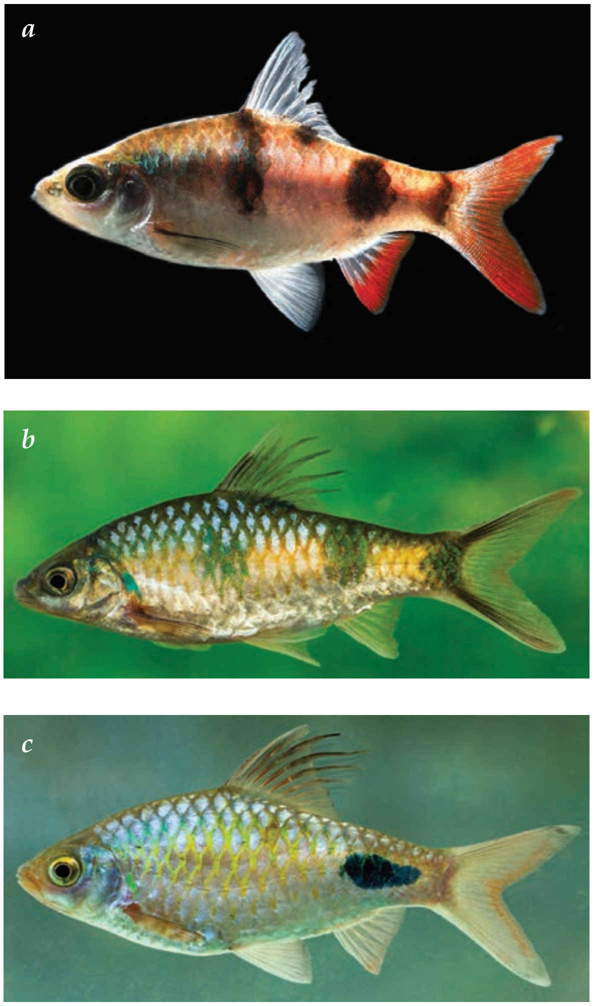
Such, however, is not the case, as we explain below. Having entered via the Malwathu-Kala system, which evidently drained the Knuckles range during the Plio-Pleistocene, several species colonized those hills. For most of their courses, however, these rivers traverse the island's vast, mostly flat, dry zone plain. This plain experiences extensive flooding during episodes of heavy rain even now, providing hydrological connectivity between adjacent basins and hence the inter-basin dispersal of fishes. This applies also to rivers traversing the wet-zone's coastal floodplain. One would expect, therefore, little geographic structure in fishes inhabiting these floodplains. We show in the case studies that follow that while the wet-zone's more complex topography results in the fish populations in its basins exhibiting greater genetic structure. Such structure is, however, attenuated in the dry zone.

We summarize below the results of recent phylogeographic analyses of individual freshwater-fish species. In many cases, these offer insights into the population structure and dispersal history of the fishes, while identifying also some hitherto unknown barriers to—and avenues of—dispersal. Where relevant, we also present phylogenies constructed from mitochondrial (and in some cases, also nuclear) markers to illustrate the relationships and evolutionary histories of these species, accompanied by haplotype networks. Metrics relating to genetic diversity are presented in Table 5.5.

The datasets on which the various generic accounts are based differ substantially. This account is intended to provide only an overview, and hence it omits details of the methods used, for which the source publications cited should be consulted.

5.4.1 *Dawkinsia*

The cyprinid genus *Dawkinsia* contains about a dozen species, two of which occur in Sri Lanka: *Dawkinsia srilankensis*, which is confined to foothill streams (80–460 m asl) draining the Knuckles hills into the Mahaweli basin; and *D. filamentosa* (Figure 5.3), which has a wide distribution in the



Mrcus Knight

Figure 5.3. Fishes of the cyprinid genus *Dawkinsia* are confined to the Western Ghats–Sri Lanka Biodiversity Hotspot. ***a,*** *Dawkinsia tambraparniei*, which occurs in the Tamiraparani River of South India; ***b,*** *D. srilankensis*, a Sri Lankan endemic occurring in streams draining to Mahaweli in the northern Knuckles Hills, near where the Malwathu River has its origins (the species does not presently occur in the Malwathu itself); and ***c,*** *D. filamentosa*, a species widely distributed across Sri Lanka and southern India.

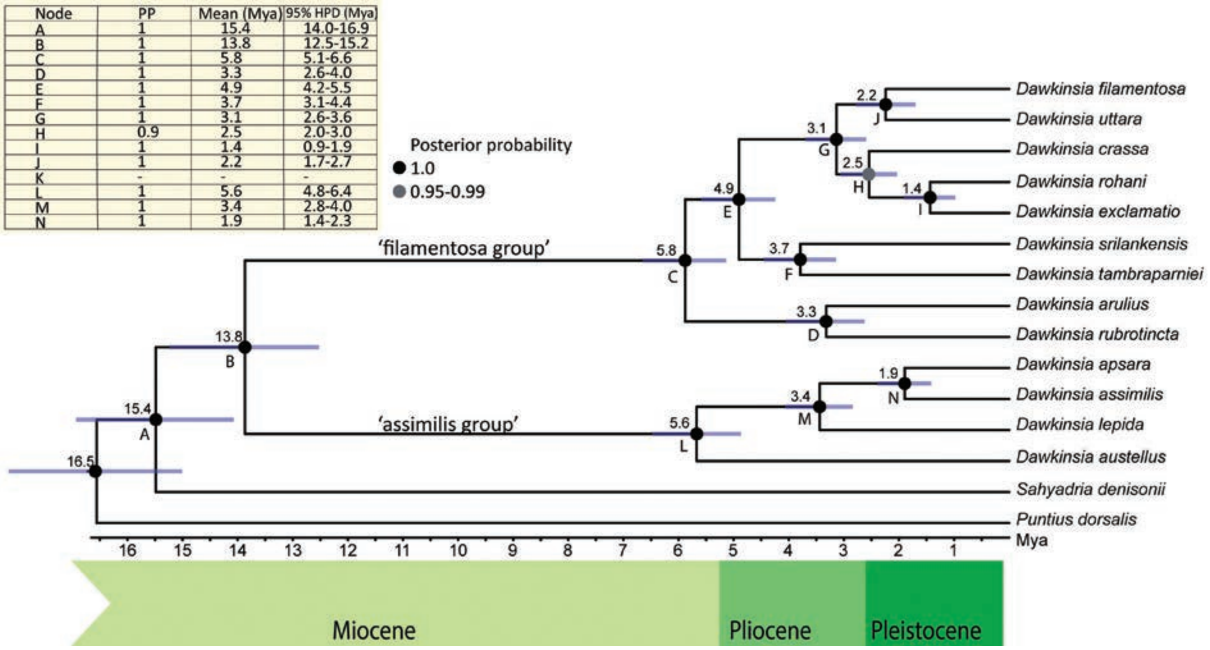
island's low- and mid-elevations (5–570 m asl) across both climatic zones. The latter occurs also in southern India, in rivers draining both the eastern and western slopes of the Western Ghats.

The phylogenetic analyses of Katwate *et al.* (2020) and Sudasinghe *et al.* (2021b) show *Dawkinsia srilankensis* and the South Indian species *D. tambraparniei* to have a well-supported sister-group relationship (Figure 5.4). The latter authors estimated a Pliocene divergence between *D. srilankensis* and *D. tambraparniei*, 3.7 (95 % HPD: 4.4–3.1) Mya. The split between the Sri Lankan and Indian lineages of *D. filamentosa* was estimated to have occurred more recently, 400 (95 % HPD: 600–200) kya, in the late Pleistocene.

Phylogeography. Sudasinghe *et al.* (2021b) showed there to have been only a modest level of haplotype sharing between the different populations of *D. filamentosa* in Sri Lanka, with haplotypes separated mostly by single mutational steps. In the *cox1* median-joining network (Figure 5.5a), no haplotypes were shared between the Sri Lankan and Indian populations, while in the *cytb* network (Figure 5.5b), a single haplotype (H3) was shared between Sri Lanka's Maha basin and India's Pampa basin, south of the Palghat Gap. Both these drain west, into the Laccadive Sea. Given the recent divergence of the Indian and Sri Lankan populations, Sudasinghe *et al.* (2021b) suspected that this outcome was more a result of under-sampling in southeast India than genetic divergence attributable to Sri Lanka's insularity. Further, these authors failed to discern a clear phylogeographic structure in *D. filamentosa* within Sri Lanka in either the *cox1* or the *cytb* median joining networks, which suggests that barriers to gene flow between basins have been weak.

Sudasinghe *et al.* (2021b) adduced evidence to support the hypothesis that the two species of *Dawkinsia* in Sri Lanka are a result of discrete dispersal across the Palk Isthmus, followed by vicariance when sea level rose or the climate of the isthmus aridified.

Dawkinsia srilankensis and its Indian sister group *D. tambraparniei* are associated with streams and rivers traversing closed forest draining the northern region of the Knuckles Hills and the eastern slopes of the Western Ghats, respectively. The latter species is confined to the Tamiraparani River, which drains toward the Indian stem of the erstwhile Palk Isthmus. Ramasamy & Saravanavel



Node	PP	Mean (Mya)	95% HPD (Mya)
A	1	15.4	14.0-16.9
B	1	13.8	12.5-15.2
C	1	5.8	5.1-6.6
D	1	3.3	2.6-4.0
E	1	4.9	4.2-5.5
F	1	3.7	3.1-4.4
G	1	3.1	2.6-3.6
H	0.9	2.5	2.0-3.0
I	1	1.4	0.9-1.9
J	1	2.2	1.7-2.7
K	-	-	-
L	1	5.6	4.8-6.4
M	1	3.4	2.8-4.0
N	1	1.9	1.4-2.3

Figure 5.4. Bayesian time-calibrated tree, using the *cytb* substitution rate, for the concatenated *cytb+cox1* dataset of *Dawkinsia* (1719 bp, Sudasinghe *et al.*, 2021b). Bars and values at nodes represent 95 % HPD and mean ages of divergence estimates, respectively.

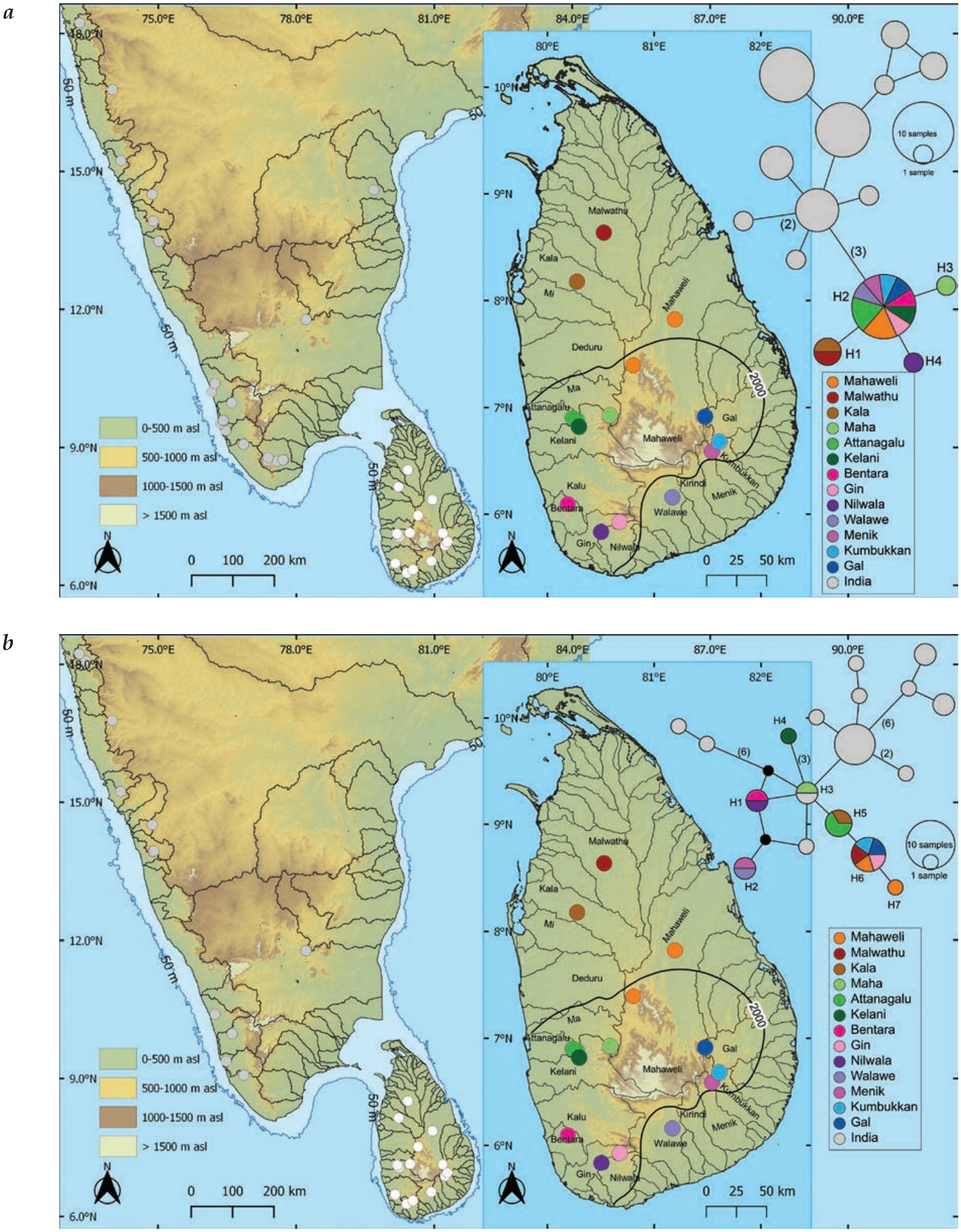


Figure 5.5. Sampling localities for *Dawkinsia filamentosa* in Sudasinghe *et al*. (2021b), and median-joining haplotype network based on the analysis of ***a,*** a 630 bp fragment of the *cox1* gene; and ***b,*** a 1089 bp fragment of the *cytb* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps > 1 is indicated in parentheses. Black circles indicate hypothetical nodes. Legend colors correspond to the river basin or the locality.

(2019) showed the Tamiraparani to have formed a Pleistocene palaeodrainage with Sri Lankan rivers draining towards the isthmus (now the Kala and Malwathu drainages). The Sri Lankan end of the Isthmus presently lies within the Malwathu basin. Deraniyagala (1958) pointed to evidence that the Kala-Malwathu basins were confluent at least until the Pleistocene, and that the headwaters of this large river in the region of the Knuckles had since been captured by the Mahaweli. *Dawkinsia srilankensis* is now confined to these headwaters, which indicates a possible route of dispersal between India and Sri Lanka of the common ancestor of *D. tambraparniei* and *D. srilankensis*. By the beginning of the Pleistocene, north-eastern Sri Lanka, which includes the Malwathu-Kala palaeobasin, had become increasingly arid (Morley, 2018): it is now among the driest regions of the island (see Figure 2.6).

It appears to have been the climatic barrier posed by an arid Palk Isthmus, rather than inundation of the land bridge itself, that was the vicariance event that separated the ancestral population that gave rise to *D. srilankensis* and *D. tambraparniei*. The isthmus was subaerial through most of the Pleistocene, but by then its climate was too arid and strongly seasonal to support the closed forests with which *D. tambraparniei* and *D. srilankensis* (and presumably their common ancestor) are associated. This aridity appears to have resulted in the extirpation of ancestral *D. srilankensis* in the Malwathu-Kala river system, isolating the population in the Knuckles Hills. This scenario may explain the distribution of another Knuckles endemic, *Labeo fisheri*, whose relationships with Indian congeners, however, remain to be worked out[*].

Unlike *Dawkinsia srilankensis, D. filamentosa* occurs in wide range of environments and habitats, such as ephemeral streams, large rivers, floodplains, estuaries and swamps, descending very nearly to sea level. It is also among the most frequent species in Sri Lanka's dry zone, including its most arid regions, such as Mannar. It could thus have dispersed between India and Sri Lanka so long as a land bridge was emergent, until the late Pleistocene. Indeed, *D. filamentosa* is among the very few cyprinid species to occur even with-

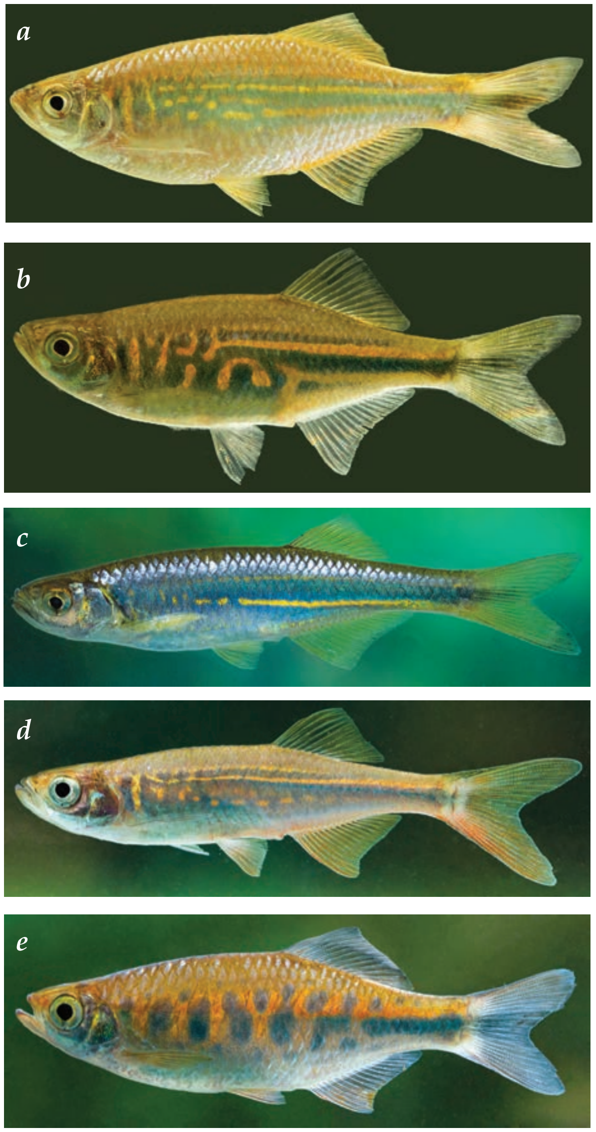


Figure 5.6. The Sri Lankan species of *Devario:* ***a,*** *D. malabaricus*, a species widely distributed in Sri Lanka and southern India; and the endemics ***b,*** *D. micronema* (Kelani to Gin basins); ***c,*** *D. memorialis* (a narrow-range endemic of the Maha basin); ***d,*** *D. monticola* (a narrow-range endemic of the Mahaweli basin in the central hills, around Agrapatana); and ***e,*** *D. pathirana* (Nilwala basin).

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[*] Anusha *et al.* (2017) reported *Labeo fisheri* from India for the first time, from Kalakkad Tiger Reserve, in the headwaters of the Tamiraparani River, unfortunately without reference to a registered voucher specimen. Sudasinghe *et al.* (2018) suggested that this taxon may have a sister-group relationship to *L. fisheri* (no other fishes confined to Sri Lanka's wet zone are shared with India). If confirmed, the record of Anusha *et al.* (2017) would lend further support to the former connectivity between the Tamiraparani and Sri Lanka's Knuckles hills, via the Malwathu-Kala basins.

in the tidal influence of rivers (pers. obs.), leading us to believe that dispersal between adjacent estuaries may have been possible during episodes of high rainfall.

5.4.2 *Devario*

Members of the cyprinid genus *Devario*, with some 40 valid species, are ubiquitous in South and Southeast Asia, between and southwards of the Indus and the Mekong basins (Fang Kullander, 2001; Kullander *et al*., 2018). Sudasinghe *et al.* (2020e) recognized five species from Sri Lanka: *D. malabaricus, D. memorialis, D. micronema, D. monticola,* and *D. pathirana* (Figure 5.6). These occur in a diversity of habitats across all eco-climatic zones, ranging from the rivers and ponds of the lowland floodplain to hill streams and torrents, from almost sea level to elevations of up to about 1580 m asl (Batuwita *et al*., 2017; Sudasinghe and Pethiyagoda, 2019; Sudasinghe *et al*., 2020e). Except for *D. malabaricus*, which occurs also in southern India, the remaining four species are endemics restricted to streams traversing the island's wet zone.

The molecular analysis of Sudasinghe *et al.* (2020e; Figure 5.7) estimated that the most recent common ancestor of the malabaricus, micronema and memorialis clades diverged from the lineage leading to the Indian species *Devario devario* ~6.2 (95 % HPD: 7.6–4.6) Mya, in the late Miocene*. The basal split between the malabaricus clade and the [micronema + memorialis] clades was estimated 5.6 (95 % HPD: 7.1–4.1) Mya, also in the late Miocene or early Pliocene.

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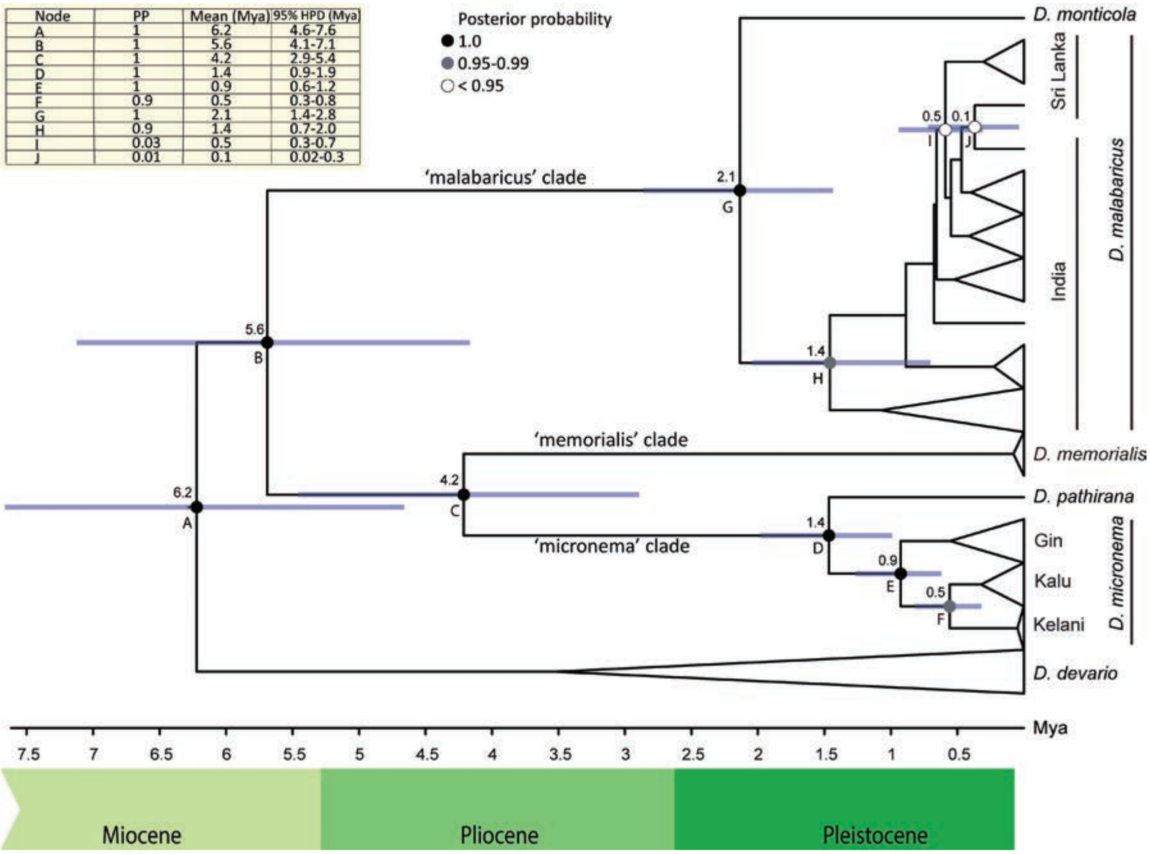
* Sea levels fell to their lowest since the Oligocene at about this time (De Boer *et al*., 2010; Hansen *et al*., 2013) and except for brief high-stands, remained below present levels until the Holocene (Bintanja & van de Wal, 2008). The time-calibrated molecular phylogeny of Beenaerts *et al.* (2010) too, estimated that a lineage of gecarcinucid (freshwater) crabs adapted to wet, open lowland habitats immigrated from India ~5.5 Mya, also in the late Miocene (see p. 137).



Node	PP	Mean (Mya)	95% HPD (Mya)
A	1	6.2	4.6-7.6
B	1	5.6	4.1-7.1
C	1	4.2	2.9-5.4
D	1	1.4	0.9-1.9
E	1	0.9	0.6-1.2
F	0.9	0.5	0.3-0.8
G	1	2.1	1.4-2.8
H	0.9	1.4	0.7-2.0
I	0.03	0.5	0.3-0.7
J	0.01	0.1	0.02-0.3

Figure 5.7. Bayesian time-calibrated tree, using the *cytb* substitution rate, for the concatenated *cytb+cox1* dataset of *Devario* (1761 bp, Sudasinghe *et al*. 2020e). Bars and values at nodes represent 95 % HPD and mean ages of divergence estimates, respectively.

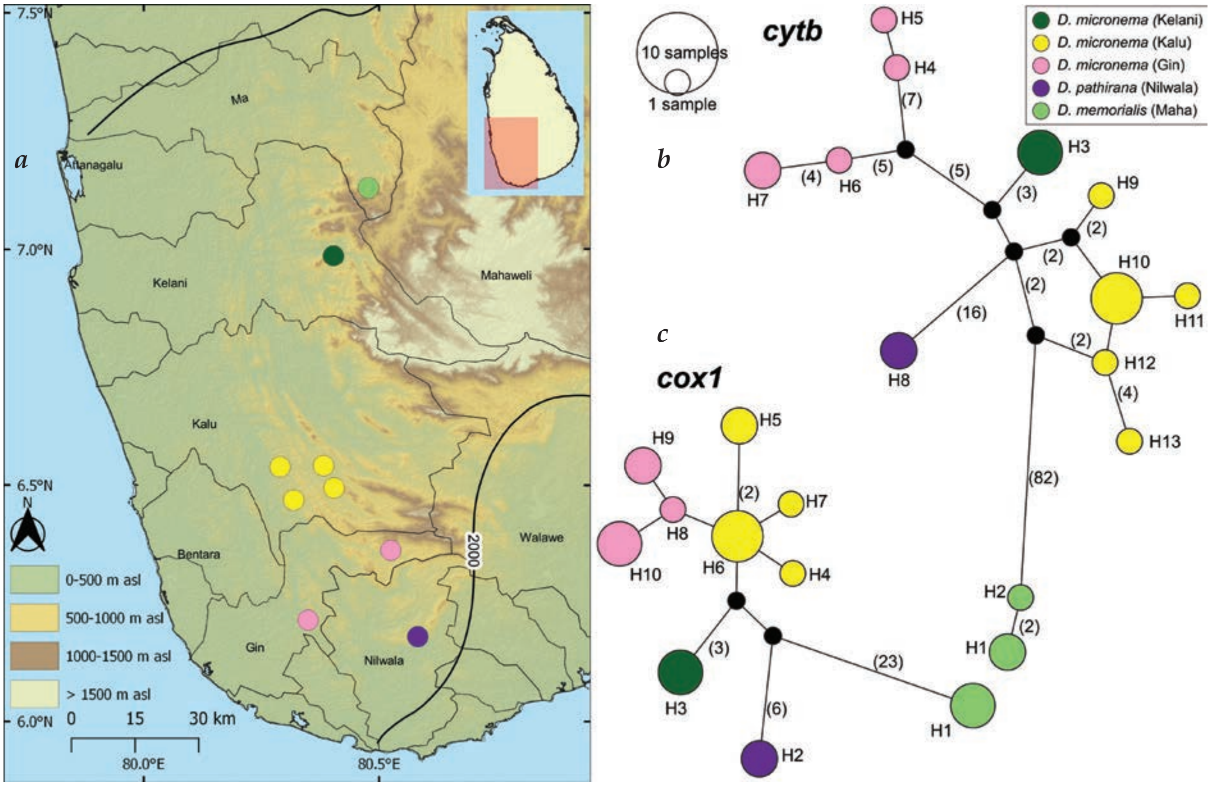


Figure 5.8. ***a***, Sampling localities and median-joining haplotype network for the micronema and memorialis clades of *Devario*, based on the analysis of ***b***, a 1092 bp fragment of the *cytb* gene, and ***c***, a 669 bp fragment of the *cox1* gene, from Sudasinghe *et al*. (2020e). The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to the river basin or the species.

The split between the micronema clade and *D. memorialis*, the oldest speciation event in the genus in Sri Lanka, occurred in the early Pliocene, dated at ~4.2 Mya, while that between *D. malabaricus* and *D. monticola* was dated to 2.1 (95 % HPD: 2.8–1.4) Mya, and that between *D. pathirana* and *D. micronema* around 1.4 (95 % HPD 1.9–0.9) Mya, in the Pleistocene. Meanwhile, the divergence between *D. micronema* from the Gin basin and its conspecific population in the Kelani and Kalu basins was dated at 0.9 (95 % HPD: 1.2–0.6) Mya (Figure 5.7). The latter two populations were estimated to have been isolated from each other for ~500 (95 % HPD: 800–300) kya.

Devario malabaricus, the only member of the genus that is shared between Sri Lanka and India, is abundant and widespread throughout the lowlands of southern peninsular India and the lowland 'floodplain' that surrounds Sri Lanka's central hills. The isolation between Sri Lankan and Indian populations of *D. malabaricus* was dated at 500 (95 % HPD: 700–300) kya and continued until ~100 (95 % HPD: 300–20) kya.

Phylogeography. Sudasinghe *et al.* (2020e) found the Sri Lankan population of the most widespread species, *D. malabaricus*, to include five *cox1* haplotypes and the Indian population to include 15. None of these is shared between the two countries. Yet, there is little phylogeographic structure in *D. malabaricus* within Sri Lanka: the species is widely distributed and appears to have enjoyed unrestricted gene flow throughout the lowlands of the island's dry and wet zones. Sudasinghe *et al.* (2020e) conjectured that it had undergone a recent population expansion, possibly a consequence of more 'open' (unshaded) habitats becoming available as a result of Holocene land-use change.

Sudasinghe *et al.* (2020e) showed the populations of *D. micronema* from the Kelani, Kalu and the Gin basins each to contain unique haplotypes, with no sharing of haplotypes between the ba-

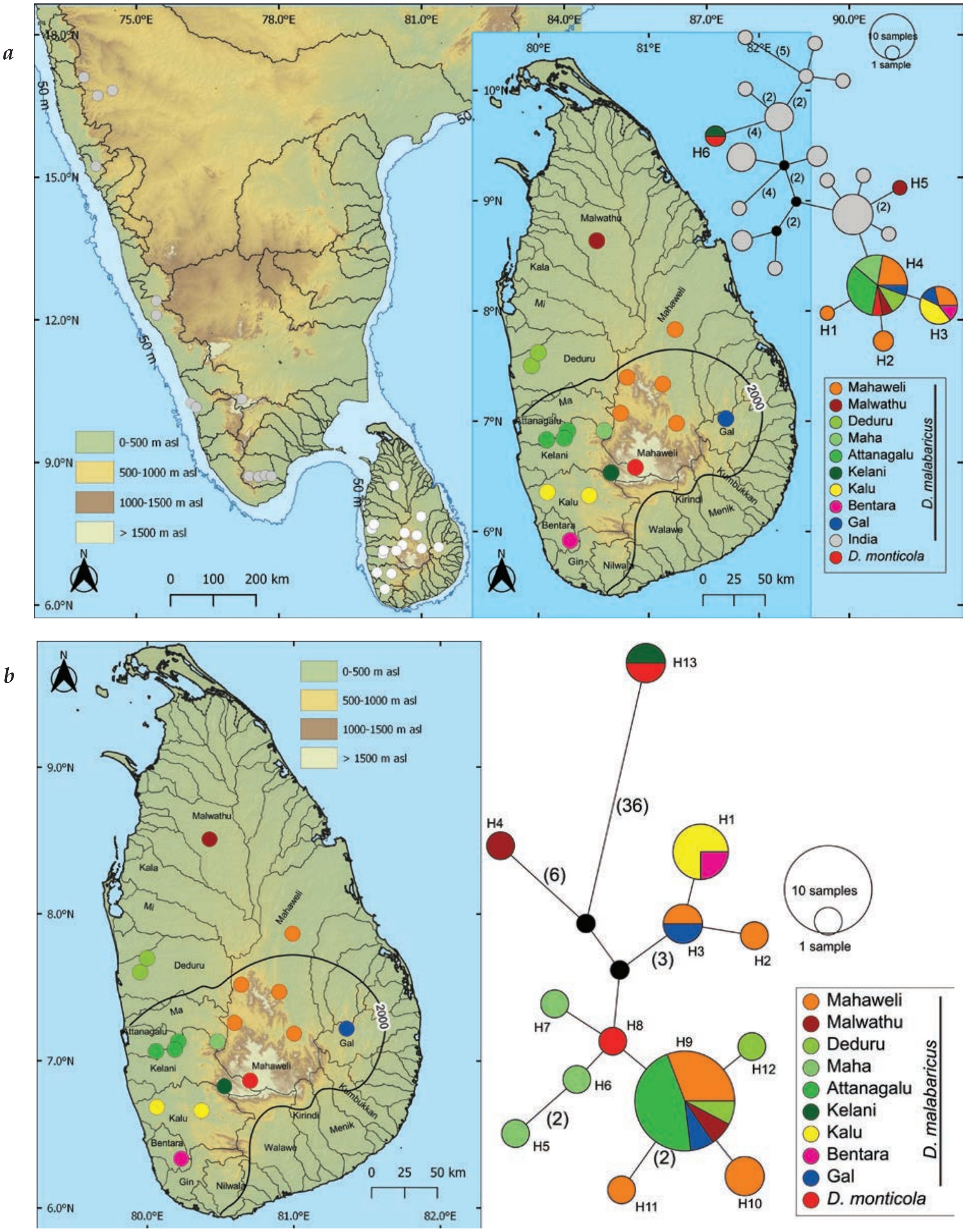


Figure 5.9. Sampling localities and median-joining haplotype network for the malabaricus clade of *Devario*, based on the analysis of **a,** a 669 bp fragment of the *cox1* gene; ***b,*** a 1092 bp fragment of the *cytb* gene, from Sudasinghe *et al*. (2020e). The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to the river basin or the locality or the species.

sins (Figure 5.8). Although *D. micronema* is the most widely distributed of the endemic species of *Devario* in Sri Lanka, it is restricted largely to shaded streams traversing lowland 'rain' forests on the slopes of the western foothills, rather than the more open habitats of the coastal floodplain, across which there are no obvious barriers to dispersal. The absence of shared haplotypes between populations of *D. micronema* in the major river basins it inhabits, all of which debouch into the Indian Ocean across a common lowland floodplain (Figure 5.8), suggests restricted gene-flow even between adjacent basins in this evidently 'forest-adapted' species. Additionally, *D. memorialis*, a species confined to the Maha River, contains two unique (H1, H2 in *cox1* and *cytb*) haplotypes, while *D. pathirana*, restricted to the Nilwala basin, contains one (H8) each in *cox1* and *cytb*.

In the case of *D. monticola* (Figure 5.9), a highland endemic apparently confined to the Bopattalawa Valley (upper Mahaweli basin), one sample contained a unique haplotype (H8 in each *cox1* and *cytb*), while another (H13 in each *cox1* and *cytb*) was shared with an example of *D. malabaricus* from Seethagangula (6.8262° N 80.5256° E) in the adjacent Kelani basin, which Sudasinghe *et al.* (2020e) suggested might result from mitochondrial introgression.

In the case of *rag1*, Sudasinghe *et al.* (2020e) found that the sample of *D. malabaricus* from Seethagangula, which nested with *D. monticola* in the mitochondrial haplotype network, shares a haplotype with *D. malabaricus* in the *rag1* haplotype network. Further, *D. micronema* from the Kelani, Kalu and Gin basins share a single haplotype with *D. pathirana*, while the sample of *D. monticola* that nested within the *cox1* and *cytb* haplotype network of *D. malabaricus* shares a haplotype with *D. memorialis*.

The results of Sudasinghe *et al.* (2020e) hint at hybridization and mitochondrial introgression in Sri Lankan *Devario*. Given the recent diversification of this group in the island, it is possible that there has been insufficient time for reproductive barriers to develop between some of the species. Hybridization and introgression may thus occur in zones of contact, or as a result of translocations or river diversions (Wikramanayake, 1990a; Sudasinghe *et al.*, 2018b).

Sudasinghe *et al.* (2020e) hypothesized, however, that hybridization and mitochondrial introgression may be more likely in closely related species pairs such *D. micronema-D. malabaricus* and *D. monticola-D. malabaricus* in their zones of contact, though this remains to be investigated.

Interestingly, of the 64 sites in Sri Lanka at which *Devario* were sampled, a congener occurred in syntopy at only at one: in the headwaters of the Maha River. Here, *D. malabaricus* occurs together with *D. memorialis*.

5.4.3 *Garra*

A feature of Sri Lanka's freshwater-fish inventory is that it is almost devoid of rheophilic fishes—fishes adapted to life in fast water (Roberts & Stewart, 1976; Lujan & Conway, 2015): see Table 5.4. Such fishes are common in the rivers of South Asia and, particularly, in southern India, where more than 20 such genera occur (see Table 4.1). Of these, only a single genus occurs in Sri Lanka, represented by a single species, *Garra ceylonensis*.

Garra are benthic algivores that exhibit multiple adaptations to life in fast-flowing waters (Lujan & Conway, 2015; Kottelat, 2020; Figure 5.10). They have depressed, fusiform bodies; unculiferous pads on the ventral surfaces of their wide, paired fins; an inferior mouth with the gular region modified to form an 'adhesive' or 'suctorial' disc; and lack—or possess only reduced or scattered—scales on their chest and belly (Stiassny & Getahun, 2007; Nebeshwar & Vishwanath, 2017; Kottelat, 2020).

While *G. ceylonensis* exhibits all these specializations, it shows no preference for torrents or high-gradient streams but occurs in a wide range of stream types. It is ubiquitous in both the wet

Figure 5.10. *Garra ceylonensis*, a Sri Lankan endemic that is ubiquitous in hard-substrate lotic environments.

and the dry zones, ranging from near sea level to upper-montane torrents (15–1575 m asl: Sudasinghe *et al.*, 2021a; up to 1800 m asl: Radda, 1973).

The evolutionary history of *Garra* in Sri Lanka came to be investigated only recently, by Sudasinghe *et al.* (2021a). Based on a sampling of 38 locations in 16 of the island's principal river basins, in addition to 36 locations in peninsular India, they generated and analyzed a multi-gene dataset of sequences at three mitochondrial and nuclear gene markers. This recovered *G. ceylonensis* and *G. mullya*, a species widely distributed in Peninsular India, as having a sister-group relationship, the estimated crown age of the Sri Lankan clade being 3.0 (95 % HPD 3.4–2.6) Mya. The analysis showed also that there had been only a single colonization event across the Palk Isthmus, in the late Pliocene, followed by an insular diversification in the Plio-Pleistocene.

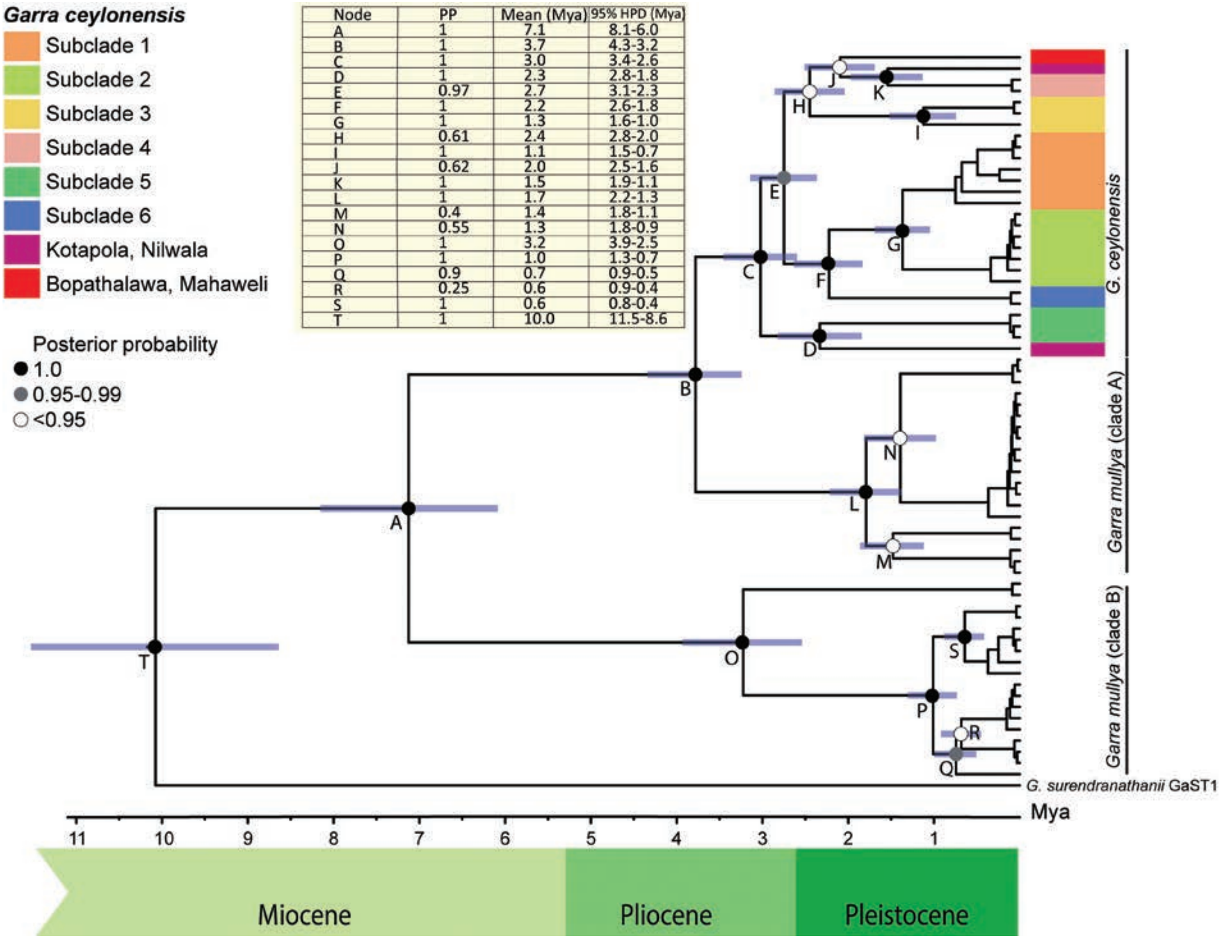
Phylogeography. Sudasinghe *et al.* (2021a) reported six subclades within *G. ceylonensis* (Figure 5.11). Subclade 1 is confined to the Kala and Malwathu basins in the northern dry zone, and up to an elevation of 1085 m asl in the Mahaweli basin, while Subclade 2 occurs in four contiguous western basins: Deduru, Ma, Attanagalu and Kelani. These two subclades show a well-supported sister-group relationship. Subclade 3 is restricted to the contiguous Kalu and Bentara basins in the southwest, with a disjunct population at Opatha in the Nilwala basin, while Subclade 4 is confined to the Gin basin. Subclade 5 was recorded from the contiguous Walawe, Kirindi and Menik basins in the island's southeast, with Subclade 6 confined to the contiguous Kumbukkan and Gal basins in the southeast.

This phylogeographic pattern is disturbed, however, by two exceptions. The first of these was represented by the samples from Bopathalawa (Mahaweli basin, 1575 m asl, the highest location at which *Garra* were recorded). All the other samples from the Mahaweli, collected from 14 locations in the elevation range 55–1085 m asl, form a well-supported monophyletic group, along with samples from the Kala and Malwathu basins (Subclade 1, Figure 5.11). The sample from Bopathalawa, however, did not nest with Subclade 1. Instead, its phylogenetic position was uncertain, exhibiting different topologies in the different analyses, always with weak node support.

The second exception to the phylogeographic pattern noted above was from Kotapola, a low elevation site (127 m asl) in the Nilwala basin. Sudasinghe *et al.* (2021a) sampled this basin at only two locations: Opatha and Kotapola. The samples from Opatha were recovered as the sister group of the Kalu-Bentara samples, which form Subclade 3. However, among the two samples from Kotapola, one was recovered, with strong node support in all the analyses, as the sister group of Subclade 4, confined to the Gin basin. The other sample from Kotapola, meanwhile, was recovered as the sister group of Subclade 5, which is confined to the Walawe, Kirindi and Menik basins.

As shown below, in *Systomus pleurotaenia* (section 5.4.6), samples from Kotapola (Nilwala basin) and Deniyaya (Gin basin) were genetically more similar to each other, while the samples from Opatha were genetically more similar to the samples from the south-western basins. Sudasinghe *et al.* (2020c) hypothesized that one lineage evolved in isolation in a Plio-Pleistocene refugium in the Nilwala basin, which was subsequently invaded by the other, possibly as a result of headwater river capture. The evidence for a Plio-Pleistocene refugium in the south-western basins (especially the Gin and Nilwala, but also the Kelani and Kalu) is further supported by the molecular phylogenies of other Sri Lankan cyprinds (see below).

The historical connectivity between the Mahaweli-Malwathu-Kala basins is reflected also in the distribution of mtDNA haplotypes in *Garra*. Among *cytb* haplotypes, one is shared between the Mahaweli and Kala, and another between the Kala and Malwathu basins. Meanwhile, a single *cox1* haplotype is confined to these three basins, emphasizing their connectivity. Given that the Malwathu-Kala river system represents the gateway into Sri Lanka for freshwater fishes, one would expect the population of *Garra* in those rivers to be basal to the diversification of the genus on Sri Lanka. However, this is not so (Figure 5.11). This suggests that *Garra* were extirpated in these dry-zone basins at some time after their initial Pliocene dispersal from India but recolonized them from the middle region of the Mahaweli subsequently, more recently than node G in Figure 5.11 (1.3,



Node	PP	Mean (Mya)	95% HPD (Mya)
A	1	7.1	8.1-6.0
B	1	3.7	4.3-3.2
C	1	3.0	3.4-2.6
D	1	2.3	2.8-1.8
E	0.97	2.7	3.1-2.3
F	1	2.2	2.6-1.8
G	1	1.3	1.6-1.0
H	0.61	2.4	2.8-2.0
I	1	1.1	1.5-0.7
J	0.62	2.0	2.5-1.6
K	1	1.5	1.9-1.1
L	1	1.7	2.2-1.3
M	0.4	1.4	1.8-1.1
N	0.55	1.3	1.8-0.9
O	1	3.2	3.9-2.5
P	1	1.0	1.3-0.7
Q	0.9	0.7	0.9-0.5
R	0.25	0.6	0.9-0.4
S	1	0.6	0.8-0.4
T	1	10.0	11.5-8.6

Figure 5.11. Bayesian time-calibrated tree, using the *cytb* substitution rate, for the concatenated *cytb+cox1* dataset of *Garra* (1746 bp, Sudasinghe *et al.*, 2021a). Bars and values on the nodes represent 95 % HPD and mean ages for divergence-time estimates, respectively.

95 % HPD 1.6–1.0) Mya. The Mahaweli drains the Knuckles Hills together with a substantial portion of the central hills, and its low, wooded valleys may have offered refugia to these fish during episodes of aridification. Indeed, the star-like pattern of the *rag1* haplotype network (Figure 5.12) seems to suggest a recent range expansion of *Garra* on the island.

An extirpation followed by recolonization is indicated also by the basal position of Subclade 5 and the discrepant sample from Kotapola. This subclade occurs in the island's southeast, diametrically opposite the point of entry of *Garra* to Sri Lanka. It would appear that desiccation led to the extirpation of *Garra* in the island's north, followed by a recolonization from the south, with the rain forests of the southern basins and the middle Mahaweli serving as drought refugia.

Sudasinghe *et al.* (2021a) found the unique *cytb* and *cox1* haplotypes of the Bopathalawa population to be separated from the other Mahaweli haplotypes by a minimum 40 and 19 mutational steps, respectively. This population is also genetically distinct from other Mahaweli populations of *Garra* by uncorrected p-distances of more than 2.3 percent for *cox1* and 3.6 percent for *cytb*. The phylogenetic position of this sample was, however, uncertain, yielding different topologies in different analyses, always with weak node support.

Sudasinghe *et al.* (2021a) surmised that the Bopathalawa lineage might be a relict of a dispersal into the montane headwaters of the Mahaweli that

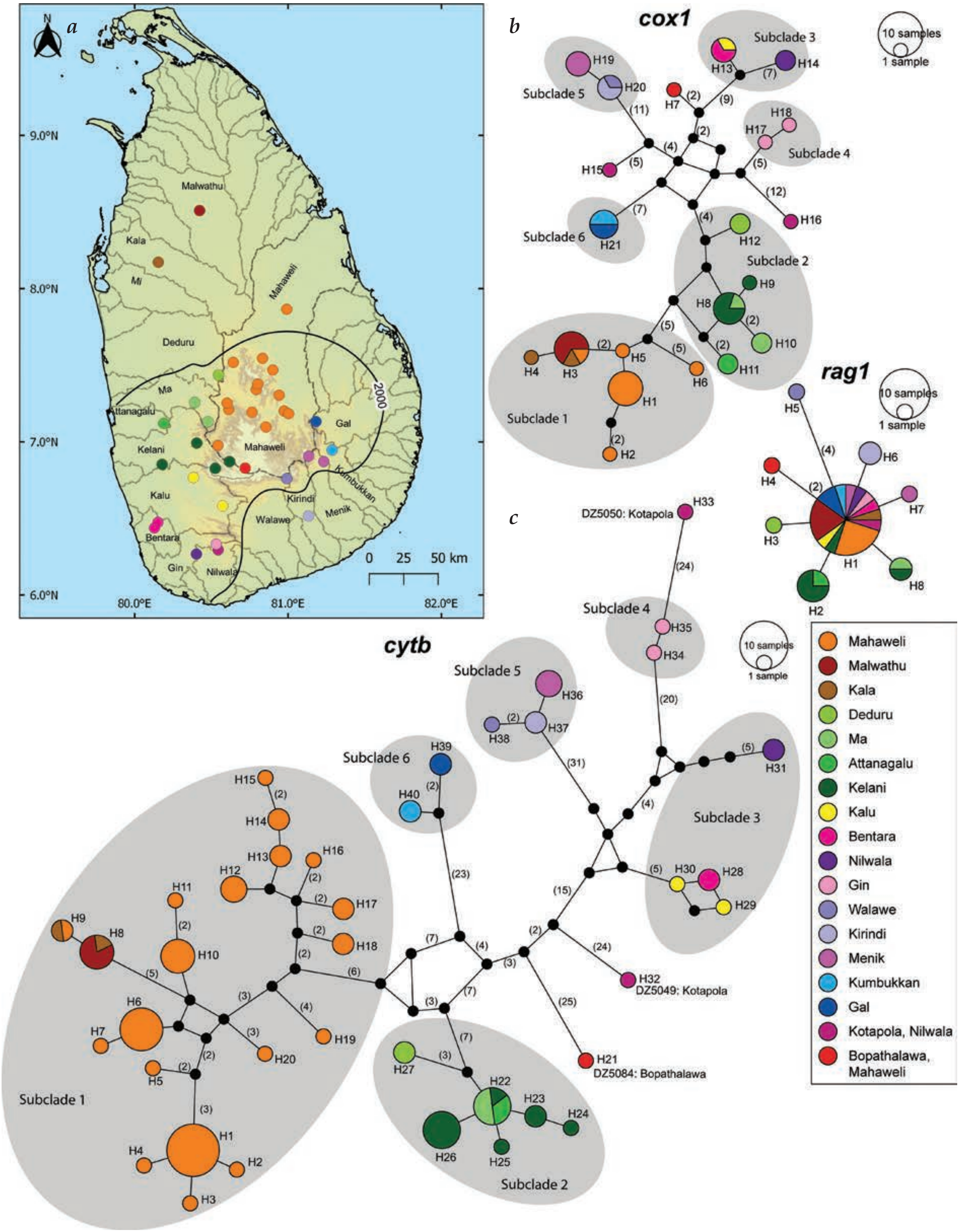


Figure 5.12. Sampling localities and median-joining haplotype network for *Garra ceylonensis*, based on the analysis of ***a,*** a 1107 bp fragment of the *cytb* gene; ***b,*** a 639 bp fragment of the *cox1* gene; and ***c,*** a 1237 bp fragment of the *rag1* gene. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to the river basin or the locality.

preceded the diversification of Subclade 1, that was subsequently extirpated in the lower reaches of the basin by aridification. Although the climatic history of Sri Lanka is poorly known, the Last Glacial Maximum at least, saw the island's humid forests decline to a fraction of their Holocene extent (Roberts *et al.*, 2018). As noted in the previous chapter, the palynological analyses of Premathilake & Risberg (2003) at Horton Plains in the central highlands (2100 m asl) too, show tropical montane cloud forest being replaced by dry forest between 24 and 18 kya, in the late Pleistocene, even as lowland forests became more open and rain forests withdrew to refugia. Such aridification events are likely to have desiccated many streams, leading to the extirpation of aquatic faunal communities. This may also explain in part why the mountain streams of Sri Lanka, unlike those of southern India, are depauperate of freshwater fishes. With a divergence time estimates of 2.1 (95 % HPD 2.8–1.4) Mya and 2.0 (95 % HPD 2.5–1.6) Mya from their lowland sister groups, respectively, *Devario monticola* and the Bopattalawa population of *Garra ceylonensis* are the oldest montane lineages in Sri Lanka, suggestive of a prior extirpation of the highland ichthyofauna.

That the Sri Lankan highlands experienced extraordinary desiccation event is evident also from the absence of lineages that are morphologically specialized to life in mountain streams, such as the balitorids and sisorids of the Western Ghats (see Table 4.1; Figure 4.2). Even now, these families range southwards as far as the Mahendragiri highlands (1654 m asl) just 30 km from Cape Comorin, and Samikuchi (80°25′48′N) (Johnson & Arunachalam, 2009). All the lineages of rheophilic fishes in the southern Western Ghats are Asian in origin. Even assuming they dispersed southwards along the mountainous Satpura route outlined by Hora (1953b), they had to cross several lowland regions between the Garo highlands of Assam and Meghalaya to the east, and the northern Western Ghats to the west, not least the Ganges-Brahmaputra lowlands (< 50 m asl) of northern Bangladesh. These fishes also crossed the Palghat and other major biogeographic gaps. Their inability to disperse across the Palk Isthmus then, would appear to be best explained not so much by an absence of hill streams as by an inhospitable climate.

In Sri Lanka, the montane ichthyofauna comprises species which are identical to—or have only recently diverged from—fishes occurring also in the lowland plains, such as the cyprinids *Garra ceylonensis, Devario malabaricus, Puntius bimaculatus* and *Rasbora dandia*, and nemacheilid *Schistura* loaches—a scenario that suggests recent colonization from the lowlands of generalist fishes tolerant of conditions in both lowland and upland streams (Sudasinghe *et al.* 2020e, 2021a).

We cannot exclude, however, the possibility that the genetic distinctiveness of the highland population of *G. ceylonensis* may be the result of positive selection of mtDNA, a phenomenon associated with high-elevation fishes (Ma *et al.*, 2015; Wang *et al.*, 2016), though this is usually observed at substantially higher elevations than 1575 m. Additionally, as pointed out by Lujan & Conway (2015), headwater populations of rheophilic fishes which have been isolated from larger downstream populations may exhibit increased rates of genetic drift.

Garra ceylonensis shows river-basin specific phylogeographic structure. Among the six subclades identified in the present study, only subclade 4 is restricted to a single basin: the Gin. The remaining subclades are each distributed within two or more contiguous basins. Strong phylogeographic structure has been observed also in rainforest-adapted cyprinids such as *Systomus pleurotaenia, Rasbora wilpita, Devario micronema,* and *Laubuka varuna,* and in the south-western wet zone of the island (Sudasinghe *et al.*, 2020c,d,e,g). In these cyprinids too, the sharing of haplotypes between adjacent river basins is limited. The authors explained this as resulting from habitat-associated philopatry restricting gene flow. In contrast to the other rainforest-adapted cyprinids, the rheophilic adaptations in *G. ceylonensis* would have aided it in dispersal to higher-elevation streams, with lateral dispersal aided by headwater river-capture, enabling gene flow between contiguous basins. Further, post-larval *G. ceylonensis* up to an age of at least two months are free-swimming midwater omnivores (Sundarabarathy *et al.*, 2005), allowing them to disperse along streams and rivers, unlike algivorous adults, which are associated exclusively with hard substrata.

It appears, however, that *Garra ceylonensis* does

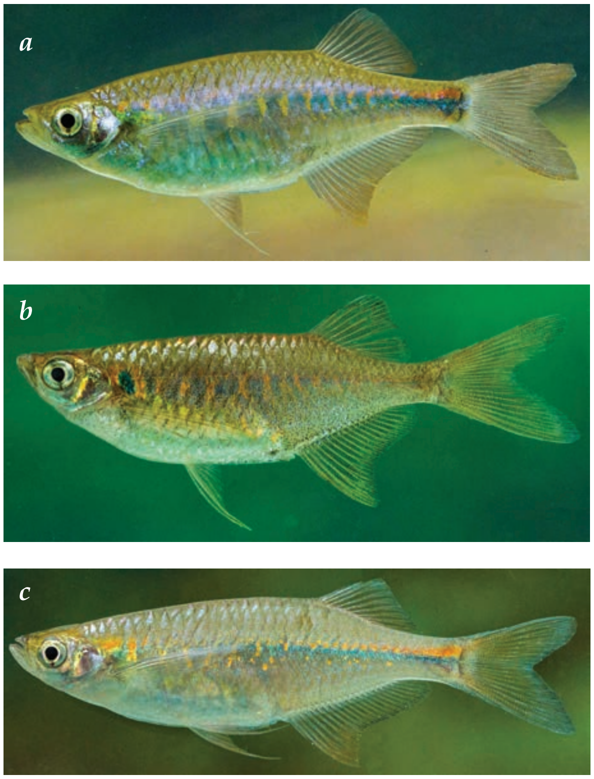


Figure 5.13. The Sri Lankan species of *Laubuka*. ***a,*** *L. lankensis,* which is widely distributed across the dry and the intermediate zones; ***b,*** *L. varuna,* which is restricted to the wet zone; and ***c,*** *L. hema,* which is restricted to the upland headwaters of the Gal basin draining the eastern slopes of the central hills.

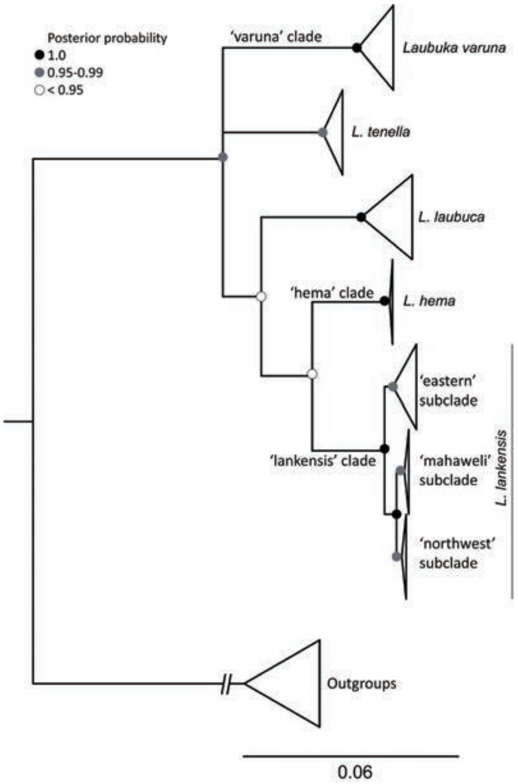


Figure 5.14. Topology of the molecular phylogenetic relationships of Sri Lankan *Laubuka*, based on Bayesian inference of the concatenated *cytb+cox1+rag1* dataset (2739 bp), after Sudasinghe *et al.* (2020g).

not disperse via the island's lowland floodplain, which offers potential hydrological connectivity between the lower reaches of adjacent river basins. The discrete phylogeographic population structure within basins and within contiguous basin clusters suggests that such dispersal did not occur or did so only exceptionally. These lowland waters are associated with soft mud, silt and sand substrates, lacking the hard, submerged surfaces that host periphyton on which adult *G. ceylonensis* feed (Costa & Fernando, 1967). Nevertheless, rheophilic adaptations appear to have aided *G. ceylonensis* to colonize widely across Sri Lanka, including up the steep torrents of the island's central mountainous region. *Garra* are among the few native fishes to inhabit high-gradient torrential streams of slope 9–23° and flow 0.5–2.5 m^3s^{-1} (Schut, *et al.*, 1984) at elevations up to 1800 m asl (Radda, 1973). No native freshwater fishes now occur above ~1600 m asl (Sudasinghe *et al.*, 2021a).

5.4.4 *Laubuka*

The cyprinid genus *Laubuka* includes about a dozen species distributed through the lowlands of tropical South and Southeast Asia (Kottelat, 2013; Kullander *et al.*, 2018). While five species occur between the Ganges basin of India and Thailand, four have been reported from the peninsula of India. While one of these is confined to the Western Ghats, three others inhabit streams and rivers draining the peninsula eastwards, to the Bay of Bengal. Sudasinghe *et al.* (2020g) showed that three species of *Laubuka* occur on Sri Lanka, all of them endemic to the island (Figure 5.13): *L. lankensis*, a species confined to the dry and intermediate zones; *L. varuna*, confined to the wet zone; and *L. hema*, a local endemic confined to the headwaters of the Gal basin draining the eastern slopes of the central hills, in the intermediate zone.

Based on a sampling of populations of *Laubuka* at 56 locations in 14 river basins representative

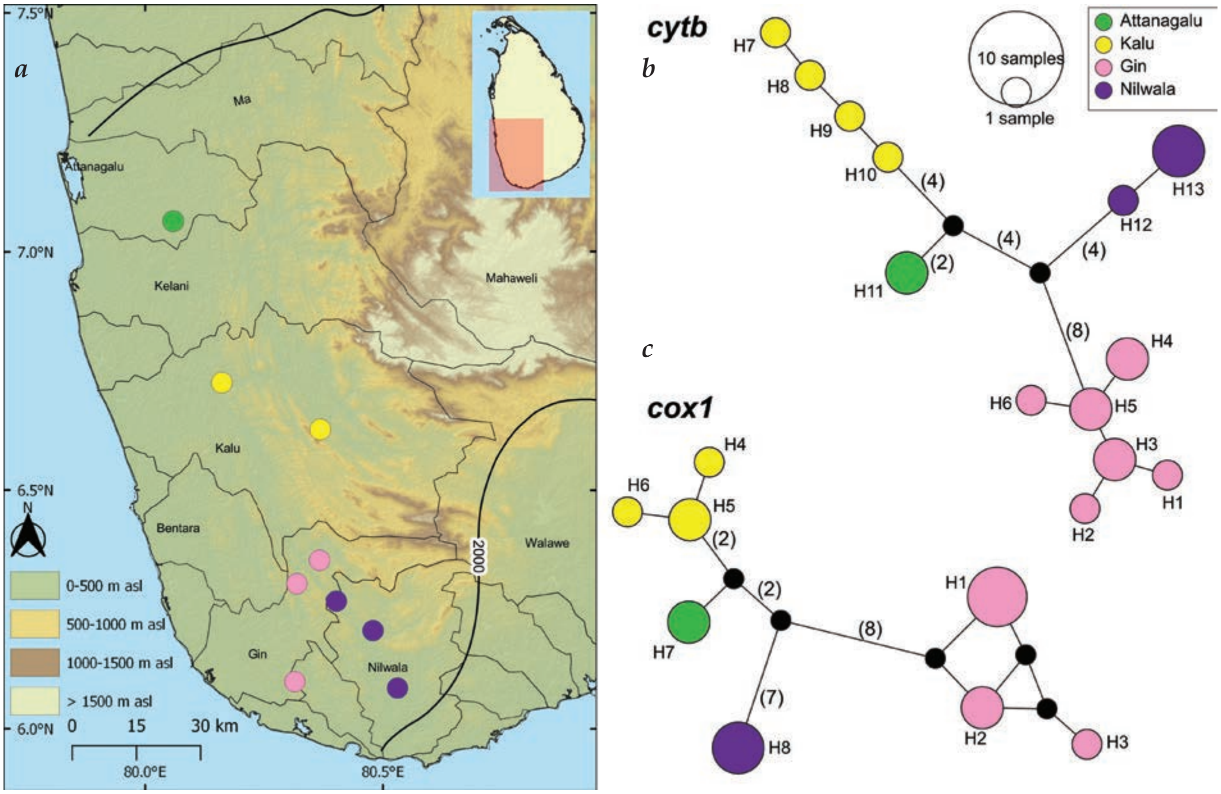


Figure 5.15. ***a,*** Sampling localities and median-joining haplotype network of *Laubuka varuna*, based on the analysis of ***b,*** a 611 bp fragment of the *cytb* gene; ***c,*** a 669 bp of the *cox1* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 are indicated in parentheses. The black circles are hypothetical nodes. Legend colours correspond to the river basin.

of Sri Lanka's main climatic zones, Sudasinghe *et al.* (2020g) presented a molecular phylogeny constructed from *cox1*, *cytb* and *rag1* sequences of the members of the genus in Sri Lanka (Figure 5.14).

The concatenated datasets presented by these authors show the three Sri Lankan species of *Laubuka* to be paraphyletic. This is suggestive of at least two dispersal or vicariance events: one involving the lineage that led to *L. varuna* in the south-western wet-zone basins, and the other, of [*L. lankensis* + *L. hema*], which are confined to the dry and intermediate zones. However, these phylogenies did not include South Indian species of *Laubuka*, such as *L. fasciata*, *L. trevori* and *L. latens*. A more robust understanding of the relationships between the species of *Laubuka* will only be possible once more comparative data from the Indian peninsula become available.

Phylogeography. Nevertheless, the haplotype network of Sri Lankan *Laubuka* presented by Sudasinghe *et al.* (2020g) illuminates their diversification within the island. *Laubuka varuna* is restricted largely to shaded streams traversing rain forests in Sri Lanka's southern and western foothills, rather than the more open habitats of the coastal floodplain, across which there appear to be no barriers to dispersal. Populations of *L. varuna* from the Attanagalu, Kalu, Gin and Nilwala basins contain one (H11), four (H7–H10), six (H1–H6) and two (H12–H13) *cytb* haplotypes, respectively (Figure 5.15a), with no sharing of haplotypes between them.

The *cox1* haplotype network too (Figure 5.15b), suggests similar inter-basin isolation: populations from the Attanagalu, Kalu, Gin and Nilwala basins represent one (H7), three (H4–H6), three (H1–H3) and one (H8) unique haplotypes, respectively, with none shared between them. Given that *L. varuna* occurs in swampy habitats in forested areas of the lowland floodplain across which these rivers debouch into the Indian Ocean, Sudasinghe

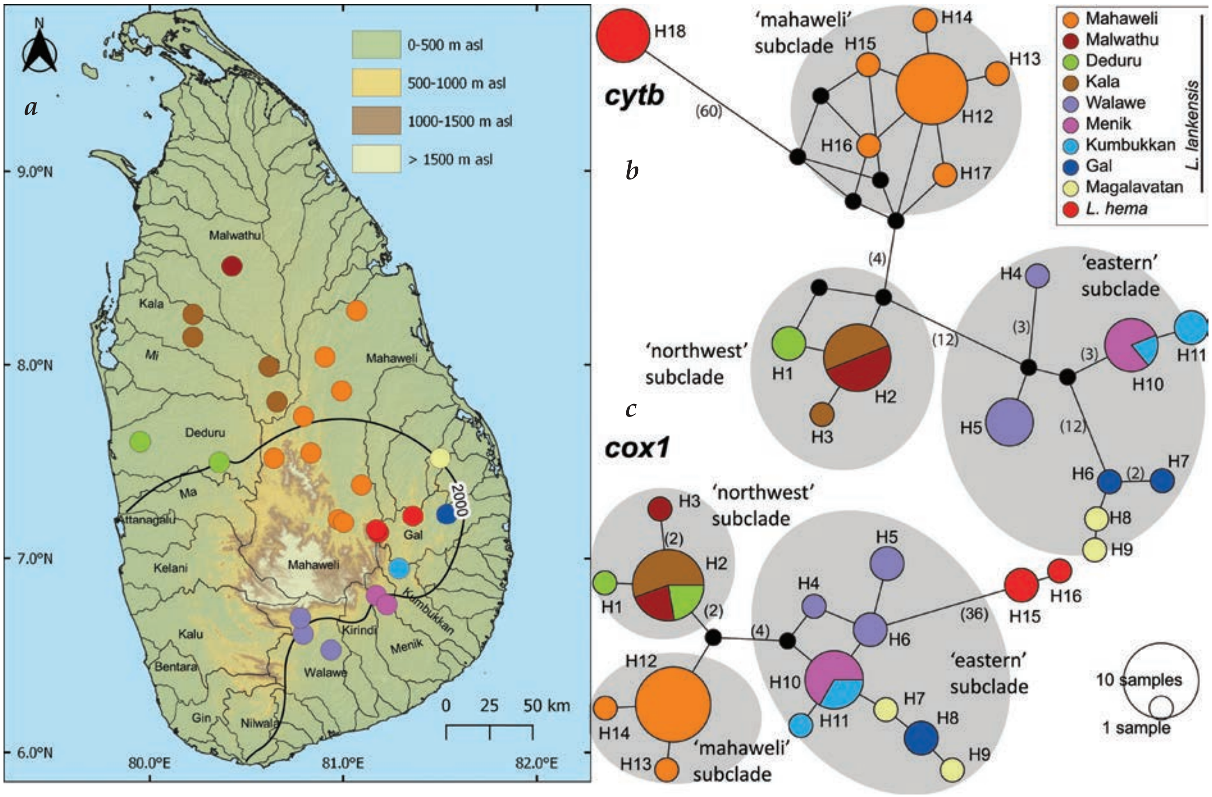


Figure 5.16. ***a,*** Sampling localities and median-joining haplotype network of *Laubuka lankensis*, based on the analysis of *b,* a 611 bp fragment of the *cytb* gene; ***c,*** a 669 bp of the *cox1* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colours correspond to the river basins or to the species, as given in the key.

et al. (2020g) were unable to explain the mechanism that restricts gene flow between adjacent basins. Instead, the species has remained confined to rainforest streams draining the lowest region of the western and southern foothills of the central mountains, in the elevation range ~10–70 m asl.

In contrast to the strong phylogeographic structure between adjacent river basins observed in *L. varuna*, such structure in *L. lankensis,* though weaker, is still discernible (Figure 5.16). The phylogeny of Sudasinghe *et al.* (2020g) showed the population of this species in the island's dry zone to comprise of three geographically characterized clades, which they labelled 'northwest', 'mahaweli' and 'eastern'. They found haplotypes of *L. lankensis* unique to the Deduru, Kala and Malwathu basins (H15 in *cytb*, H18 in *cox1*) in the northwest clade; and the Menik and Kumbukkan basins (H23 in *cytb*, H13 in *cox1*) in the eastern clade. The remaining haplotypes, though unique to each basin, were separated by only one or a few mutational steps from those of the adjacent river basins in these three regions (Figure 5.16b,c). They concluded that the star-like pattern observed in the haplotype networks of the Mahaweli population of *L. lankensis* is consistent with a rapid population expansion in the recent past, following a population bottleneck (Milá *et al.*, 2017).

Laubuka hema, which has the smallest distribution among the Sri Lankan species, contains two unique *cox1* (H8–H9) haplotypes and a single unique *cytb* (H25) haplotype. The species appears to be confined to the upper reaches of the Gal basin. Sudasinghe *et al.* (2020g) identified samples from Iginiyagala, further downstream, as *L. lankensis*. Outside the Gal basin, they recorded *L. hema* from only a single location, in the headwaters of the Hepola Oya (a stream), a tributary of the Mahaweli, near Bibile. This location is proximal to the boundary between the Mahaweli and Gal ba-

Figure 5.17. The Sri Lankan species of *Rasbora*. ***a,*** *R. dandia* and ***b,*** *R. microcephala*, which occur also in southern India; and the Sri Lankan endemics, ***c,*** *R. naggsi* (upland regions of basins from the Kalu to the Kirindi,), ***d,*** *R. adisi* (uplands Gal, Heda, Kumbukkan, Menik and Mahaweli basins), ***e,*** *R. armitagei* (a narrow-range endemic in the uplands of the Kalu basin), and ***f,*** *R. wilpita* (lowland rain forests within the Kalu, Bentara, Gin and Nilwala basins).

sins and appears to be the result of river-capture between their headwaters.

5.4.5 *Rasbora*

With some 80 valid species, the freshwater-fish genus *Rasbora* is among the most speciose cyprinid genera occurring in tropical Asia (Britz & Tan, 2018; Kottelat, 2013). The genus has its greatest diversity in Southeast Asia, with only five valid species reported from the peninsula of India west of the Ganges basin: *R. daniconius*, ranging from the Ganges westwards across the northern region of the peninsula; *R. labiosa*, from the northern part of the Western Ghats; *R. neilgherriensis*, from ~700–2000 m asl elevation in the Western Ghats; *R. microcephala*, from the south eastern lowlands of Sri Lanka and peninsular India; and *R. dandia*, a species distributed widely across Sri Lanka and the Indian peninsula (Frick *et al.*, 2021). Four species are endemic to Sri Lanka: *R. adisi, R. armitagei, R. naggsi* and *R. wilpita* (Silva *et al.*, 2010; Sudasinghe *et al.*, 2020d) (Figure 5.17).

Rasbora adisi is confined to the uplands (~25–700 m asl) of the south- and east-draining Gal, Heda, Kumbukkan, Menik and Mahaweli basins, the headwater regions of which are contiguous, while *R. armitagei* is a narrow-range endemic confined to a single steam, Indika Dola, near Weralugahamula, in the Walawe basin (~300 m asl, 6.487°N, 80.599°E). *Rasbora naggsi* occurs in the uplands of basins from the Kalu to the Kirindi, inclusive (the headwater regions of these are contiguous), whereas *R. wilpita* occurs in rain forests on the slopes of the foothills (~50–115 m asl) in the Kalu, Bentara and Gin basins, which have contiguous headwater regions*.

Sudasinghe *et al.* (2020d) sampled populations of *Rasbora* at 90 sites representative of the major climatic and hydrological regions of Sri Lanka. Their concatenated (*cytb+cox1+rag1+irbp*) dataset, whether using the maximum likelihood or Bayes-

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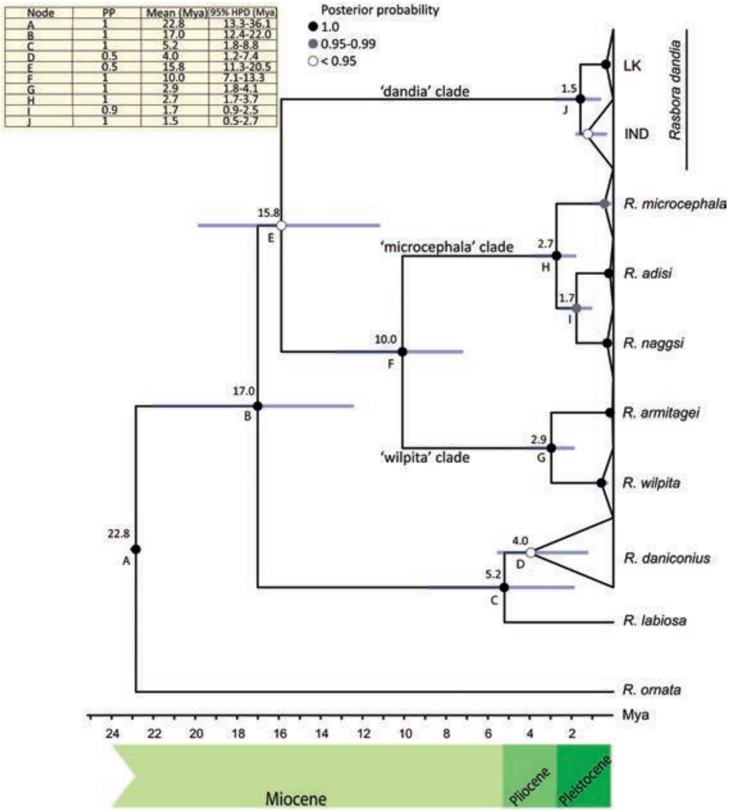
* Though not recorded in our sampling, the species may occur also in parts of the Nilwala and Kelani basins.



Node	PP	Mean (Mya)	95% HPD (Mya)
A	1	22.8	13.3-36.1
B	1	17.0	12.4-22.0
C	1	5.2	1.8-8.8
D	0.5	4.0	1.2-7.4
E	0.5	15.8	11.3-20.5
F	1	10.0	7.1-13.3
G	1	2.9	1.8-4.1
H	1	2.7	1.7-3.7
I	0.9	1.7	0.9-2.5
J	1	1.5	0.5-2.7

Figure 5.18. Bayesian time-calibrated tree of Sri Lankan and Indian *Rasbora*, based on the concatenated *cytb+cox1* (1227 bp) dataset of Sudasinghe *et al*. (2020d). Bars and values at nodes represent 95 % HPD and mean ages of divergence estimates, respectively. Note that in Sudasinghe *et al*. (2020d) and the text herein, the median values for divergence times are given. LK, Sri Lanka; IN, India.

ian inference, showed the Sri Lankan species as being divided into three main clades which they labeled (i) the 'dandia clade', (ii) the 'microcephala clade', and (iii) the 'wilpita clade' (Figure 5.18).

Sudasinghe *et al.* (2020d) showed the Sri Lankan and Indian populations of *R. dandia* to have diverged during the Pleistocene: 1.5 (95 % HPD 2.7–0.5) Mya. Although the Palk Isthmus was subaerial for most of the Pleistocene when sea level was substantially below that at present (Miller *et al.*, 2005: Figure 3.63), it appears to have been too arid to facilitate the dispersal of rainforest-associated fishes. *Rasbora dandia*, however, is arguably the most ubiquitous and abundant species of South Asian *Rasbora*, occurring even in the driest regions of the island. Consistent with a such adaptability, it does not exhibit detectable phylogeographic structure within Sri Lanka (Figure 5.19). Nevertheless, no mitochondrial haplotypes are shared between its Sri Lankan and Indian populations. This could be because the analysis of Sudasinghe *et al.* (2020d) lacked samples from southernmost eastern India.

Sudasinghe *et al.* (2020d) estimated the divergence between *R. naggsi* and *R. adisi* at 1.7 (95 % HPD 2.5–1.0) Mya; and between the rainforest-associates *R. wilpita* and *R. armitagei* at 2.9 (95 % HPD 4.1–1.8) Mya. Given the absence of Indian samples, however, they were unable to estimate a divergence time for the split between Indian and Sri Lankan *R. microcephala*. The presence of this species even in the arid Northern Province of Sri Lanka, and the ~0.9 Mya crown age of its Sri Lankan population, suggests that dispersal between India and Sri Lanka occurred in the late Pleistocene, perhaps coincident with that of *R. dandia*.

The analysis of Sudasinghe *et al.* (2020d) showed that the Sri Lankan species of *Rasbora* can be reliably distinguished from one another by details of their colour patterns, despite the superficial simi-

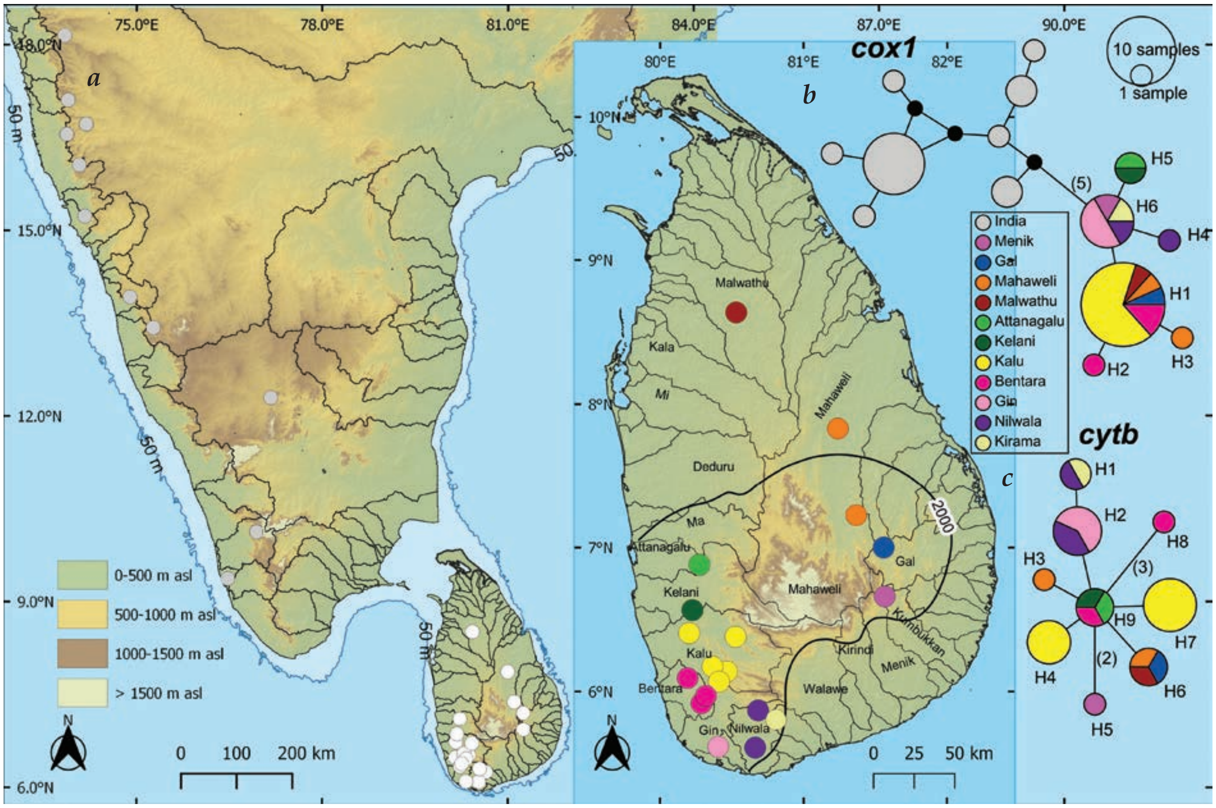


Figure 5.19. ***a,*** Sampling localities and median-joining haplotype network for the Sri Lankan species of *Rasbora* in the dandia clade, based on the analysis of ***b***, a 636 bp of the *cox1* gene; and ***c,*** a 591 bp fragment of the *cytb* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to the river basins, region or species.

larity of coloration in the six species (Figure 5.17). Interestingly however, they found that some individuals belonging to the members of the *Rasbora microcephala* group show substantial morphological disparity. Of the specimens of *R. microcephala* from the Malwathu, Kala, Mi, Deduru, Attanagalu, and Kalu basins in the island's northwest quadrant, most possess a superior mouth with a ventral projection of the dentary articulation and ½5 scales between lateral line and origin of dorsal fin. In contrast, specimens of *R. adisi* in the Gal, Heda, Kumbukkan and Menik basins usually possess a terminal mouth, lack a ventral projection of the dentary articulation, and have ½4 scales between lateral line and origin of dorsal fin. Among specimens from the Mahaweli basin, however, most possess a superior mouth and about half exhibit a ventral projection of the dentary articulation, similar to *R. microcephala*. In contrast, about a quarter of the *R. microcephala* specimens from the Mahaweli had lateral scalation consistent with that of *R. adisi*.

Similarly, despite specimens of *Rasbora* from the Kirindi basin nesting phylogenetically with *R. naggsi*, they exhibited morphological characters that align them with either *R. microcephala* or *R. naggsi* while diverging in several respects from topotypical *R. naggsi* from the Walawe and Kalu basins. In the latter basins, most examples of *R. naggsi* possess a terminal mouth and lack a ventral projection of the dentary articulation, whereas most of those from the Kirindi possess a superior mouth and about half exhibit a ventral projection of the dentary articulation. Despite these morphological disparities, coloration in all these populations was consistent with their genetic identity.

Sudasinghe *et al*. (2020d) attributed the morphological incongruities between *R. microcephala* with *R. naggsi* and *R. adisi* in the Kirindi and Mahaweli basins, respectively, to the possibly incipient na-

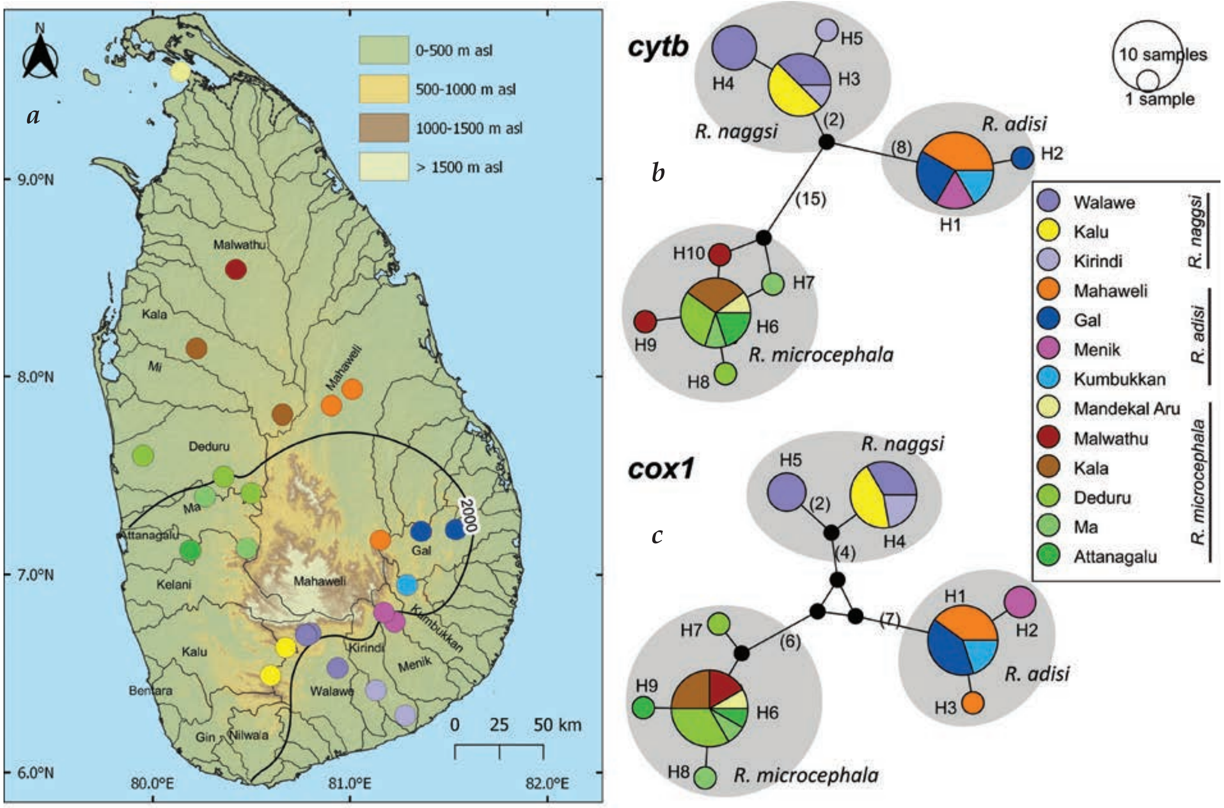


Figure 5.20. *a,* Sampling localities and median-joining haplotype network for the Sri Lankan species of *Rasbora* in the micocephala clade, based on the analysis of **b,** a 591 bp fragment of the *cytb* gene; and **c,** a 636 bp of the *cox1* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to the river basins, region or species.

ture of speciation, there having been insufficient time for reproductive isolation. It is possible that anthropogenic activities, such as habitat modification and hydrological diversions, may have affected the evolutionary processes operating among these species (Otto, 2018).

Phylogeography. The *cytb* haplotype network of Sudasinghe *et al.* (2020d) (Figure 5.19b) shows *R. dandia* to contain eight haplotypes (H16–H23), among which H17 is a high-frequency haplotype present in samples from both the wet zone and the dry zone: it appears to signal an ancestral condition of *R. dandia* in Sri Lanka.

Rasbora microcephala (Figure 5.20) contains five *cytb* haplotypes (H8–H12) in a star-like pattern. H8 is represented in samples from the Mandekal, Kala, Maha, Deduru and Attanagalu basins, and appears to represent an ancestral condition of *R. microcephala* in Sri Lanka.

Samples of *R. naggsi* from the Kalu and Walawe contain two haplotypes (H13, H14). These basins share a haplotype (H13) with the Kirindi population, to which the H15 haplotype is unique.

Samples of *R. adisi* include two haplotypes, of which H6 is shared between the Gal, Menik, Kumbukkan and Mahaweli basins, while H7 is restricted to the Gal River.

Consistent with other wet-zone endemics, populations of *R. wilpita* (Figure 5.21) from the Kalu, Bentara and Gin basins contain two (H2, H3), one (H5) and one (H4) haplotypes, respectively, with no sharing of haplotypes between them (Figure 5.21b). Meanwhile, its sister group, the micro-endemic *R. armitagei*, possesses a single, unique haplotype (H1).

The *cox1* haplotype network of Sudasinghe *et al.* (2020d) (Figure 5.19) shows Sri Lankan samples of *R. dandia* to represent six haplotypes (H13–H18), while the Indian *R. dandia* represents eight (H19–

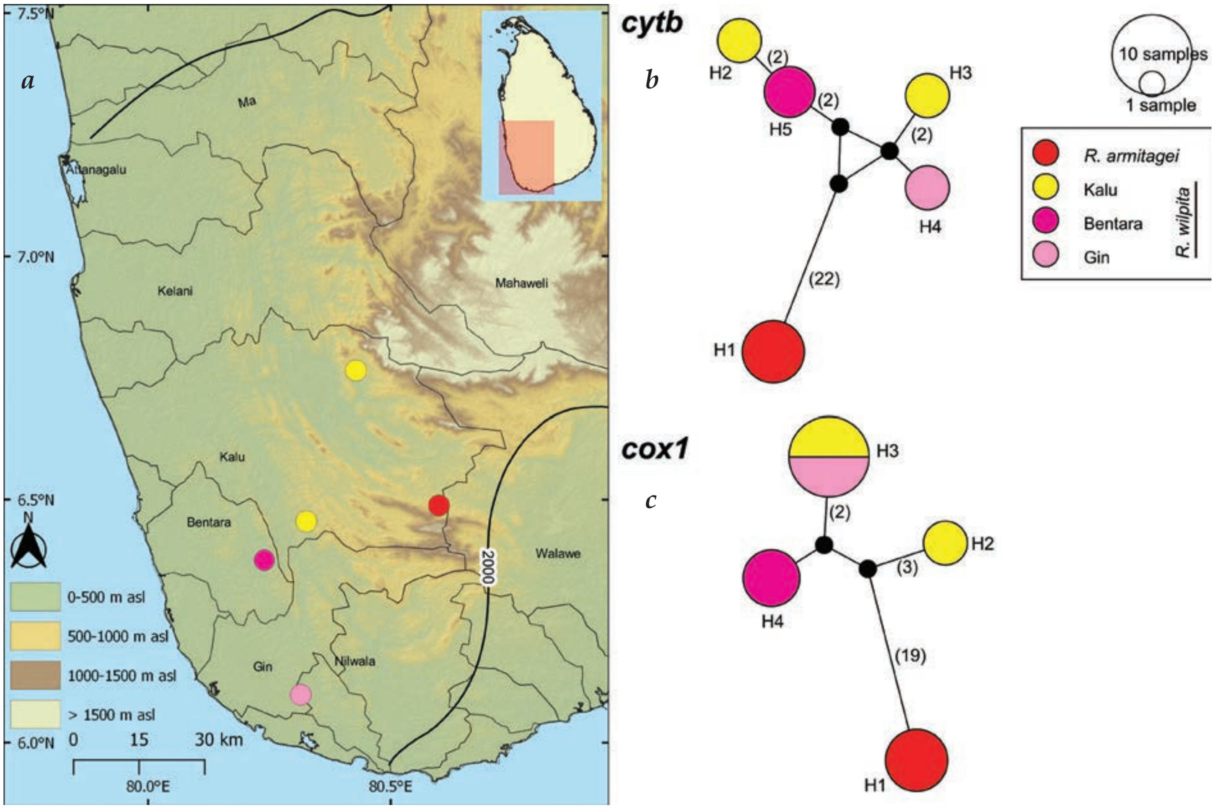


Figure 5.21. ***a,*** Sampling localities and median-joining haplotype network for the Sri Lankan species of *Rasbora* in the wilpita clade, based on the analysis of **b,** a 591 bp fragment of the *cytb* gene; and **c,** a 636 bp of the *cox1* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to the river basins or species.

26). No *R. dandia* haplotypes are shared between Sri Lanka and India; they are separated minimally by six mutational steps. Within the Sri Lankan populations of *R. dandia*, H13, a high-frequency haplotype represented in samples from all three climatic zones, appears to signal an ancestral condition of the species in the island.

Rasbora microcephala (Figure 5.20) contains four haplotypes (H8–H11) in a star-like pattern. Haplotype H8, present in samples from Mandekal, Malwathu, Kala, Maha, Deduru and Attanagalu basins, apparently represents an ancestral condition in *R. microcephala* in Sri Lanka.

Meanwhile, *R. naggsi* shares the H11 haplotype between the Kalu, Walawe and Kirindi basins, and has a unique haplotype, H12, in the Walawe.

Rasbora adisi contains only a single shared haplotype, H5, present in samples from the Gal, Kumbukkan and Mahaweli basins, in addition to two unique haplotypes H6 and H7 in the Mahaweli and Menik basins, respectively.

Broadly reflecting the topology of the *cytb* network, populations of *R. wilpita* (Figire 5.21) in the Bentara basin contain a single unique haplotype (H3), while those from the Kalu form a unique (H2) haplotype and another (H4) shared with the Gin basin.

As in the case of *cytb*, *R. armitagei* has a single, unique *cox1* haplotype (H1).

The Sri Lanka species of *Rasbora* appear to show the highest degree of philopatry in the case of wet-zone endemics such as *R wilpita,* less so in the case of species with distributions extending into the dry zone, such as *R. naggsi*, and almost none at all in the case of the recent dispersants from India, *R. microcephala* and *R. dandia.*

5.4.6 *Systomus*

Phylogeography. The three endemic species of *Systomus* (*S. asoka, S. pleurotaenia* and *S. martenstyni*: Figure 5.22) form a monophyletic group whose common ancestor dispersed to Sri Lanka in the early Miocene (see Figure 5.23 for divergence times). *Systomus asoka* is a narrow-range endemic, owing to ecological or physiological constraints that are not yet understood, while *S. martenstyni* is confined to the rivers and larger streams draining the Knuckles and adjacent hills. The fourth species, *S. sarana*, has a wide distribution throughout the lowlands of both Sri Lanka and India.

Systomus asoka and *S. martenstyni* each exhibit only a single *cytb*, *cox1* and *rag1* haplotype: their restricted ranges limit discussion of their phylogeography.

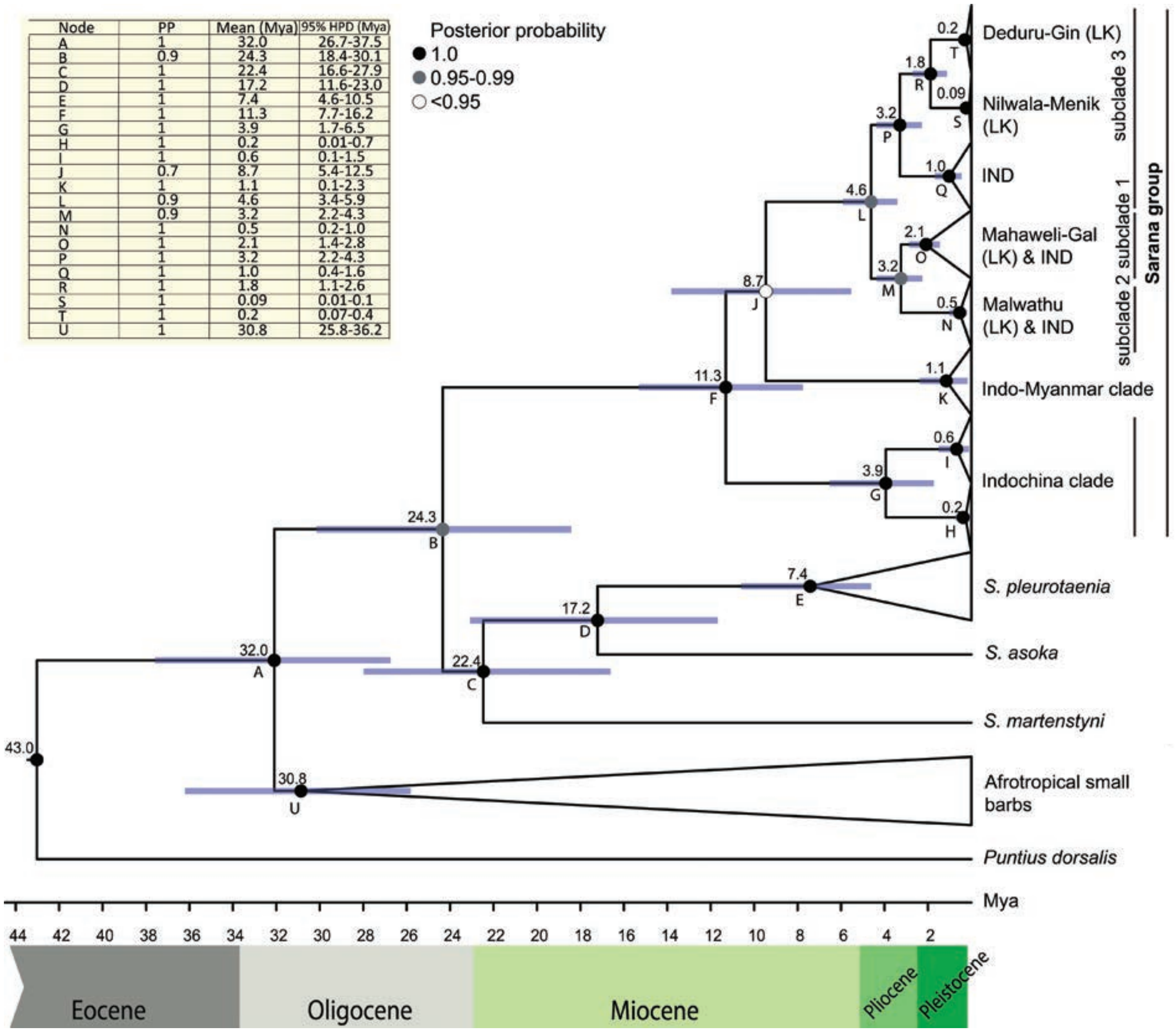
Sudasinghe *et al.* (2020c) estimated the split between the South- and the Southeast Asian subclades of the sarana group (node F in Figure 5.23) to have occurred 10.8 (95 % HPD: 15.0–7.6) Mya. *Systomus sarana* entered Sri Lanka for the first time, however, substantially later: ~3.1 Mya (95 % HPD: 4.2–2.2 Mya; see node P in Figure 5.23). Although the Palk Isthmus was frequently inundated during the Pliocene, it was also subaerial for extensive periods (Figure 3.63) and *S. sarana* dispersed across it on three occasions. Unlike the endemic species of *Systomus*, it is a habitat generalist which is not dependent on rainforest contexts, although it does occur also in rain forests (Kortmulder *et al.*, 1982; Moyle & Senanayake, 1984).

***Systomus sarana*.** Three geographically and genetically distinct populations of *Systomus sarana* are represented in Sri Lanka, which Sudasinghe *et al.* (2020c) labelled Subclades 1–3 (Figure 5.23).

Subclade 3 is confined to the western and southern lowlands from the Deduru to the Menik basins, with the Sri Lankan and Indian (Tamil Nadu, Kerala) members of the subclade exhibiting a sister-group relationship. Sudasinghe *et al.* (2020c) dated the split between the Indian and Sri Lankan populations to 3.1 (95 % HPD: 4.2–2.2) Mya, with the western and southern populations diverging 1.8 (95 % HPD: 2.6–1.1) Mya. This subclade exhibits a distinct haplotype distribution (Figure 5.24). A unique *cytb* haplotype is shared between the southern Walawe, Kirindi and Menik basins, while another is restricted to the Kirindi, while a unique *cox1* haplotype is shared among basins from Nilwala to Kirindi, inclusive. Meanwhile, the Deduru, Attanagalu, Kalu and Bentara populations share a *cytb* and *cox1* haplotype each.

Subclade 1 has a wide distribution across the northern Western Ghats and central India. It occurs also in the Mahaweli and Gal basins, which drain the island's east and northeast, respectively. This subclade is descended from an ancestor which entered Sri Lanka in the early Pleistocene, 2.2 (HPD: 2.9–1.6) Mya. The close relationship between Mahaweli and Gal Oya samples suggests a former connection between these two basins,

Figure 5.22. Sri Lankan species of *Systomus*. ***a,*** *S. sarana,* which ranges widely through Sri Lanka and India; ***b,*** *S. pleurotaenia,* which ranges from the Attanagalu to the Nilwala basins in the south-western wet zone; ***c,*** *S. martenstyni,* which is endemic to streams draining the northern Knuckles Hills, within the Mahaweli basin; and ***d,*** *S. asoka,* known from two locations in the middle region of the Kelani basin.



Node	PP	Mean (Mya)	95% HPD (Mya)
A	1	32.0	26.7-37.5
B	0.9	24.3	18.4-30.1
C	1	22.4	16.6-27.9
D	1	17.2	11.6-23.0
E	1	7.4	4.6-10.5
F	1	11.3	7.7-16.2
G	1	3.9	1.7-6.5
H	1	0.2	0.01-0.7
I	1	0.6	0.1-1.5
J	0.7	8.7	5.4-12.5
K	1	1.1	0.1-2.3
L	0.9	4.6	3.4-5.9
M	0.9	3.2	2.2-4.3
N	1	0.5	0.2-1.0
O	1	2.1	1.4-2.8
P	1	3.2	2.2-4.3
Q	1	1.0	0.4-1.6
R	1	1.8	1.1-2.6
S	1	0.09	0.01-0.1
T	1	0.2	0.07-0.4
U	1	30.8	25.8-36.2

Figure 5.23. Bayesian time-calibrated tree, using the *cytb* substitution rate, for the concatenated *cytb+cox1* dataset of *Systomus* (1736 bp, Sudasinghe *et al*., 2020c). Bars and values at nodes represent 95 % HPD and mean ages of divergence estimates, respectively. Note that in Sudasinghe *et al*. (2020c) and the text herein, the median values for divergence times are given.

perhaps in the context of a historical river-capture event, as evidenced also by *Laubuka*.

Subclade 2 ranges across eastern peninsular India to West Bengal, being represented in Sri Lanka only in the Malwathu drainage in the north-western dry zone. It is the most recent lineage of *Systomus* to have dispersed to Sri Lanka, 2.1 (HPD: 3.2–1.1) Mya, and shows no *cytb* or *cox1* haplotype diversity within the island.

As expected, the *rag1* haplotype diversity within *S. sarana* is more conservative: the Mahaweli and Gal basins (Subclade 1) share a unique haplotype, as does the southern population of Subclade 3 (Kirindi and Menik). The western population of Subclade 3, however, shares a haplotype with Subclade 2 (Malwathu).

Systomus pleurotaenia. *Systomus pleurotaenia,* the most widely distributed species of *Systomus* endemic to Sri Lanka, shows strong phylogeographic structure (Figure 5.25b,c). It is ubiquitous in shaded, clearwater rainforest streams from the Attanagalu to the Nilwala basins.

Cytochrome-b haplotypes of *S. pleurotaenia* are shared only between the Attanagalu and Kelani, and the Nilwala and Gin (Figure 5.25b). The head-

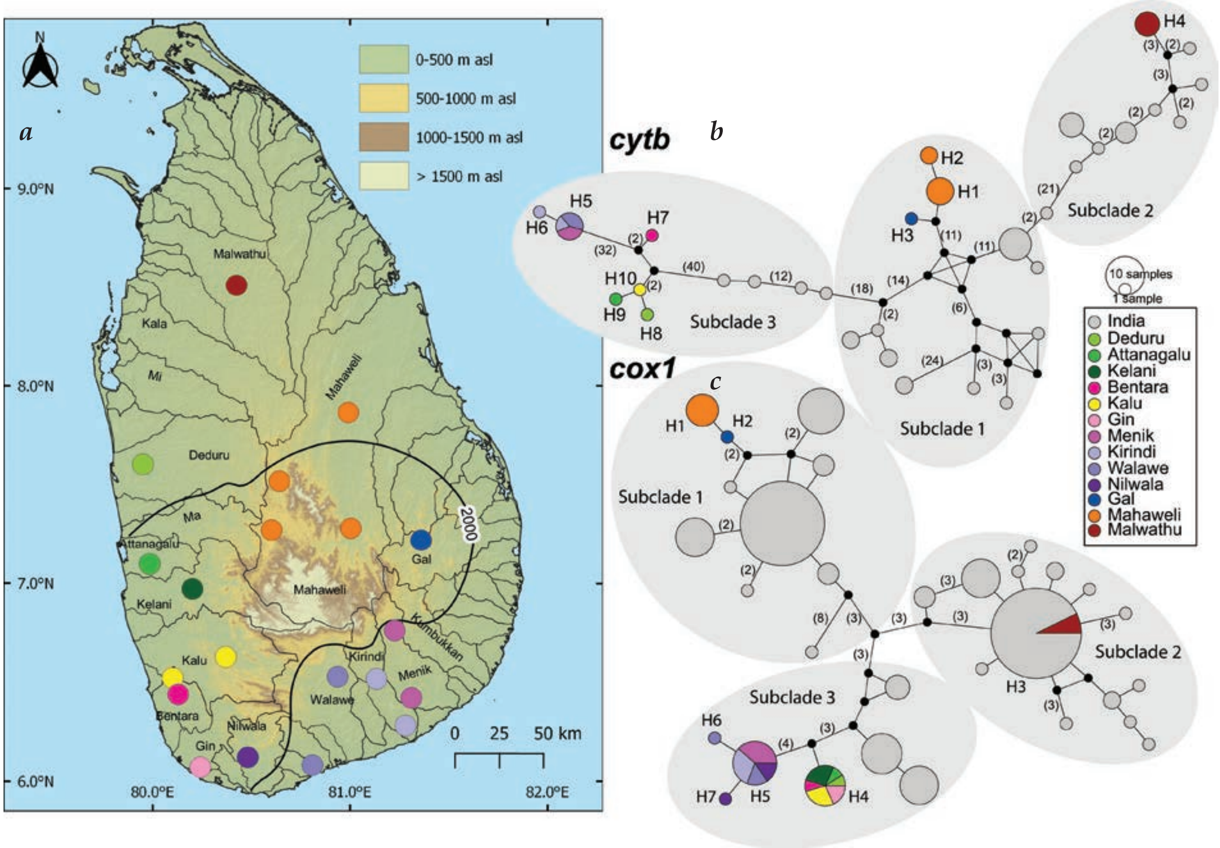


Figure 5.24. ***a,*** Sampling localities and median-joining haplotype network for the Indo-Sri Lanka clade of the sarana group, based on the analysis of ***b,*** a 1082 bp fragment of the *cytb* gene; and ***c,*** a 654 bp fragment of the *cox1* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to the river basins or the regions.

waters of these basin pairs are contiguous, and gene flow likely occurred through river capture. Although this species occurs even at elevations as low as 20 m, it does not enter the floodplain and hence, evidently does not disperse across it.

The population from the Kalu basin contains three unique *cox1* haplotypes, while the Kelani and Attanagalu populations share a further one. Two samples from Opatha (Nilwala basin) share a single haplotype; however, those from Kotapola (Nilwala) and Deniyaya (Gin) share another, which differs from the remaining haplotypes by a substantial 36 or more mutational steps, and from samples from Opatha by 37.

The *cytb* haplotype network resembles that of *cox1*. Populations of *S. pleurotaenia* from the Kalu basin contain three haplotypes, while the Kelani and Attanagalu populations share one. Samples from Opatha (Nilwala basin) share two haplotypes while, remarkably, those from Kotapola (Nilwala) and Deniyaya (Gin) share another. The last-mentioned haplotype differs from all others by at least 68 mutational steps, and from those from Opatha by 83–84 mutational steps.

In the *rag1* haplotype network, populations of *S. pleurotaenia* from the Attanagalu, Kelani and Kalu, and one sample from Opatha in the Nilwala basin, form a shared haplotype; a further sample from Opatha and two from Kotapola, in the same basin, however, each possess a unique haplotype.

Sudasinghe *et al.* (2020c) concluded that the unusual haplotype distribution in *S. pleurotaenia* appears to be the result of long-isolated populations within individual basins mixing as a result of river capture. It suggests that such capture events occurred between the Nilwala and Gin basins, and the Kelani and Attanagalu basins.

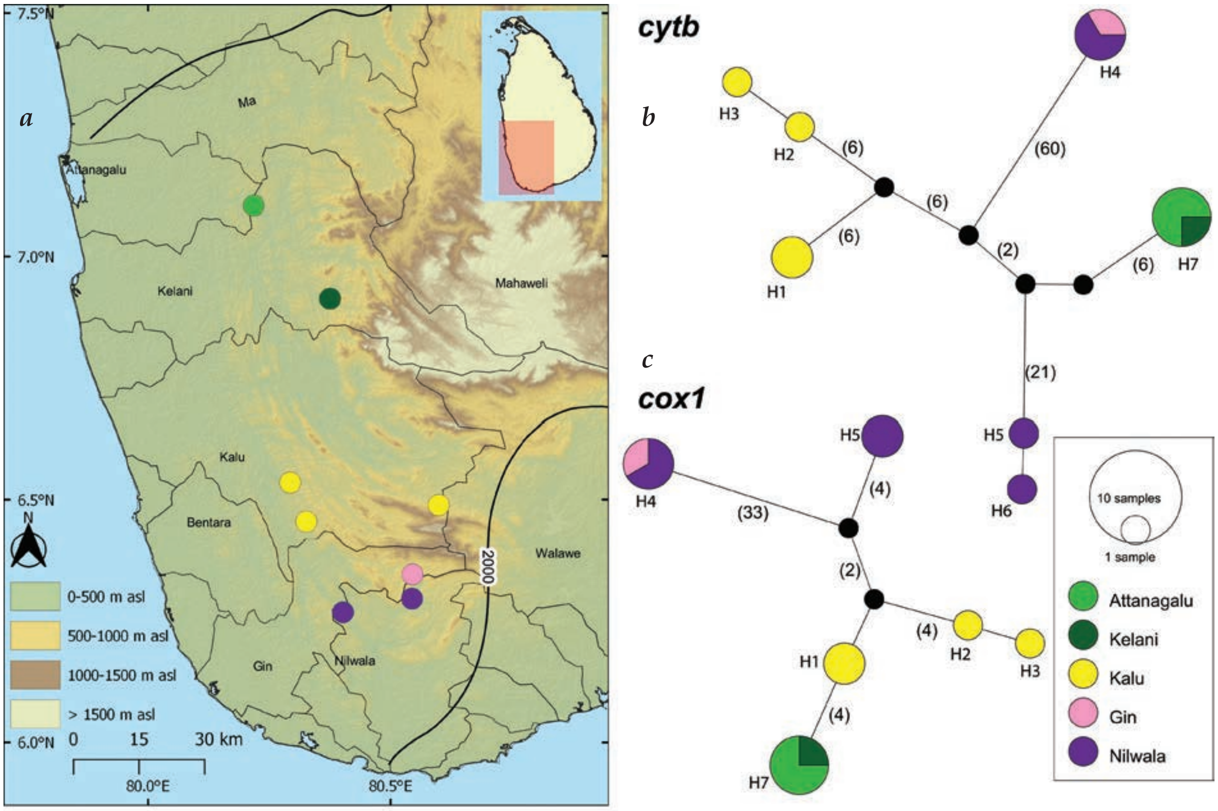


Figure 5.25. ***a,*** Sampling localities and median-joining haplotype network for *Systomus pleurotaenia*, based on the analysis of ***b,*** a 1082 bp fragment of the *cytb* gene; and ***c,*** a 654 bp fragment of the *cox1* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to river basins.

5.4.7 *Pethia*

The genus *Pethia,* which presently includes some 43 valid species, has a distribution ranging from Sri Lanka across India and on to Myanmar. These are colourful, usually sexually dimorphic fishes that have long been popular in the ornamental-fish trade, in which the Sri Lankan endemic *Pethia nigrofasciata* was for decades a favourite. Five species of *Pethia* are known from Sri Lanka, all of them endemic to the island (Figure 5.26).

With a range spanning the Kelani and Walawe basins, *P. nigrofasciata* is the most widely distributed species of *Pethia* in the wet zone, while *P. bandula*, a narrow-range endemic, is confined to a single small stream near the northern boundary of the Kelani basin. *Pethia cumingii* and *P. reval* are a parapatric species pair. The former has a distribution ranging from the Kalu to the Walawe basins, while *P. reval* ranges from the Kelani in the wet zone, northwards to the Deduru basin, in the intermediate zone. It appears that a zone of contact between *P. cumingii* and *P. reval* may exist in the Kalu basin (discussed below). These four species inhabit mainly lowland streams (*P. nigrofasciata,* 1–520 m asl[*†]; *P. bandula,* 170 m asl; *P. cumingii,* 15–190 m asl; *P. reval,* 10–125 m asl[†]). The fifth species, *P. melanomaculata*, is confined to—but widely distributed across—the intermediate zone and the dry zone plains, in the elevation range 25–295 m asl.

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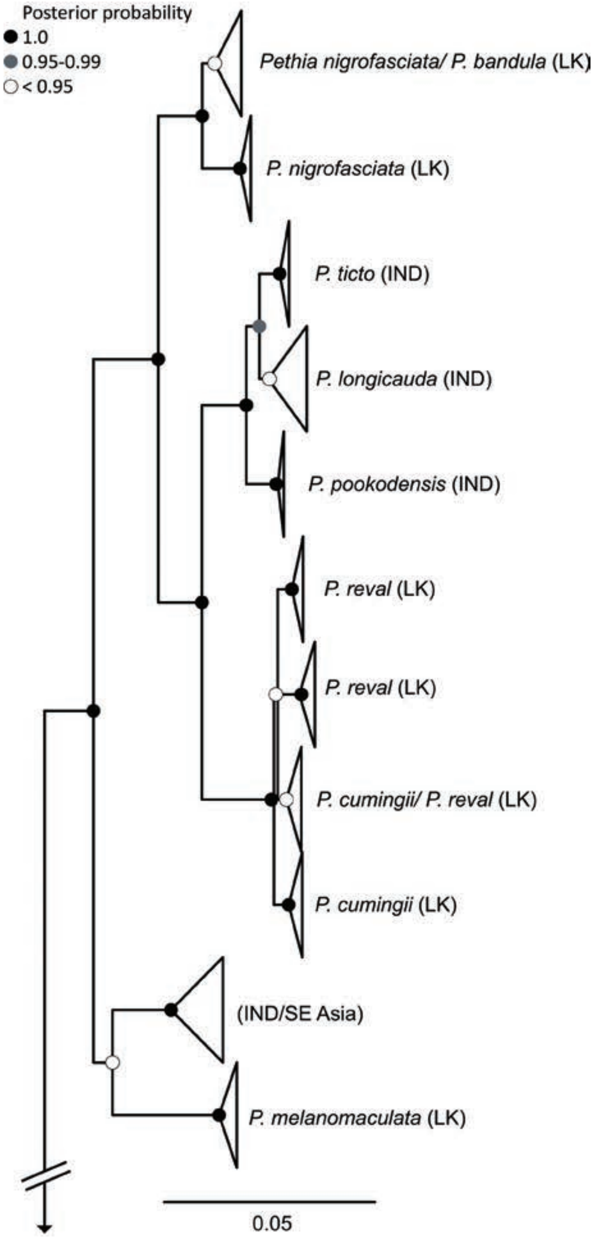
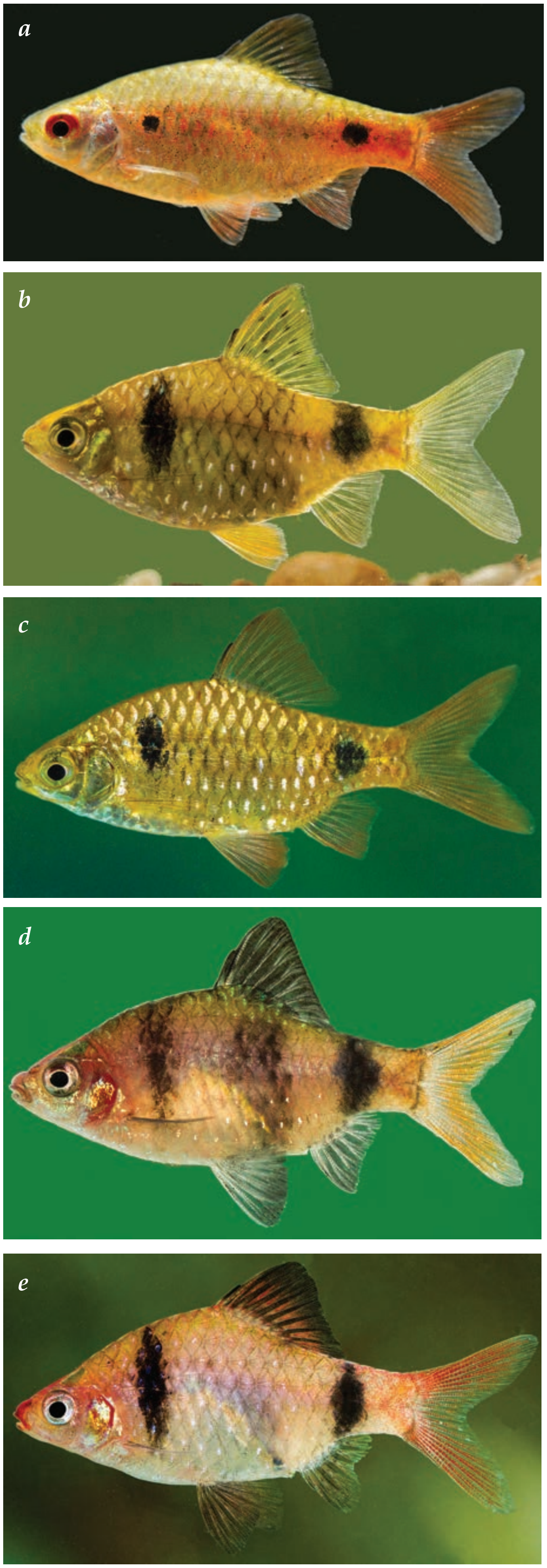
[*] 590 m asl if the population at Pambahinna is naturally occurring.

[†] In the Mahaweli basin, to which it has been introduced, the species reaches elevations of up to 660 m asl.



▲ **Figure 5.27.** Topology of the molecular phylogenetic relationships of Sri Lankan *Pethia*, based on Bayesian inference of the concatenated *cytb+rag1* dataset (2572 bp), after Sudasinghe *et al*. (2021c).



◄ **Figure 5.26.** The Sri Lankan species of *Pethia*. ***a,*** *P. melanomaculata,* a species widely distributed across the dry zone lowlands, entering also the western and eastern intermediate zones; ***b,*** *P. cumingii,* which ranges from the Kalu to the Gin basins; ***c,*** *P. reval,* which extends from the Deduru to the Kelani basin, with a translocated population in the Mahaweli; ***d,*** *P. nigrofasciata,* distributed from the Attanagalu to the Walawe basins, with a feral population in the Mahaweli; and ***e,*** *P. bandula,* a narrow-range endemic in the Kelani basin.

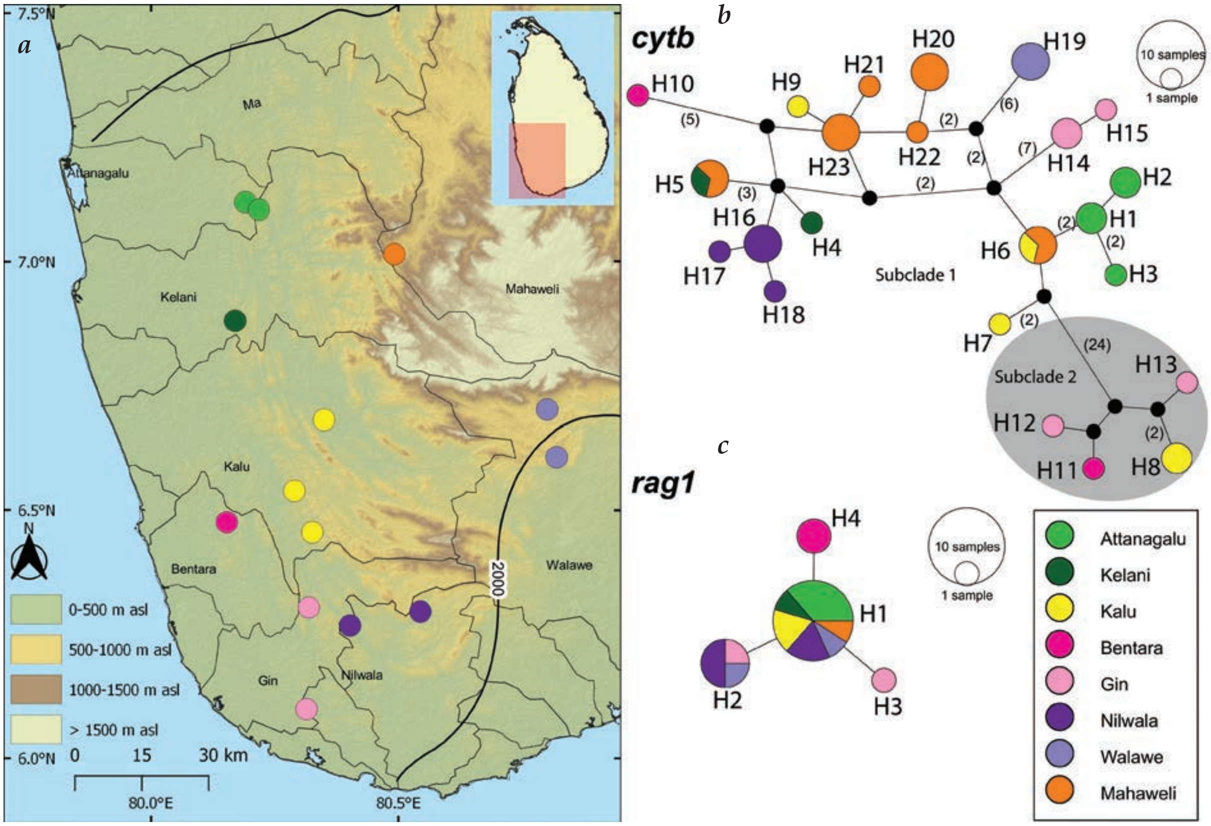


Figure 5.28. ***a,*** Sampling localities for *Pethia nigrofasciata* for the molecular analysis in Sudasinghe *et al*. (2021c). Median-joining haplotype network for *P. nigrofasciata*, based on the analysis of ***b,*** a 1082 bp fragment of the *cytb* gene, and ***c,*** a 1490 bp fragment of the *rag1* gene. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colours correspond to river basins.

Phylogeography. The phylogenetic analysis of Sudasinghe *et al.* (2021c) recovered the Sri Lankan species of *Pethia* not as a monophyletic diversification but deriving either from three separate dispersal events from India, or from two such events in addition to a back-migration to India (Figure 5.27). Although no timing analysis was provided in that study, the species' present habitat associations suggest a pattern similar to that of other such species in the island (*e.g., Laubuka varuna*). Assuming there were three dispersals from India, the common ancestor of *P. nigrofasciata* and *P. bandula* dispersed across the Palk Isthmus when its climate was relatively aseasonal, supporting rain forests, close to the Miocene-Pliocene boundary, while that of *P. reval* and *P. cumingii* arrived towards the end of the Pliocene, but before the isthmus aridified in the Pleistocene. If, however, only two India-Sri Lanka dispersal events were involved, then the common ancestor of the four south-western species must have dispersed at around the Miocene-Pliocene boundary. Given the wide distribution of *P. melanomaculata* in even the more arid regions of the dry zone, its ancestor is presumed to have arrived in the Pleistocene. Indeed, most of the dry zone's fishes appear to derive from India-Sri Lanka dispersal events during this time, suggestive of an extirpation of the earlier fauna.

The haplotype network of *P. nigrofasciata* presented by Sudasinghe *et al.* (2021c) indicates strong phylogeographic structure, with no *cytb* haplotypes shared between basins and only one *rag1* haplotype shared disjunctively among all except the Bentara and Gin basins (Figure 5.28). While their concatenated *cytb+rag1* phylogeny recovered *P. nigrofasciata* as two well-supported subclades, one spanning the distribution of the

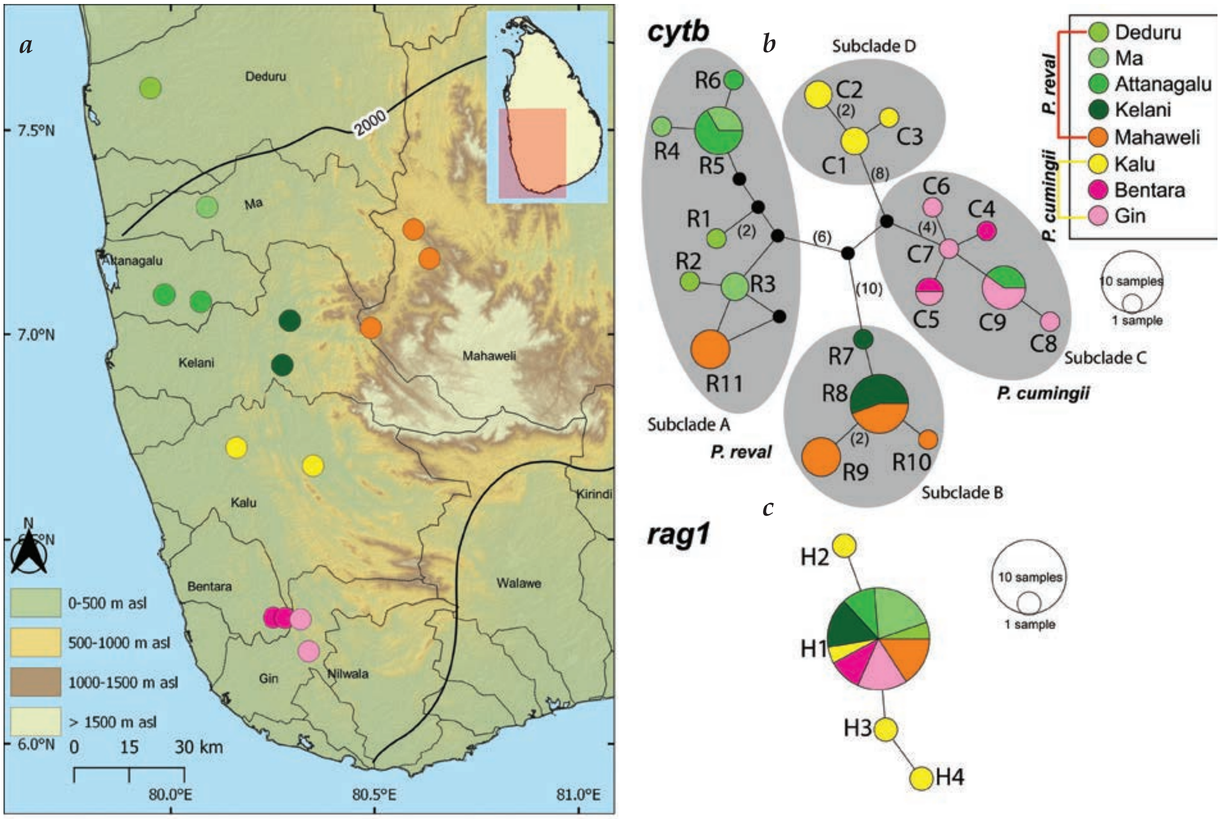


Figure 5.29. ***a,*** Sampling localities for *Pethia reval* and *P. cumingii* for the molecular analysis in Sudasinghe *et al.* (2021c). Median-joining haplotype network for *Pethia reval* and *P. cumingii*, based on the analysis of ***b,*** a 1082 bp fragment of the *cytb* gene, and ***c,*** a 1490 bp fragment of the *rag1* gene. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colours correspond to river basins.

species from the Attanagalu to the Walawe basins, and the other confined to the region between the Kalu and Gin basins, inclusive, no haplotypes are shared between the two; instead, each subclade has haplotypes unique to individual basins. Unlike in the previously mentioned cyprinids, there is no evidence of inter-basin gene flow through headwater capture events in *Pethia*, for example, between the Kalu and Walawe rivers.

While *P. cumingii* and *P. reval* are not obligatory rainforest associates, three of the four subclades of this species pair each exhibit distinct phylogeographic structure (Figure 5.29). Subclades A and B contain haplotypes unique to *P. reval* and subclade D contains haplotypes unique to *P. cumingii*. Subclade C, however, includes haplotypes shared between both *P. reval* and *P. cumingii*. One *cytb* haplotype, R5, is shared between the adjacent Maha and Attanagalu basins, while another, C5, is shared between the Bentara and Gin basins. C9, however, is disjunct between the Attanagalu and Gin basins*. Interestingly, three *cytb* and three *rag1* haplotypes are unique to the Kalu basin, which shares no haplotypes with any other basin. Thus, the species of *Pethia* confined to the south-western wet and intermediate zones exhibit little inter-basin gene flow (Sudasinghe *et al.* 2021c).

By contrast, most of Sri Lanka's dry zone fishes investigated until now exhibit relatively weak phylogeographic structure (*e.g.*, Sudasinghe *et al.* 2019a–c, 2020c–g, 2021a,b). In a scenario reminiscent of *Laubuka lankensis, Pethia melanomaculata* presents as three regional haplogroups (Figure 5.30): the north-western dry-zone basins, the Mahaweli basin, and the eastern basins. These are separated weakly, by relatively few mutational steps, and low haplotype and nucleotide diversity (Table 5.5).

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* This may be an ancestral haplotype that has not yet been fixed in the intervening populations.

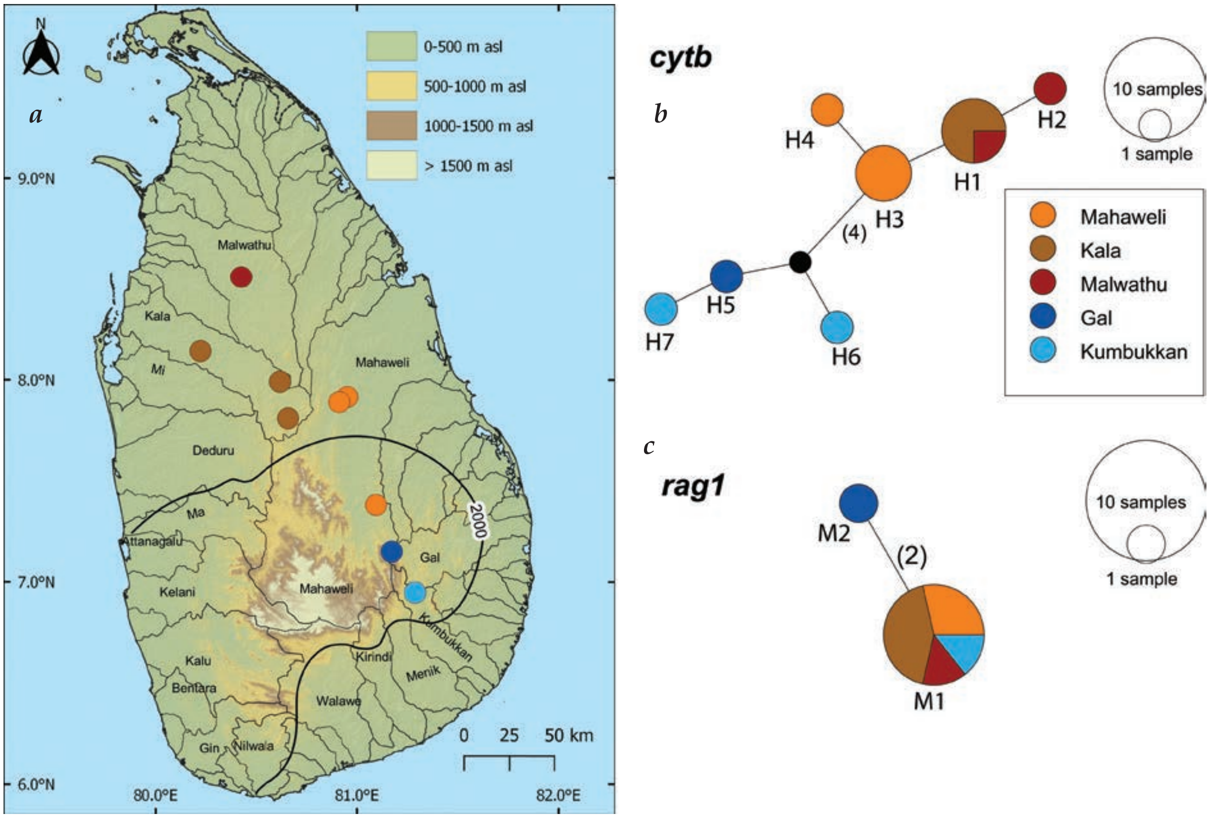

Figure 5.30. ***a,*** Sampling localities for *Pethia melanomaculata* in the molecular analysis of Sudasinghe *et al*. (2021c). Median-joining haplotype network for *P. melanomaculata*, based on the analysis of ***b,*** a 1082 bp fragment of the *cytb* gene, and ***c,*** a 1490 bp fragment of the *rag1* gene. The number of mutational steps >1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colours correspond to river basins.

The haplotype networks of both *P. nigrofasciata* and *P. reval* indicate shared mitochondrial haplotypes (N5 and R8, respectively) between the west-draining Kelani and east-draining Mahaweli basins. These basins share a common boundary along a 40 km long, 600–2000 m-high ridge that extends from Ginigathena to Horton Plains. Sudasinghe *et al.* (2020a) reported a shared haplotype between populations of the dwarf snakehead *Channa orientalis* between them (see section 5.4.9, below), suggesting that gene flow between them is possible. In the case of *Pethia*, however, Wikramanayake (1990a) recorded a translocation experiment in which both *P. nigrofasciata* and *P. reval* (his '*P. cumingii*') were introduced to a stream near Ginigathena (6.987°N, 80.499°E). Whether stemming from this or other undocumented ones, both *P. nigrofasciata* and *P. reval* now occur as far as 40 km downstream, at Peradeniya.

The haplotype network of Sudasinghe *et al*. (2021c; Figure 5.29b,c) revealed that the Mahaweli population of *P. reval* stems from multiple sources, as is the case also in *P. nigrofasciata*. In *P. reval,* haplotype R11 from Mahaweli, for example, though not shared with any other basins, falls within subclade A. Meanwhile, haplotypes R8–R10 are nested in subclade B. The remaining samples of subclade A are from the Deduru, Ma and Attanagalu basins, whereas those of subclade for B are from Kelani. The multiple origins of the Mahaweli populations is unsurprising given that one population was present by the 1920s (Deraniyagala, 1930) and another was introduced in the 1980s (Wikramanayake, 1990a). Haplotypes R9–R11 of *P. reval* in the Mahaweli are unique. This too, suggests that the haplotype diversity of the natural populations of *P. reval* is underrepresented in the sampling of Sudasinghe *et al*., 2021c. Further, Figure 5.28 shows the population of *P. nigrofasciata* in the Mahaweli to contain several unique *cytb* haplotypes (N20–N23); this too, reflects a limitation of the sampling density.

The phylogeography of Sri Lanka's species of *Pethia* pose multiple questions that can probably be answered only by future research. Primary among these are the machanisms by which within-basin genetic integrity is maintained. As noted above, the range of *P. nigrofasciata* very nearly reaches the coastal floodplain, while that of *P. reval* actually extends well into it. What then, inhibits inter-basin dispersal via the floodplain? As the introductions of these two species to the Mahaweli show, they have been able to disperse widely within that basin in only a few decades. However, dispersal within their native range appears more restricted. Nowhere is this clearer, perhaps, than in the case of *P. bandula*, the global range of which is a 3-km stretch of a small stream traversing an agricultural landscape. Credible accounts exist of the species having been successfully translocated to nearby streams in the same locality by well-meaning conservationists (though regrettably, with no documentation). Given that the precise locations at which these introductions were made and the provenance of the stocked fishes have never been published, the success of these introductions cannot be assessed. It means that future ichthyologists will have to invest considerable 'detective work' to establish whether the parent stock of these populations originated from the type locality of *P. bandula* or were derived from aquarium stock that might have been contaminated through hybridization with other species of *Pethia*.

The possible zones of hybridization between *P. reval* and *P. cumingii* in the Kalu basin (Meegaskumbura *et al*., 2008), and between *P. nigrofasciata* and *P. bandula* in headwaters of the Attanagalu basin (Sudasinghe *et al*., 2021c) too, remain to be evaluated.

5.4.8 *Rasboroides*

As explained in Chapter 4, the common ancestor of the genera *Rasboroides* and *Horadandia* appears to have been among the earliest among cypriniform lineages to disperse into Sri Lanka, probably as early as the late Eocene (Sholihah *et al*., 2021b). Two species are recognized in each genus of these miniature fishes: *R. vaterifloris* and *R. pallidus*, both confined to rain forests in Sri Lanka's wet zone (Figure 5.31); and *H. atukorali* and *H. brittani*, with wide distributions in the lowlands of Sri Lanka and southern India, respectively.

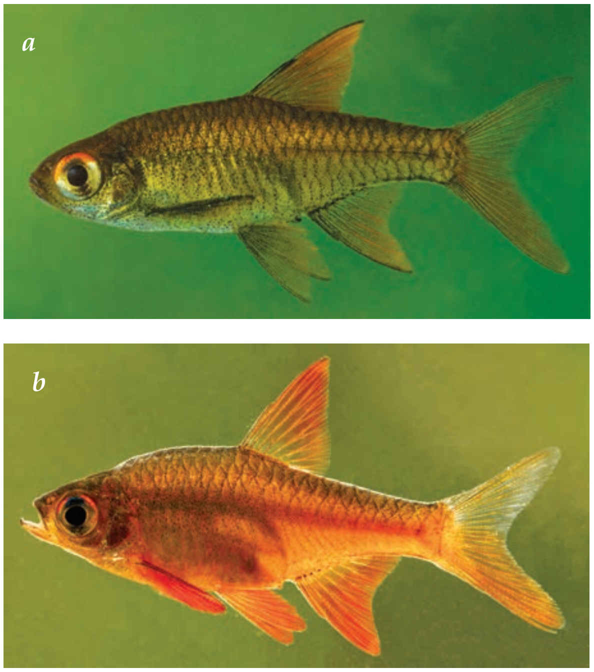

Figure 5.31. The species of *Rasboroides*: ***a***, *R. vaterifloris*, which occurs in the Kalu and Kelani basins; and ***b***, *R. pallidus*, which ranges from the Kalu to the Nilwala basin.

Within Sri Lanka, *R. vaterifloris* is distributed in the Kalu basin and also the southern parts of the Kelani, while *R. pallidus* has a wider range spanning the Bentara and Nilwala basins. It also occurs at a few locations within the Kalu basin, and it remains unknown whether these populations are native or the result of unintended releases, especially given that *R. pallidus*, owing to its striking coloration, was for many decades preferentially harvested for the ornamental fish trade.

Phylogeography. Sudasinghe *et al.* (2018a) investigated the phylogeography of *Rasboroides* across the range of the genus except for the Kelani and Nilwala basins (Figure 5.32). Their results showed no shared *cox1* or *cytb* haplotypes between *R. vaterifloris* and *R. pallidus*. Populations of *R. vaterifloris* in tributaries within the same basin (*e.g.*, at Gilimale and Athwelthota, both within the Kalu basin), meanwhile, contained unique haplotypes. In the case of *R. pallidus*, the *cox1* H1 haplotype is shared by the Kalu and Bentara basins, while the

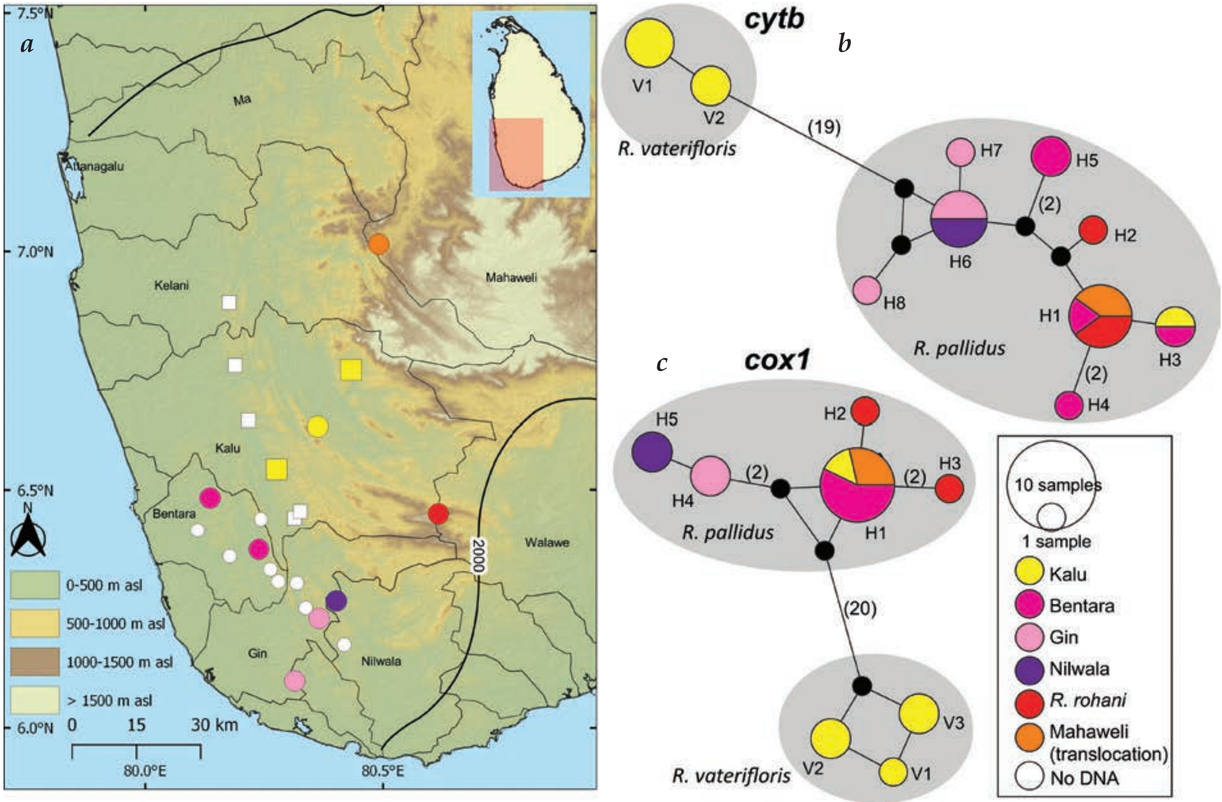

Figure 5.32. ***a,*** Sampling localities for *Rasboroides vaterifloris* (squares) and *R. pallidus* (circles) from the molecular analysis of Sudasinghe *et al*. (2018a) and unpublished sequences: white symbols represent locations at which, though the species was recorded, no samples for genetic analysis were collected; ***b,*** haplotype networks, based on a 609 bp fragment of the *cytb* gene; and ***c,*** a 669 bp fragment of the *cox1* gene. The sizes of the circles are proportional to the number of individuals sharing a given haplotype. The black circles are hypothetical nodes. Legend colours correspond to river basins.

Gin and Bentara populations have the H6-H7 and the H5 haplotypes, respectively, unique to them, suggestive of isolation.

This study served also to show that the populations of *Rasboroides* in the Walawe and Mahaweli basins, which had previously been identified as *R. rohani* (Batuwita *et al.,* 2013) and *R. vaterifloris* (Wikramanayake, 1990a), respectively, are both in fact translocated populations of *R. pallidus.* The former resulted from an undocumented introduction, while the latter derives from an introduction made in 1981 (Wikramanayake, 1990a).

5.4.9 *Channa orientalis*

The endemic pelvic-fin-less snakehead *Channa orientalis* (Figure 5.33) has a wide range within the wet zone of Sri Lanka, from the Attanagalu to the Nilwala, and the Mahaweli basin. Though associated primarily with rainforest habitats, it is commonly encountered in clearwater streams in the elevation range 5–1315 m asl.

Phylogeography. Based on specimens sampled at 16 locations in the major river basins in which the species occurs, Sudasinghe *et al*. (2020a) conducted a morphological and molecular analysis, based on sequences of the *cox1* barcoding gene. Their results were surprising: *Channa orientalis* comprises two genetically distinct populations, separated by a substantial uncorrected p-distance of 6.9–8.1 percent, a divergence magnitude usually associated with morphologically distinct species of snakeheads. However, they found the two populations to be morphologically indistinguishable. The molecular analysis of Ekanayake *et al*. (2021) too, corroborated the findings of Sudasinghe *et al*. (2020a).

One lineage, which Sudasinghe *et al*. (2020a) referred to as the ‘Southern’, occurs in the Gin and

Figure 5.33. Examples of *Channa orientalis:* ***a,*** from the Southern lineage (Kalu to Nilwala basins); and ***b,*** from the Northern lineage (Attanagalu to Kalu basin, and Mahaweli basins).

Nilwala basins. The other, the 'Northern' lineage, occurs in the Attanagalu, Kelani, Bolgoda and Mahaweli basins.

Although both lineages appear to occur in the Kalu basin, they may nevertheless be allopatric. The samples from the lower reaches of Kalu sampled so far represent the northern lineage, while the population in the upper reaches of basin represent the southern lineage. The uncorrected p-distances within the southern and northern lineages were 0.0–2.7 percent and 0.0–2.5 percent, respectively. Interestingly, the two populations differed from their genetically closest congener, *Channa kelaartii*, by only 6.1 percent and 5.1 percent, respectively, a lesser pairwise *cox1* distance than exists between the morphologically indistinguishable northern and southern populations of *C. orientalis*.

In the median-joining network (Figure 5.34), the haplotypes of the southern and northern lineages of *C. orientalis* are separated by a minimum of 40 mutational steps. The northern lineage includes seven haplotypes (N1–N7), among which N1 and N2 are shared between the headwaters of Kelani and the Mahaweli, while N3, N4, N5 and N6-N7 are unique to the Mahaweli, Attanagalu, Bolgoda and Kalu basins, respectively.

The southern lineage, meanwhile, includes eight haplotypes (S1–S8). Samples from the Gin basin contain two (S4, S5), while those from the Kalu and Nilwala contain three each (S1–S3 and S6–S8, respectively). None of these is shared between the basins.

Channa orientalis, along with *Belontia signata* and *Clarias brachysoma,* are the only Sri Lankan endemics that appear to have a natural distribution spanning the central mountains, between the eastward-draining Mahaweli and the westward-draining basins of the south-western wet zone. Sudasinghe *et al.* (2020a) pointed out that *C. orientalis* occurs at elevations as high as 1300 m asl at Dick Oya, in the Kelani basin. The sharing of haplotypes in *C. orientalis* between the headwaters of Kelani and Mahaweli may suggest that gene flow across the Ginigathena-Horton Plains ridge, which separates the Kelani and Mahaweli basins, may have occurred through a river-capture event. The authors eliminated the possibility of a recent inter-basin translocation by drawing attention to museum specimens collected in the Mahaweli prior to 1874.

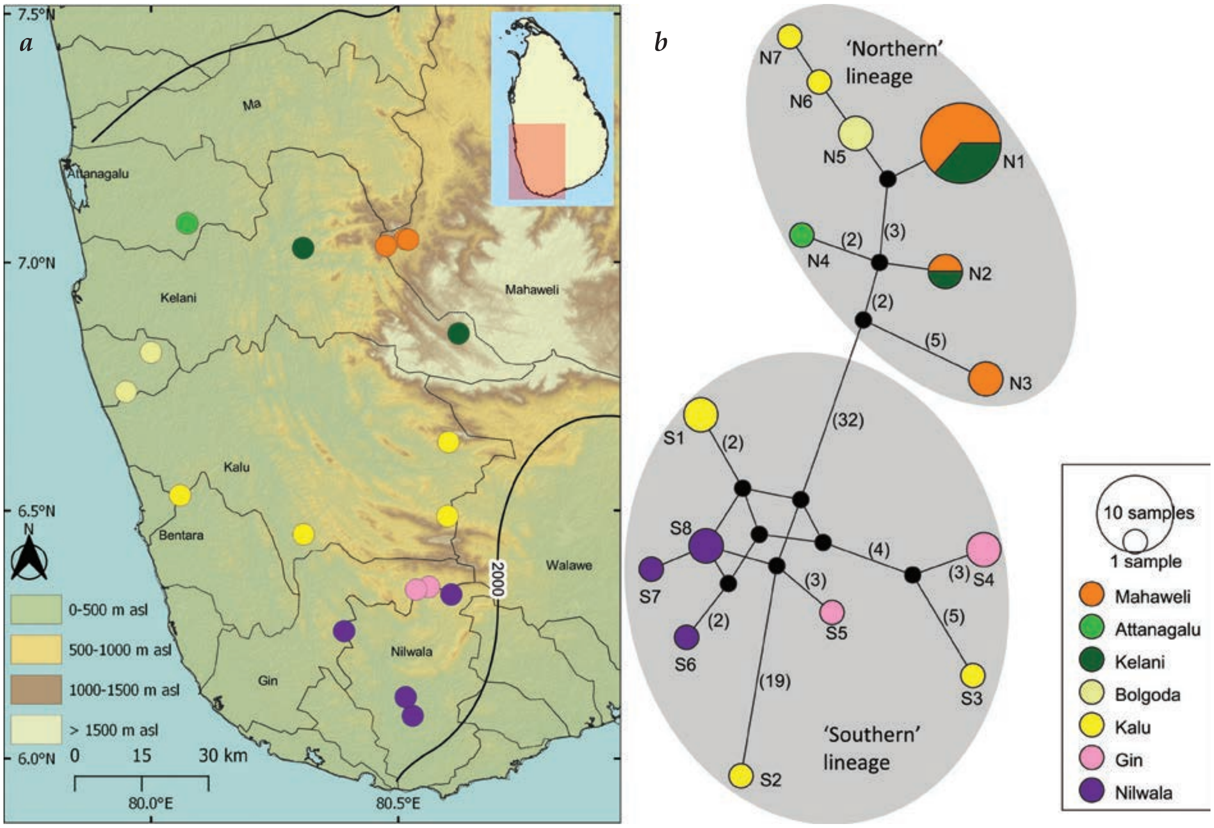

Figure 5.34. ***a,*** Sampling localities; and **b,** median-joining haplotype network for *Channa orientalis*, based on the *cox1* sequences reported on by Sudasinghe *et al.* (2020a) and Ekanayake *et al.* (2021). The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps > 1 is indicated in parentheses. The black circles are hypothetical nodes. Legend colors correspond to the basin.

5.4.10 *Channa kelaartii*

The ~20 species of snakeheads of the *Channa gachua* group are relatively small (< 250 mm SL) and widely distributed across a wide range, from eastern Iran to Taiwan, and southwards to Sundaland and across India to Sri Lanka. Conte-Grand *et al.* (2017) showed through a molecular analysis that the Sri Lankan fish referred to as *Channa gachua* was in fact not that species. Following from that work, and based on samples drawn from across Sri Lanka and southern India, Sudasinghe *et al.* (2020f) provided a morphological and molecular characterization of the species, while showing that the name *C. kelaartii*, provided by Albert Günther in 1861, was available for it (Figure 5.35). They also showed that *C. kelaartii* was separated from *C. orientalis*, the only other member of the *C. gachua* group in Sri Lanka by a minimum uncorrected p-distance of 5.1 % in the barcoding *cox1* gene (Sudasinghe *et al.*, 2020a).

Phylogeography. The results of Sudasinghe *et al.* (2020f) showed *C. kelaartii* not to be endemic to Sri Lanka but present also in southern India. The Sri Lankan and Indian sequences of *C. kelaartii* (Figure 5.36) formed five and four haplotypes, respectively, none of them shared between the two countries. The Sri Lankan sequences of *C. kelaartii* from the southwestern wet zone (Kelani, Kalu and Gin river basins), the northern intermediate zone (Maha basin), and the northern dry zone (Malwathu basin) form a single shared haplotype (H1), along with two specimens of uncertain provenance. Sequences of *C. kelaartii* from the Mahaweli basin and the eastern dry zone (Gal, Kumbukkan and Walawe basins) are separated from those of the south-western and northern dry-zone populations of Sri Lankan *C. kelaartii* by a minimum of three mutational steps. The Sri Lankan sequences of *C. kelaartii* show an intraspecific genetic diversity of 0.0–1.3 percent in the *cox1* gene and differ

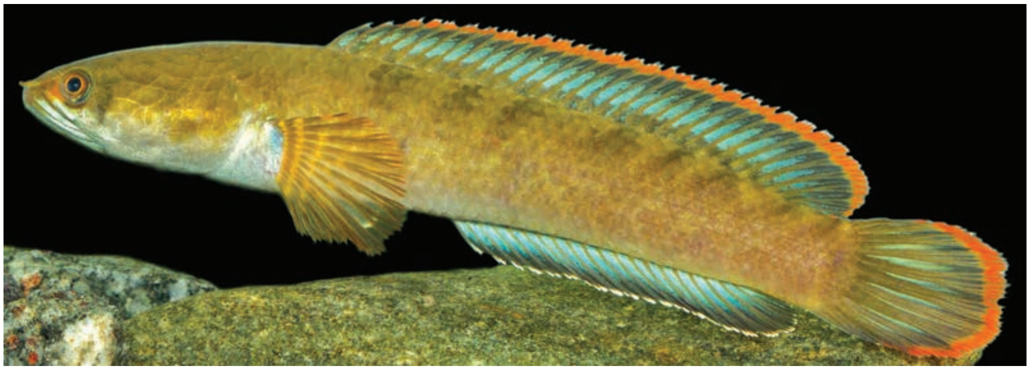

Figure 5.35. *Channa kelaartii*, a species widely distributed through Sri Lanka and southern India.

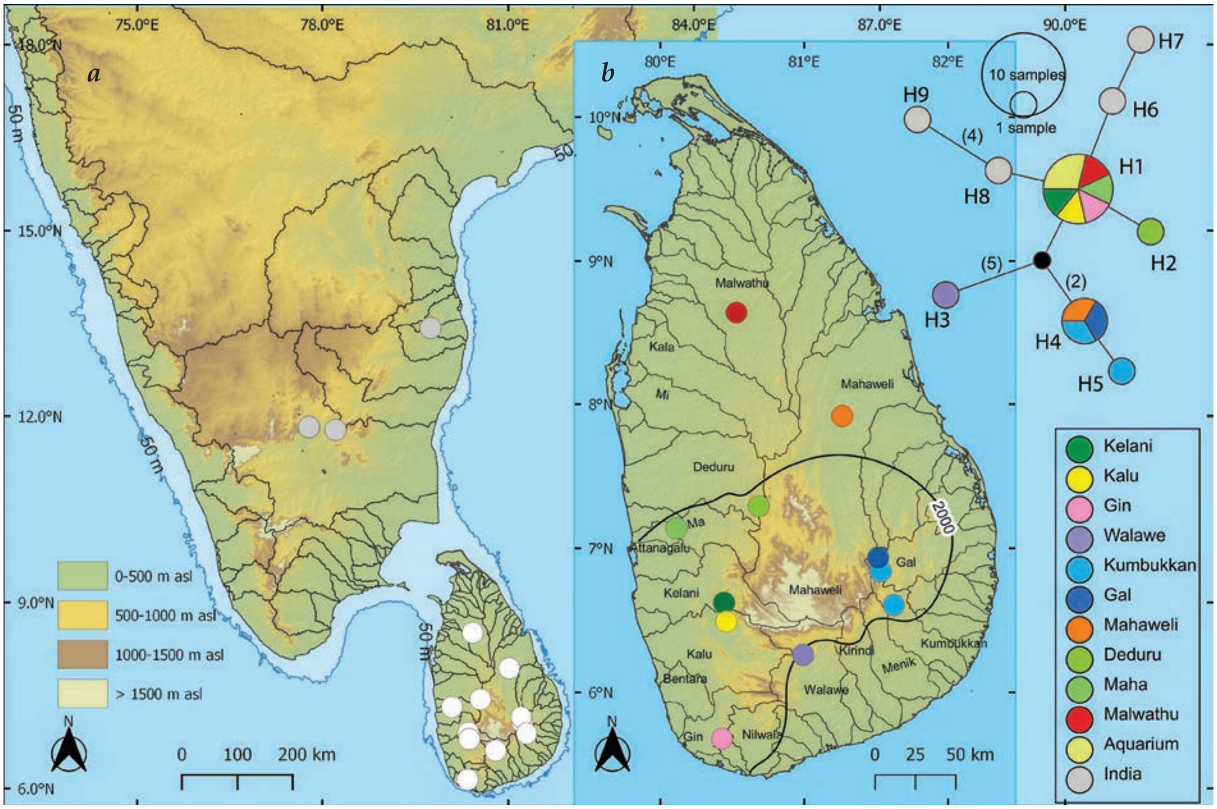

Figure 5.36. ***a***, Sampling localities of *Channa kelaartii* in Sudasinghe *et al*. (2020f). The black lines represent drainage margins; and **b,** the median-joining haplotype network is based on the analysis of a 654 bp fragment of the *cox1* gene. The areas of the circles are proportional to the number of individuals sharing a given haplotype. The number of mutational steps > 1 is indicated in parentheses. Black circles are hypothetical nodes. Legend colours correspond to the river basins or region as indicated in the key.

from Indian sequences of *C. kelaartii* by a modest 0.2–1.1 percent. Further, a pairwise genetic distance of 7.9–8.8 percent separates *C. kelaartii* from the Indian *C. gachua*.

5.4.11 Giant snakeheads

Sudasinghe *et al.* (2020b) showed there to be two distinct species of giant snakeheads* in Sri Lanka: *Channa marulius,* distributed in the north-western dry zone, and *C. ara*, in the middle and lower regions of the Mahaweli basin (see Figure 1.8). The two species are separated by an uncorrected pairwise distance of 3.6 percent in the *cox1* barcoding gene. These authors reported also a further putative species in the group, from the island's south-western wet zone, reporting it as a 'puzzling third component of the Marulius group's diversity': *Channa* cf. *ara*. Though genetically more similar to *C. marulius*, *C.* cf. *ara* is distinguished from it in morphology. Paradoxically, it is morphologically more similar to *Channa ara*, from which it diverges by an uncorrected *cox1* pairwise distance of 3.7 percent.

Phylogeography. Sudasinghe *et al.* (2020b) identified three haplotypes within the Sri Lankan giant snakeheads, corresponding to *Channa ara* from the Mahaweli Basin (H1), *C.* cf. *ara* from the south-western wet zone (H2), and *C. marulius* from the northern dry zone (H3). The haplotype of *C. ara* differs from those of *C.* cf. *ara* and *C. marulius* by a minimum of 22 mutations. *Channa ara* is marginally more similar genetically to continental *C. marulius* (3.6–4.2 %) and Sri Lankan *C.* cf. *ara* (3.7 %) than it is to Sri Lankan *C. marulius* (4.6 %). Meanwhile, the Sri Lankan *C. marulius* differs from continental *C. marulius* by 1.6–2.3 percent. Although modest, this is twice the intraspecific *cox1* genetic divergence previously reported in its populations across India and western Myanmar. In contrast, the Sri Lankan *C.* cf. *ara* differs less from continental *C. marulius* (uncorrected p-distance 1.0–1.6 %) than it does from the Sri Lankan *C. marulius* (2.0 %).

Although a fuller understanding of the interrelationships within Sri Lanka's giant snakeheads must await sequencing of more loci across a more representative sample, the *cox1* analysis of Sudasinghe *et al.* (2020b) suggests that Sri Lanka's giant snakeheads occur as at least three genetically distinct populations, each of which may derive from a separate dispersal across the Palk Isthmus. The separation between the north-western Malwathu and north-eastern Mahaweli populations is especially noteworthy, given that some other dry-zone species (*e.g., Dawkinsia, Garra*) possess haplotypes that are shared across this boundary. Nevertheless, given that the *cox1* barcoding gene has its greatest utility not in discerning phyogenetic relationships but in identifying species (and even then with limitations: Hubert & Hanner, 2015; Pedraza-Marrón *et al.*, 2019), the relationships of Sri Lanka's giant snakeheads must be a subject of future study.

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* Giant snakeheads are uncommon in Sri Lanka, for which reason the present account is constrained by limited sampling.

SUPPLEMENT 7

Refugial value of riparian habitats

The riparian habitats beside the streams, rivers and marshes of the wet zone appear to have long served as refuges during arid periods in the region's past. Of the 16 angiosperm genera endemic to Sri Lanka, (see footnote on p. 23) at least five are riparian or aquatic associates: *Adrorhizon* (Orchidaceae), *Championia* (Gesneriaceae), *Chlorocarpa* (Achariaceae), *Farmeria* (Podostemaceae) and *Hortonia* (Monimiaceae), while the available information on a further two, *Dicellostyles* (Malvaceae) and *Diyaminauclea* (Rubiaceae), suggests that they too, may be associated principally with riparian environments.

Indeed, Ashton (2014: 391), considered the resilience to aridification conferred on *Hortonia* by its riparian association to have been a key to its persistence in Sri Lanka since the Cretaceous, noting that 'Its partially riverine ecology could explain how it might have persisted through the lowland desert climate that must have prevailed while the Indian Plate rafted through the Horse Latitudes'. The absence of *Hortonia*—and indeed, the Monimiaceae as a whole—from India, however, remains a mystery (see also p. 95). To the east, the family recurs only from the Nicobars across Malesia, in monimiace lineages not closely related to *Hortonia*. The relationships of *Hortonia* remain enigmatic, with different analyses recovering it as near-basal to the Monimiaceae or nested deeply within the family: Bobrov *et al.* (2017: fig. 7).

Figure S7.1. Riparian habitats typical of rainforest streams, in Deniyaya, south-western Sri Lanka.

6

Conclusions

Only too often in this book, we find ourselves unable to explain the mechanisms that gave rise to the many disjunctions we observe between Sri Lanka's biota and those of Asian region and former Gondwanan terranes. Notwithstanding the many unexplained gaps*, however, there is much we can learn from the growing body of biogeographic research now being focused on Asia.

As we explain in the Preface, we wrote this book because Sri Lanka has up to now lacked a framework on which to test biogeographic hypotheses. We hope this text provides such a framework. Based on the hundreds of studies we review in this book, what then, is the picture that emerges?

First, despite Sri Lanka having been terrestrially linked to Africa, Madagascar and the Seychelles between the Middle Jurassic and early Paleogene (~160–65 Mya), it shares with them very few animal lineages that reflect this antiquity. Nevertheless, the handful of disjunct lineages whose divergence dates unambiguously to rifting from those terranes, such as the heterometrine scorpions, petalid spiders and acavid snails, provide evidence that Gondwanan vicariance played an important part in shaping the island's fauna. That fauna had, however, at some point prior to the Eocene, been all but lost. The lack of fossils from Sri Lanka between the late Cretaceous and late Pleistocene means we cannot know when this extinction took place. Tentatively, therefore, we implicate the Cretaceous-Plaeogene cataclysm and Deccan volcanism for leaving in Sri Lanka a very nearly blank slate on which a new evolutionary story, rooted mainly in Southeast Asia, came to be be written.

The preponderance of timing studies on lineages that exhibit autochthonous diversifications in the island recover crown ages no earlier than the Oligocene, which suggests that dispersals into the country were few until then. This suggests that following the inferred extinction ~66 Mya, and contact between India and Asia ~55 Mya, a biotic link with the mainland may not have existed until the Oligocene. Regrettably, almost no divergence-timing studies have been done for the dozens of flowering-plant taxa whose distributions show tantalising disjunctions. The dipterocarp genus *Cotylelobium* and crypteroniace genus *Axinandra*, for example, are two lineages of great antiquity which are disjunct between Sri Lanka's wet zone and perhumid Malesia. Yet, we have no idea when they diverged. Similarly, *Hortonia* appears to be a 'Noah's Ark' taxon; but is it?

It seems clear that despite the vicissitudes of climate, Sri Lanka's south-western wet zone has been, at least in part, a uniquely valuable biotic refuge through the past ~30 My. During that entire period, it lay within ±6° latitude, well inside the humid intertropical convergence zone. Nevertheless, the island's biota appears to have suffered repeated extirpations, survived only by refugial populations in moist valleys in the southern and central mid-hill regions.

Trimen's Floral Disparity

The different relationships of Sri Lanka's wet-zone flora—the montane plants being similar to those of the southern Western Ghats whereas the lowland ones are rooted in Malesia—remain to be studied. We are not aware of any research on this question since Henry Trimen first made this observation in 1885. If true, these distributions allow diverse hypotheses on historical climate, extinctions and dispersal patterns to be tested†.

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* We have usually avoided choosing between dispersal and vicariance. Only too often, hypotheses involving one or the other are treated as fact, reminiscent of Friedrich Nietzsche's observation, "… *in jede Lücke hatten sie ihren Wahn gestellt, ihren Lückenbüßer, den sie Gott nannten*" [… into every gap they put their delusion, their stopgap, which they called God]. This is perhaps as true of biogeography as it is of theology.

† The desiccation-tolerance and seed dormancy studies of Sri Lankan montane plants by Athugala *et al.* (2021a,b), could inform such hypotheses.

We hypothesize that Trimen's disparity results from an extinction in Sri Lanka's central mountains. Indeed, multiple lines of evidence, including from freshwater fishes (Chapter 5), support the idea that the Sri Lankan highlands suffered one or more severe extinctions, most recently during the Pleistocene, and most probably as a result of aridification. The present montane flora then, would be assumed to have dispersed across the Palk Strait since that event. But, as we show from multiple lines of evidence, it is unlikely that wet-adapted plant lineages could have crossed the Isthmus during the Plio-Pleistocene. Besides, the island's contemporary montane flora is rich in endemic species, though not endemic supra-specific taxa that are not represented also in the lowland rainforests: *i.e.*, it is young.

It would seem then, that the extirpation of the highland flora occurred at some time during the late Miocene. We therefore hypothesize that the present flora could have been derived from only three sources. (1), lineages that dispersed from lower elevations and therefore have lowland sister groups. As climate warmed following the Last Glacial Maximum, such upward dispersal must certainly have occurred. (2), recolonization of the highlands from the Western Ghats by lineages with terrestrial seed dispersal could only have taken place prior to the Pliocene aridification of the Palk Isthmus. (3), lineages which arrived within the last ~5 My must be capable of dispersal by zoochory or by wind.

Such a scenario seems to be supported by a floristic study in the southern Western Ghats[*] which found that while there were no species shared across a high-elevation wet evergreen forest and a dry deciduous forest, species from these two forest types showed much closer evolutionary relationships than expected. Additionally, a study in Sumatra[†] showed that at about the same latitude as Sri Lanka, montane forests retreated 700–750 m during glacial maxima, which offers a mechanism for the rapid altitudinal dispersal of plants.

It is also noteworthy that while numerous plant lineages occur only in the South Indian and Sri Lankan hills, this is not so in the case of nonvolant montane vertebrates: they were evidently unable to disperse across the isthmus even during cool phases during the Plio-Pleistocene. Despite dozens of high-elevation plants being shared between the Western Ghats and Sri Lanka, no high-elevation fishes, amphibians or mammals are.

The Palk Isthmus

Part of our motivation to give this former land bridge between India and Sri Lanka a name was to identify it as an important locus of biogeographic investigation. So neglected was this crucial biogeographic conduit that a name was coined for it only as recently as 2018[‡]. The former climate and vegetation of the Isthmus have been little examined until now. The idea that it has been strongly seasonal for the past five million years, and arid for the past three, is also new. While this scenario appears to be supported by a several studies, it is certainly not supported by all. It deserves further investigation, especially through the palynological examination of submarine sediment cores from the seafloor of the Palk Strait.

The fishes

Sri Lanka's south-western wet zone is a hotspot of freshwater-fish diversity and endemism. Within this region, streams draining rainforests on the foothills and uplands up to 500 m asl are of special importance. Most wet zone endemics show strong phylogeographic structure, with little or no haplotype-sharing between basins (*e.g., Devario micronema, Rasbora wilpita, Systomus pleurotaenia, Laubuka varuna, Pethia nigrofasciata, P. cumingii, Channa orientalis*). These species also show a greater nucleotide and haplotype diversity compared with their close relatives whose ranges extend to the dry zone. In cases where haplotypes are shared between basins in these wet-zone endemics, they are mostly between basins with contiguous headwaters. It appears that gene flow between basins, across the lowland floodplains, has been inhibited by habitat-associated philopatry.

In contrast, the generalist species that have wide distributions in the island show little phylogeographic structure. For these, it appears that dispersal occurs via the littoral floodplain that connects the wet, intermediate and dry zones (*e.g., Devario malabaricus, Dawkinsia filamentosa, Rasbora dandia, Channa kelaartii*). The only exceptions to this among the widespread generalists are *Systomus sarana* and *Garra ceylonensis*. Despite the ab-

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[*] Divya *et al.* (2020).

[†] Shaney *et al*. (2020).

[‡] Sudasinghe *et al.*,2018b.

sence of obvious barriers to dispersal, *S. sarana* exhibits modest phylogeographic structure within the different climatic zones. Further, compared with other generalist taxa, the divergences associated with *Systomus sarana* occurred substantially earlier.

Pethia melanomaculata and *Laubuka lankensis*, which are distributed in the intermediate and dry zones of the island, show a similar phylogeographic structure. In both these species, three haplogroups reflecting their geographic distribution can be identified: Northwest, Mahaweli, and Eastern. These haplogroups, however, are separated by only a few mutational steps. In both species, the Eastern haplogroup exhibits the highest haplotype and nucleotide diversity. Given the dry zone's uniform topography, the barriers that limit the dispersal of these haplogroups are still not known.

The foothills of the Kelani, Kalu, Gin and Nilwala basins appear to have served as refugia during Plio-Pleistocene aridification event/s, as evidenced by the phylogeographic structure and phylogenies of *Pethia nigrofasciata, Devario micronema, D. pathirana, Laubuka varuna, Systomus pleurotaenia* and *Garra ceylonensis*. This warrants investigation across different taxa, including plants, as it is likely that the region deserves greater conservation attention than it presently attracts. The greater genetic diversity associated with the eastern basins, compared with the other dry- and intermediate-zone basins also supports this conjecture.

The intermediate zone, which was largely marginalized in earlier studies (*e.g.*, Senanayake, 1980; Pethiyagoda, 1991), emerges as a region of special interest. The ranges of two endemics, *Pethia reval* and *Ompok argestes*, extend from the south-western wet zone into northern intermediate zone. *Laubuka hema* is confined to the headwaters of the Gal Oya basin of the intermediate zone of the eastern slopes of the central mountains. The rivers of this region call for further biodiversity exploration.

The Knuckles endemics *Dawkinsia srilankensis* and *Labeo fisheri* support the conclusion of Deraniyagala (1958a), based on a different body of evidence, that these hills, which now lie within the east-flowing Mahaweli basin, drained into the west-flowing Malwathu-Kala system until some time in the Pleistocene. Such a conclusion is supported also by the phylogeographic structure of *Garra ceylonensis*. Divergence-time estimates derived from studies cited in Chapter 5 suggest that the Knuckles Hills and Malwathu River may have had a shared hydrography in the Pliocene, as inferred from the 3.7 (95% HPD: 4.4–3.1) Mya divergence between *D. srilankensis* and *D. tambraparniei*[*]. The former confluence of the Malwathu and Kala rivers is supported also by the phylogeography of *Garra ceylonensis, Laubuka lankensis, Systomus sarana,* and *Pethia melanomaculata*[†].

Several patterns in phylogeographic structure provide possible evidence for headwater capture events in some Sri Lankan river basins (*e.g., Laubuka hema, Rasbora adisi* and *Systomus sarana* between the Mahaweli and Gal basins; *Channa orientalis*, between the Mahaweli and Kelani; *Systomus pleurotaenia* and *Garra ceylonensis*, between the Nilwala and Gin; and *S. pleurotaenia* between Kelani and Attanagalu). It is likely, once these river systems are sampled more finely, that a clearer picture of historical river capture events will emerge.

In the absence of a clear Gondwanan signature in its freshwater fishes, the earliest freshwater-fish dispersals into Sri Lanka appear to have occurred in the Oligocene (*e.g.,* the ancestors of *Belontia* and *Malpulutta*), if not already by the late Eocene as, perhaps, in the case of *Rasboroides*[‡]. Most other rainforest-adapted endemics derive from dispersals from India in the vicinity of the Miocene-Pliocene boundary, which appears to be the last period[§] in which a perhumid climate occurred on and around the Palk Isthmus (*e.g.*, the common ancestor of *Devario micronema, D. pathirana,* and *D. memorialis*: 6.2 Mya (95% HPD 7.6–4.6 Mya).

Lineages that dispersed to Sri Lanka after the early Pliocene are widely distributed in the dry zone and seem adapted to a xeric and strongly seasonal climate: *e.g., Rasbora dandia* (~1.4 Mya, 95% HPD 2.7–0.5 Mya) and *Systomus sarana* ~3.1 Mya (95% HPD: 4.2–2.2 Mya). Most likely owing to aridity, the Palk Isthmus appears to have served more as a filter of—than as a conduit for—biotic dispersal as the Plio-Pleistocene advanced.

Sri Lanka appears to have suffered at least three major extinctions of its freshwater fishes. The first of these is inferred from the absence of lineages on the island that predate the late Oligocene. The second appears to have occurred around or prior to the Miocene-Pliocene

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[*] Sudasinghe *et al*. (2021b).

[†] Sudasinghe *et al*. (2020b,g; 2021a,c).

[‡] Sholihah *et al.,* 2021b

[§] There is fossil evidence from the Indian Peninsula that suggests that aridification was widespread and prolonged. Patnaik (2015) infers from Siwalik fossils, for example, a gradual change from C_3 dominated trees and shrubs to C_4 dominated warm-season grasses at around the Miocene-Pliocene transition with, among mammals, browsers being replaced by grazers.

boundary, following which period many of its endemic diversifications derive. Lineages that survived (*e.g., Malpulutta, Rasboroides, Belontia,* and the endemic diversification of *Systomus*), appear to have done so in refugia in moist valleys among the foothills of the island's south-western perhumid zone and the Knuckles Range. Then, a subsequent event, probably in the early Pleistocene, extirpated the fishes of the central mountains and dry zone. In consequence, the fishes that now occur in the hills have closely related sister groups in the lowlands, from which they diverged only in the Pleistocene.

For their part, the species that now inhabit the dry zone are almost all shared with India. Regrettably, the dearth of molecular analyses of freshwater fishes from the east-draining rivers of the Indian Peninsula, such as the Cauvery, Vaigai, Vaippar and Tamiraparani, handicap studies of the timing of dispersal events across the Palk Isthmus.

As suggested by their haplotype networks, dry zone species such as *Laubuka lankensis* and *Rasbora microcephala* appear to have undergone rapid population expansions, which too, are consistent with such a scenario. The paucity of rheophilic fishes and clades adapted to montane streams, in contrast to southern India, support a widespread extirpation of such fishes on the island. While several such extinction events appear to have taken place, it is noteworthy that the divergence of *Devario monticola* and the Bopattalawa population of *Garra ceylonensis* from their lowland sister groups date to about 2 Mya, which suggests they dispersed to the highlands after a desiccation event that occurred in or prior to the early Pleistocene.

Channa orientalis is the only endemic species hitherto shown to have dispersed across the central mountains, between the west-flowing Kelani basin and the east-flowing Mahaweli basin. This distribution may be reflected also in *Belontia signata* and *Clarias brachysoma* which, however, have not yet been investigated.

In addition to shedding light on the genetic structure of populations, phylogeographic studies such as those summarized in Chapter 5 have also helped trace the provenance of populations of species that have been translocated, intentionally or otherwise.

Biodiversity science in Sri Lanka in the 1970s and '80s focused largely on ecology, while the period since the 1990s has seen increasing attention devoted to inventory-building. Little attention was given to understanding intra- and inter-specific variation, whether based on genetic or morphological data. The results we present in Chapter 5 (*e.g.*, the diversifications of *Devario* and giant snakeheads) suggest that non-overlapping morphological characters, or differences in p-distances for a single marker, should not by themselves decide the recognition of species. The picture is often more nuanced than that. Similarly, as seen in *Channa orientalis*, overlaps in morphological characters or genetic distances is not uncommon even between putative species. We emphasize therefore, the importance of thinking in terms of micro- and macro-evolutionary processes, phylogeny and phylogeography in order to understand the process of speciation in a broader—and genuinely, rather than nominally—integrative context.

Implications

We hope that a key message readers of this book take away from it is, *all species are not equal*. Sri Lanka is home to a small number of ancient endemic lineages which, owing to their extraordinary phylogenetic diversity, deserve conservation priority. Unfortunately, none of these is a big, charismatic animal. But taxa such as *Acavus, Aneuretus, Pettalus, Rasboroides, Rhysida* and *Srilankametrus*, each at the end of a long branch of the Tree of Life, carry fascinating evolutionary histories dating back tens of millions of years. They are by far the most unique elements of Sri Lanka's biodiversity.

Sadly, it is equally true that the tools of molecular phylogenetics, now more than three decades old, have barely begun prying into the island's plants. The floral disjunctions remaining to be explained and timed have been known to botanists, in most cases, for the past century. Yet, the surface has barely been scratched in seeking to understand their historical biogeography using the tools of molecular biology. What is more, when it comes to the phylogeography of plants—in which geographic, climatic and edaphic associations, for example, can more easily be analysed—virtually nothing has been done up to now. Vast fields of research, therefore, yet await the advent of curious minds.

The past 30 years have seen the flourishing of biodiversity exploration in Sri Lanka, and unprecedented taxonomic productivity. It is time, perhaps, to begin thinking about where all these plants and animals came from, how they got here, and how they went about occupying the land. In an age of rapid climate change, the answers to such questions are not purely academic: they stand to describe how the biodiversity on which our civilization depends will respond to the stresses of the future, just as it did to those of the past.

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