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REVIEW ARTICLE

Integrative Taxonomy in the Indian Subcontinent: Current Progress and Prospects

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Abstract | The term "integrative taxonomy", or the use of multiple lines of evidence in the delimitation and naming of new species, was independently introduced in two papers in 2005. This paper aims to provide a brief review of integrative taxonomy and the growth of molecular tools in systematics, with special reference to its prevalence and scope for biodiversity research in India. We review the literature to understand the state of progress in systematics from India since 2005 using both vertebrate and invertebrate examples. We end by summarising best practises and a workflow for integrative taxonomy, as well as emphasizing the need for a national strategy for taxonomy and systematic research with an outline on how to achieve this.

1 Background

Among the most fundamental disciplines in biology is systematics, the study of biological diversity and its evolutionary origins. It includes the discovery of species, reconstructing the evolutionary relationships among species, naming and classifying biodiversity (taxonomy), studying patterns of diversification, functional traits and distribution through time[136]. The practical endeavour of cataloguing biological diversity is by no means trivial, with estimates of the proportion of species that remain unnamed as high as 85%[111]. There have been repeated appeals and efforts to document biodiversity, including the Systematics Agenda 2000 to inventory life on earth over the next 25 years (2000–2025)[39]. These efforts have been in response to the ongoing biodiversity crisis, which is a loss of biodiversity at an alarming rate, rivalling extinction rates of the five mass extinctions[22].

Species form the fundamental units of analysis in the biological sciences for reproducibility, and comparative studies. Species are also equally important in agriculture, the medical sciences and even in legislation. Therefore, understanding what species are remains important for a broader audience than just biologists[41]. However, how many species actually exist and where they are distributed remains unknown for most taxonomic groups as well as in the most biodiverse regions of the world, known as the Linnean and Wallacean shortfalls[73]. This has also been referred to as the Taxonomic Crisis or Impediment (see: www.biodiv.org). A myriad of causative factors has been identified leading to this Impediment, including the lack of sustained efforts in both taxonomic research and training the next generation of taxonomists, besides a lack of funding and exploration in poorly known parts of the world[34,39,73]. An additional exacerbating factor is the very definition of a species, with a multitude of species concepts. Thus, understanding what constitutes a species and how to define them has remained a challenging problem in biology.

2 Species and Species Concepts: A Brief Overview

Species have traditionally been recognised using morphological characteristics and that remains the most prevalent metric in defining and describing new species. However, the two main tasks of a taxonomist are delimitation and identification of species[135]. The former task invokes a species concept, which is a philosophical treatise on what a species is, while the latter merely looks

Systematics: as defined by one of the leading journals in the field Systematic Biology—"Systematics is the study of biological diversity and its origins. It focuses on understanding evolutionary relationships among organisms, species, higher taxa, or other biological entities such as genes, and the evolution of properties of taxa including intrinsic traits, ecological interactions, and geographic distributions. An important part of systematics is the development of methods for various aspects of phylogenetic inference and biological nomenclature/classification."

Taxonomy: is the science of delineating, classifying, and naming taxa including both living and fossilised taxa.

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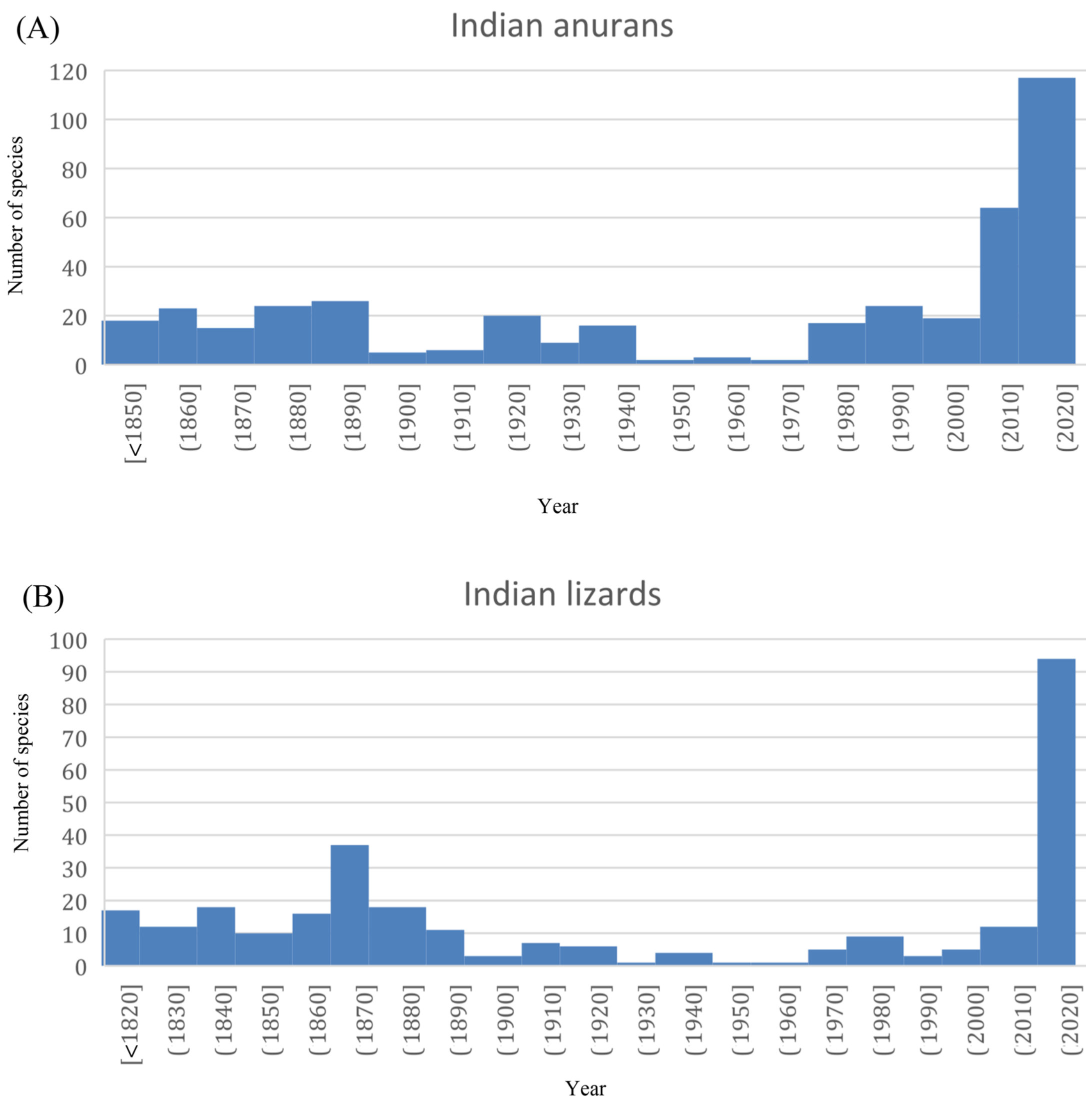

Figure 1: Species descriptions of mainland Indian (**A**) anurans and (**B**) lizards over the last two centuries

for the characters that are useful in identifying and distinguishing species ([46,50–53]). A plethora of species concepts has been proposed, with as many as 34 listed in one review[40,101,50–53,154]. The most prevalent and influential is the Biological Species Concept (BSC), which considers species to be reproductively isolated metapopulations[102]. There are numerous issues with the BSC, a review of which are outside the scope of this article, but two main problems which stand out are: its non-universality, as in the case of asexual organisms, and that reproductive isolation is almost always inferred through proxy rather than experimentally tested, such as lack of gene flow leading genetic or morphological divergence ([50,51]).

The Evolutionary Species Concept (ESC) explicitly incorporated evolutionary thinking in systematics and defined a species as "a single lineage of ancestor–descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate"[138]. The use of molecular data allowed an extension of the ESC to the Phylogenetic Species Concept (PSC), where species can be identified based on reciprocal monophyly synthesized many of the alternative species concepts along with BSC and proposed a unified species concept with the operational criteria being that species are "separately evolving (segments of) metapopulation lineages" ([50,52,53]). This is also known as the "General Lineage Concept" (GLC). The GLC recognises a potential species as a unique lineage based on one or more criteria, many of which correspond to different species

Biological Species Concept: species are groups of interbreeding natural populations that are reproductively isolated from other such groups[102].

Evolutionary Species Concept: an evolutionary species is a single lineage of ancestor–descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. ([138]:153).

Lineage: an ancestor–descendant series.

Phylogenetic Species Concept: a recognizable monophyletic group "A cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." (Cracraft 1989).

Species concepts: a definition to delimit species based on certain criteria.

concepts. These criteria and species concepts correspond with different stages of divergence and trajectories of the speciation process ([50,51]: Fig. 2,[83]: Fig. 1). There is a growing consensus among systematic biologists that species delimitation aims to identify independently evolving lineages. To do this one needs to identify operational criteria to delineate lineages based on these species concepts using independent datasets including DNA, morphology, and species distribution models, among others. The term Integrative Taxonomy emerged to encompass these conceptual and methodological developments, with species boundaries defined by congruence across multiple lines of evidence[46,151].

3 Integrative Taxonomy

An integrative taxonomic framework uses the GLC to discover independently evolving lineages and then tests different species hypotheses based on multiple datasets. It argues that the independent lineages should be recognised when multiple lines of evidence converge and identify distinct species/lineages. Dayrat[46] and Will et al.[151] used the term integrative taxonomy simultaneously, though in slightly different contexts. DNA barcoding was proposed as a method that would revolutionise taxonomy, with divergence along a single mitochondrial locus (mostly cytochrome oxidase I—COI) considered sufficient to delimit species. Originally proposed as a panacea to taxonomic issues, Will et al.[151] argued strongly that DNA barcoding was a "back-slide into phenetics" and argued for examining multiple data sources while defining species. Dayrat[46] set out guidelines for taxonomists when using integrated data for the naming of species, some of which are now common practise in integrative taxonomy (e.g. 'species should only be named when their limits are supported by multiple lines of evidence or that 'types preserved so that molecular data can be extracted'). Though these two publications formalised the term "Integrative Taxonomy" which has led to a cascade of publications using the term since, others have argued that taxonomy has long been integrative[146].

The very definition of integrative taxonomy encompasses quantitative approaches to define species across different datasets and strives to go beyond qualitative comparisons. Integrative taxonomy has since then evolved to encompass multiple datasets while delimiting species either by integrating by congruence or by accumulation[119]: Fig. 1. A common practice while using an integrative taxonomic framework has been to assess molecular (mitochondrial DNA and nuclear DNA: mtDNA and nucDNA), morphological, climatic, distributional, and behavioural (acoustic, chemical/pheromonal) data while delimiting species[46,120,151]). The idea is to identify a priori putative species based on each of the datasets and then evaluate the status of each of species with operational criteria to identify distinctness and uniqueness[135].

There are multiple ways to delineate species using molecular data with species delimitation methods, which broadly try and distinguish between intra- and inter-specific variation. These may use either genetic distance or branch lengths in the case of tree-based methods, without invoking explicit species concepts. The other species delimitation methods rely on the phylogenetic species concept to identify and delineate species. Many of these methods either use a coalescent approach, birth–death models, or Poisson models in a likelihood or Bayesian framework using largely DNA sequence data and phylogenies (See review by[95] for details on methods). Some of the commonly used discovery methods (where a priori species are not defined) based on phylogenetic trees are the Generalized Mixed Yule Coalescent (GMYC) model[62,123] and the Poisson tree processes (PTP) model[81,155] and its extension multi-rate PTP[81]. mPTP is an extension of the PTP which allows more variation in parameters, is much faster and helps account for sampling bias/ variation in intraspecific genetic diversity. The validation methods, wherein a priori species are defined and then the uniqueness of these is assessed, are Bayesian coalescent method in the software BPP (Bayesian Phylogenetics and Phylogeography)[152] and also multi-species coalescent analyses can be carried out in *BEAST [57].

Species delimitation or identification of putative species based on morphological data can also be done in a phylogenetic framework (Parsimony or Maximum Likelihood) or using multidimensional analyses to identify unique entities[140]. There has been some debate on whether morphological characters should be used to delineate species boundaries or use them merely as diagnostic characters to describe species. The latter has been extensively used and demonstrated its value through Linnean taxonomy[151]. Species delimitation methods require comparable character states and discrete variation which is often lacking in morphological characters[150]. However, there are studies which delineate species boundaries based on morphological data[140]. The ecological

Integrative Taxonomy: The term integrative taxonomy was introduced by Dyrat and Will et al. simultaneously in 2005—**integrative taxonomy** is defined as the science that aims to delimit the units of biodiversity using multiple and complementary perspectives (phylogeography, comparative morphology, population genetics, ecology, development, behaviour, etc.). —Dyrat, 2005 **and integrative taxonomy** which uses a large number of characters including DNA and many other types of data, to delimit, discover and identify meaningful, natural species and taxa at all levels—[151].

DNA barcoding: is a method of species identification using a short section of DNA from a specific gene or genes (iBOL).

A Brief Description of Biodiversity Hotspots in India:

1. Peninsular India has a distinct geological history, forming part of the Gondwanan supercontinent around 200 million years ago, sequentially breaking away from Africa, Madagascar and Seychelles before drifting northward to its current position. Peninsular India is flanked by mountain ranges: the **Western Ghats** is a series of ranges that run along the west coast escarpment, forming part of the Western Ghats-Sri Lanka Biodiversity Hostpot; the **Eastern Ghats** are more arid and include a series of isolated low mountain ranges along the east coast; and the Satpuda-Vindhya ranges form the northern boundary. In between these regions are largely arid, savanna habitats including numerous plateaus and lowlands.
2. The **Himalayas** were formed by the collision of the Indian Plate and Eurasia, which began ~ 50 million years ago ([15,33]. Outlining the Indian plate with the tallest mountains in the world, the Himalayan ranges are a topographically and climatically heterogeneous landscape. The main ranges of the Western and Eastern Himalayas form the **Himalaya Hotspot,** while the eastern syntaxis is part of the **Indo-Burma Hotspot**[108].
3. **Northeast India** includes the regions east of Sikkim—the Eastern Himalayas in the north, the eastern syntaxis of the Himalayas in the east, the Shillong plateau to the south, and the Brahmaputra and Teestha River drainages running through lowland areas. Northeast India is incredibly diverse, though the discoveries of numerous distinct vertebrates in the recent past indicate how poorly studied the region remains (e.g.[7,19,35,45,96,98,99,142]).
4. The **Andaman and Nicobar archipelago** has 556 islands and rocky outcrops of varied sizes distributed over an area of 8249 km^2. It harbours high biodiversity and endemicity, but each island group has unique biogeographic affinities—the Andaman Islands are a part of the **Indo-Burma biodiversity hotspot,** and the Nicobar Islands are a part of the **Sundaland biodiversity hotspot.** There have been a few studies examining distribution patterns of plants, birds and herpetofauna from these islands, and most of the region remains unexplored and its biodiversity undiscovered.

(niche), distributional or any other trait data can be used to identify distinct units using multivariate analyses (examples: birds–[132], centipedes–[78], lizards–[131], primates–[17]). However, intra and interspecific variation for individual data types may not always be congruent. Therefore, only if multiple data sources support the uniqueness of a species/lineage are they recognised as distinct species, leading to a robust species hypothesis.

An integrative taxonomic framework can also be useful in cases where species are young, for example, nucDNA and other slow evolving neutral genetic markers may not be able to detect recent divergence. Also, in cases where there is incomplete lineage sorting or secondary gene flow, there is likely to be incongruence of different genetic markers leading to discordance between gene and species trees. In these cases, the use of morphological traits along with distributional or ecological trait data is very valuable. Similarly, there may not be any diagnostic morphological characters in the case of cryptic species that may be divergent in other traits such as ecological niches, acoustic signal, or any other behaviour; or in cases where there is high phenotypic plasticity and/ or potential for convergent evolution in morphological traits[91,59,135]. Therefore, integrating multiple independent data sources is useful to detect potential conflict among the data sets while defining species boundaries. This approach is a step forward from simply enumerating biodiversity because while identifying and delineating species, it also informs the underlying processes which may have shaped biodiversity[59]. This approach of discovery and then hypothesis testing across multiple datasets leads to a more informed, more rigorous, and accurate assessment of biodiversity.

4 Integrative Taxonomy and Biodiversity Assessment in India

The biodiversity of the Indian subcontinent has been assembled over hundreds of millions of years, with both ancient and young lineages, taxa that have dispersed from the east and west, Gondwanan relics, and numerous *in-situ* radiations ([82] and references therein). The complex geological past of the Indian plate and contemporary climatic and topographic heterogeneity plays an important role in shaping its biodiversity[3,76,77,83] and references therein). India encompasses four global biodiversity hotspots, namely Western Ghats—Sri Lanka, Himalayas, Indo-Burma region, and Sundaland (Andaman and Nicobar Islands)[112]. Understanding biodiversity is fundamental not only to the biological sciences but also in conservation planning in our constantly changing world, through both anthropogenic activities and due to climate change. India is a megadiverse country that also has an incredibly high human population density, placing wild landscapes and biodiversity under extreme pressure[104].

Most of the current understanding of species diversity and its distributional limits in India is from 19 and 20th-century naturalists' observations. For many taxa, especially terrestrial small vertebrates and invertebrates, a large number of species remain known from only the original description and there have been no revisions since then. However, the enumeration of biodiversity has received attention in recent years, yielding many new species discoveries and collection/collation of distribution records. For example, 174/ 410 Indian anuran species and 105/ 290 mainland Indian lizards have been described since 2005 (see methods; Table 1; Fig. 1 and 2). Many of the new species discoveries are from one global biodiversity hotspot, the Western Ghats in southern India, and other biodiversity hotspots and biogeographic regions in India remain to be explored (Table 1). For example, among amphibians 129/ 174 of the new species discovered since 2005 are from the Western Ghats, while new descriptions of lizards since 2005 include 39 and 53 respectively from the Western Ghats and peninsular India (out of 105 new species named since 2005). Many studies use morphology in conjunction with molecular phylogenies to study systematics across taxonomic groups. However, a small proportion of these studies have carried out explicit species delimitation analyses either on molecular or morphological or ecological data.

While assessing biodiversity in one of the most biodiverse parts of the world may seem like a daunting task, the use of an integrative framework wherein multiple lines of evidence are used to define species offers a systematic and robust approach to deal with a problem of this scale. It is abundantly clear that we lack a fundamental understanding of biodiversity across the Indian subcontinent i.e., the biodiversity suffers from both Linnean (many unknown species) and Wallacean (poor distribution data) shortfalls, where an integrative taxonomy will be very useful. Also, integrative taxonomy will not only help generate taxonomic and distributional data but will help also in addressing another important shortfall, Darwinian shortfall, where molecular data will allow to assess the evolution of species and their phenotypic (morphological) traits (Diniz-Filho et al. 2013). In addition, the use

Table 1: An exhaustive list of species from India which were delineated using an integrative taxonomic framework across animal groups.

Taxa	Genus	Species	Year	Region	Molecular Data		SDM- DNA		Morphology		Distribution	ENM	BD	NR	References
					mttDNA	nucDNA	DM	VM	MDD	SDM					
Phylum: Arthropoda															
Centipedes—Scolopendridae	*Digitipes*	*barnabasi*	2013	WG	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	No	No	78,75
	Digitipes	*jangii*	2013	WG	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	78,75
	Digitipes	*nudus*	2013	WG	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	78,75
	Digitipes	*jonesii*	2013	WG	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	78,75
	Digitipes	*coonoorensis*	2013	WG	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	No	No	78,75
	Ethmostigmus	*sahyadrensis*	2018	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	76
	Ethmostigmus	*praveeni*	2018	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	76
	Ethmostigmus	*coonooranus*	2018	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	No	76
	Ethmostigmus	*tristis*	2018	EG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	No	76
	Ethmostigmus	*agasthyamalaiensis*	2018	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	76
	Otostigmus	*ruficeps*	2013	WG	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	No	No	78,75
	Rhysida	*longipes*	2020	OR	Yes	Yes	Yes	No	Yes	No	Yes	No	No	No	79
	Rhysida	*konda*	2020	EG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	79
	Rhysida	*assispina*	2020	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	No	79
	Rhysida	*pazhuthara*	2020	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	79
	Rhysida	*trispinosa*	2020	PI	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	79
	Rhysida	*lewisi*	2020	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	79
	Rhysida	*immarginata*	2020	SEA	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	79
	Rhysida	*sp1*	2020	EG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	No	79
	Rhysida	*sp2*	2020	PI	Yes	Yes	Yes	No	Yes	No	Yes	No	No	No	79
	Rhysida	*sada*	2020	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	79
	Rhysida	*aspinosa*	2020	WG	Yes	Yes	Yes	No	Yes	No	Yes	No	No	No	79
	Rhysida	*ikhalama*	2020	NEI	Yes	Yes	Yes	No	Yes	No	Yes	No	No	Yes	79

Table 1: (continued)

Taxa	Genus	Species	Year	Region	Molecular Data		SDM- DNA		Morphology		Distribution	ENM	BD	NR	References
					mttDNA	nucDNA	DM	VM	MDD	SDM					
Butterflies—Nymphalidae	*Polyura*	*bharata*	2015	IN	Yes	Yes	Yes	Yes	Yes	No	Yes	No	No	Yes	144
Crickets—Gryllidae	*Itaropsis*	*tenella*	2011	WG	Yes	Yes	No	No	Yes	Yes	Yes	No	Yes	No	74
Phylum: Chordata															
Birds—Muscicapidae	*Montecincla*	*jerdoni*	2017	WG	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	Yes	132
	Montecincla	*cachinnans*	2017	WG	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	Yes	132
	Montecincla	*fairbanki*	2017	WG	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	Yes	132
	Montecincla	*meridionalis*	2017	WG	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	Yes	132
	Sholicola	*major*	2017	WG	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	Yes	132
	Sholicola	*albiventris*	2017	WG	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	Yes	132
	Sholicola	*ashambuensis*	2017	WG	Yes	Yes	No	Yes	Yes	Yes	Yes	No	Yes	Yes	132
Primates – Colobinae	*Semnopithecus*	*schistaceus*	2020	HI	Yes	Yes	No	Yes	Yes	No	Yes	Yes	No	Yes	17
	Semnopithecus	*entellus*	2010	IN	Yes	Yes	No	No	Yes	No	Yes	Yes	No	Yes	84,113,114
	Semnopithecus	*priam*	2014	IN	Yes	Yes	No	No	Yes	No	Yes	Yes	No	Yes	18,113,114
	Semnopithecus	*hypoleucos*	2014	IN	Yes	Yes	No	No	Yes	No	Yes	Yes	No	Yes	18,113,114
Rats—Muridae	*Millardia*	*kondana*	2020	WG	Yes	Yes	No	No	Yes	Yes	Yes	Yes	No	No	20
Fishes—Cyprinidae	*Waikhomia*	*hira*	2020	WG	Yes	No	No	No	Yes	No	Yes	No	No	No	85
	Waikhomia	*sahyadriensis*	2020	WG	Yes	No	No	No	Yes	No	Yes	No	No	No	85
Amphibians -															
Bufonidae	*Xanthophryne*	*tigerina*	2009	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	28
Dicroglossidae	*Euphlyctis*	*aloysii*	2009	WG	Yes	No	No	No	Yes	No	No	No	Yes	Yes	80
Dicroglossidae	*Euphlyctis*	*karaavali*	2016	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	125
Dicroglossidae	*Euphlyctis*	*mudigere*	2009	WG	Yes	No	No	No	Yes	No	No	No	Yes	Yes	80
Dicroglossidae	*Minervarya*	*caperata*	2008	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	93
Dicroglossidae	*Minervarya*	*cepfi*	2017	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	64
Dicroglossidae	*Minervarya*	*goemchi*	2018	WG	Yes	No	No	No	Yes	No	Yes	No	No	Yes	54
Dicroglossidae	*Minervarya*	*gomantaki*	2015	WG	Yes	Yes	No	No	Yes	No	Yes	No	No	Yes	55

Table 1: (continued)

					Molecular Data		SDM- DNA		Morphology						
Taxa	Genus	Species	Year	Region	mttDNA	nucDNA	DM	VM	MDD	SDM	Distribution	ENM	BD	NR	References
Dicroglossidae	*Minervarya*	*granosa*	2008	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	93
Dicroglossidae	*Minervarya*	*kadar*	2017	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	64
Dicroglossidae	*Minervarya*	*kalinga*	2018	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	129
Dicroglossidae	*Minervarya*	*krishnan*	2018	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	129
Dicroglossidae	*Minervarya*	*kudremukhensis*	2008	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	93
Dicroglossidae	*Minervarya*	*manoharani*	2017	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	64
Dicroglossidae	*Minervarya*	*marathi*	2019	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	122
Dicroglossidae	*Minervarya*	*mudduraja*	2008	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	93
Dicroglossidae	*Minervarya*	*neilcoxi*	2017	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	64
Dicroglossidae	*Sphaerotheca*	*magadha*	2019	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	124
Dicroglossidae	*Sphaerotheca*	*pashchima*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	118
Megophryidae	*Megophrys*	*awuh*	2020	NEI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	98
Megophryidae	*Megophrys*	*dzukou*	2020	NEI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	98
Megophryidae	*Megophrys*	*flavipunctata*	2018	NEI	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	97
Megophryidae	*Megophrys*	*himalayana*	2018	NEI	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	97
Megophryidae	*Megophrys*	*numhbumaeng*	2020	NEI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	98
Megophryidae	*Megophrys*	*oreocrypta*	2018	NEI	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	97
Megophryidae	*Megophrys*	*periosa*	2018	NEI	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	97
Micrixalidae	*Micrixalus*	*adonis*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*candidus*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*frigidus*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*kodayari*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*kurichiyari*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*mallani*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*nelliyampathi*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30

Table 1: (continued)

Taxa	Genus	Species	Year	Region	Molecular Data mttDNA	Molecular Data nucDNA	SDM- DNA DM	SDM- DNA VM	Morphology MDD	Morphology SDM	Distribution	ENM	BD	NR	References
Micrixalidae	*Micrixalus*	*nigraventris*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*niluvasei*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*sairandhri*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*sali*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*specca*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*spelunca*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Micrixalidae	*Micrixalus*	*uttaraghati*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	30
Microhylidae	*Microhyla*	*darreli*	2018	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	67
Microhylidae	*Microhyla*	*eos*	2019	NEI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	32
Microhylidae	*Microhyla*	*kodial*	2018	WG	Yes	No	No	No	Yes	No	No	No	Yes	Yes	149
Microhylidae	*Microhyla*	*laterite*	2016	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	137
Microhylidae	*Micryletta*	*aishani*	2019	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	44
Microhylidae	*Mysticellus*	*franki*	2019	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	66
Nyctibatrachidae	*Astrobatrachus*	*kurichiyana*	2019	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	148
Nyctibatrachidae	*Nyctibatrachus*	*athirappillyensis*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	64
Nyctibatrachidae	*Nyctibatrachus*	*kumbara*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	71
Nyctibatrachidae	*Nyctibatrachus*	*manalari*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	65
Nyctibatrachidae	*Nyctibatrachus*	*mewasinghi*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	92
Nyctibatrachidae	*Nyctibatrachus*	*minimus*	2007	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	26
Nyctibatrachidae	*Nyctibatrachus*	*pulivijayani*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	65
Nyctibatrachidae	*Nyctibatrachus*	*radcliffei*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	65
Nyctibatrachidae	*Nyctibatrachus*	*robinmoorei*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	65
Nyctibatrachidae	*Nyctibatrachus*	*sabarimalai*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	65
Nyctibatrachidae	*Nyctibatrachus*	*webilla*	2017	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	65
Ranidae	*Hydrophylax*	*bahuvistara*	2015	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	117

Table 1: (continued)

					Molecular Data		SDM- DNA		Morphology						
Taxa	Genus	Species	Year	Region	mttDNA	nucDNA	DM	VM	MDD	SDM	Distribution	ENM	BD	NR	References
Ranidae	*Indosylvirana*	*caesari*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	31
Ranidae	*Indosylvirana*	*doni*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	31
Ranidae	*Indosylvirana*	*indica*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	31
Ranidae	*Indosylvirana*	*magna*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	31
Ranidae	*Indosylvirana*	*sreeni*	2014	WG/PI	Yes	No	No	No	Yes	No	No	No	No	Yes	31
Ranidae	*Indosylvirana*	*urbis*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	31
Ranixalidae	*Indirana*	*bhadrai*	2016	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	63
Ranixalidae	*Indirana*	*chiravasi*	2014	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	116
Ranixalidae	*Indirana*	*duboisi*	2016	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	43
Ranixalidae	*Indirana*	*paramakri*	2016	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	63
Ranixalidae	*Indirana*	*salelkari*	2015	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	109
Ranixalidae	*Indirana*	*sarojamma*	2016	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	43
Ranixalidae	*Indirana*	*tysoni*	2016	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	43
Ranixalidae	*Indirana*	*yadera*	2016	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	43
Ranixalidae	*Walkerana*	*muduga*	2020	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	56
Rhacophoridae	*Ghatixalus*	*asterops*	2008	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	27
Rhacophoridae	*Ghatixalus*	*magnus*	2015	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	2
Rhacophoridae	*Mercurana*	*myristicapalustris*	2013	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	1
Rhacophoridae	*Pseudophilautus*	*amboli*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Pseudophilautus*	*kani*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*akroparallagi*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*archeos*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	147
Rhacophoridae	*Raorchestes*	*aureus*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	147
Rhacophoridae	*Raorchestes*	*blandus*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	147
Rhacophoridae	*Raorchestes*	*chlorosomma*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25

Table 1: (continued)

Taxa	Genus	Species	Year	Region	Molecular Data		SDM- DNA		Morphology		Distribution	ENM	BD	NR	References
					mttDNA	nucDNA	DM	VM	MDD	SDM					
Rhacophoridae	*Raorchestes*	*chotta*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*chromasynchysi*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*coonoorensis*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*echinatus*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	147
Rhacophoridae	*Raorchestes*	*emerald*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	147
Rhacophoridae	*Raorchestes*	*flaviocularis*	2014	WG	Yes	No	No	No	Yes	No	No	No	Yes	Yes	147
Rhacophoridae	*Raorchestes*	*ghatei*	2013	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	115
Rhacophoridae	*Raorchestes*	*honnametti*	2016	WG	Yes	No	No	No	Yes	No	No	No	Yes	Yes	125
Rhacophoridae	*Raorchestes*	*indigo*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	147
Rhacophoridae	*Raorchestes*	*jayarami*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*kaikatti*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*kollimalai*	2020	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	70
Rhacophoridae	*Raorchestes*	*lechiya*	2016	WG	Yes	No	No	No	Yes	No	No	No	Yes	Yes	153
Rhacophoridae	*Raorchestes*	*leucolatus*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	147
Rhacophoridae	*Raorchestes*	*marki*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*munnarensis*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Rhacophoridae	*Raorchestes*	*primarrumpfi*	2014	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	147
Rhacophoridae	*Raorchestes*	*resplendens*	2010	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	29
Rhacophoridae	*Raorchestes*	*silentvalley*	2016	WG	Yes	No	No	No	Yes	No	No	No	Yes	Yes	153
Rhacophoridae	*Raorchestes*	*sushili*	2009	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	25
Lizards –															
Agamidae	*Calotes*	*zolaiking*	2019	NEI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	68
Agamidae	*Monilesaurus*	*acanthocephalus*	2018	WG	Yes	Yes	No	No	Yes	No	Yes	No	No	Yes	121
Agamidae	*Monilesaurus*	*montanus*	2018	WG	Yes	Yes	No	No	Yes	No	Yes	No	No	Yes	121
Agamidae	*Sarada*	*darwini*	2016	WG/PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	47

Table 1: (continued)

					Molecular Data		SDM- DNA		Morphology						
Taxa	Genus	Species	Year	Region	mttDNA	nucDNA	DM	VM	MDD	SDM	Distribution	ENM	BD	NR	References
Agamidae	*Sarada*	*superba*	2016	WG/PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	47
Agamidae	*Sitana*	*attenboroughii*	2018	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	133
Agamidae	*Sitana*	*dharwarensis*	2020	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	16
Agamidae	*Sitana*	*gokakensis*	2018	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	49
Agamidae	*Sitana*	*laticeps*	2016	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	47
Agamidae	*Sitana*	*marudhamneydhal*	2016	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	47
Agamidae	*Sitana*	*spinaecephalus*	2016	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	47
Agamidae	*Sitana*	*thondalu*	2018	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	49
Agamidae	*Sitana*	*visiri*	2016	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	47
Gekkonidae	*Cnemaspis*	*ajijae*	2018	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	134
Gekkonidae	*Cnemaspis*	*amba*	2019	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	87
Gekkonidae	*Cnemaspis*	*amboliensis*	2018	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	134
Gekkonidae	*Cnemaspis*	*bangara*	2020	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	14
Gekkonidae	*Cnemaspis*	*chengodumalaensis*	2020	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	42
Gekkonidae	*Cnemaspis*	*flaviventralis*	2016	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	134
Gekkonidae	*Cnemaspis*	*graniticola*	2020	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	14
Gekkonidae	*Cnemaspis*	*koynaensis*	2019	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	87
Gekkonidae	*Cnemaspis*	*limayei*	2018	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	134
Gekkonidae	*Cnemaspis*	*magnifica*	2020	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	88–90
Gekkonidae	*Cnemaspis*	*mahabali*	2018	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	134
Gekkonidae	*Cnemaspis*	*rishivalleyensis*	2020	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	13
Gekkonidae	*Cnemaspis*	*shevaroyensis*	2019	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	87
Gekkonidae	*Cnemaspis*	*stellapulvis*	2020	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	88–90
Gekkonidae	*Cnemaspis*	*thackerayi*	2019	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	87
Gekkonidae	*Cnemaspis*	*yelagiriensis*	2020	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	14

Table 1: (continued)

Taxa	Genus	Species	Year	Region	Molecular Data		SDM- DNA		Morphology		Distribution	ENM	BD	NR	References
					mttDNA	nucDNA	DM	VM	MDD	SDM					
Gekkonidae	*Cnemaspis*	*zacharyi*	2020	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	42
Gekkonidae	*Cyrtodactylus*	*bhupathyi*	2018	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	10
Gekkonidae	*Cyrtodactylus*	*chamba*	2018	WH	Yes	No	No	No	Yes	No	No	No	No	Yes	7
Gekkonidae	*Cyrtodactylus*	*guwahatiensis*	2018	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	9
Gekkonidae	*Cyrtodactylus*	*jaintiaensis*	2018	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	9
Gekkonidae	*Cyrtodactylus*	*kazirangaensis*	2018	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	9
Gekkonidae	*Cyrtodactylus*	*montanus*	2018	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	9
Gekkonidae	*Cyrtodactylus*	*nagalandensis*	2018	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	9
Gekkonidae	*Cyrtodactylus*	*rishivalleyensis*	2016	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	3
Gekkonidae	*Cyrtodactylus*	*septentrionalis*	2018	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	9
Gekkonidae	*Cyrtodactylus*	*srilekhae*	2016	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	3
Gekkonidae	*Cyrtodactylus*	*tripuraensis*	2018	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	10
Gekkonidae	*Cyrtodactylus*	*urbanus*	2020	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	127
Gekkonidae	*Cyrtodactylus*	*varadgirii*	2016	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	6
Gekkonidae	*Dravidogecko*	*douglasadamsi*	2019	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	36
Gekkonidae	*Dravidogecko*	*janakiae*	2019	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	36
Gekkonidae	*Dravidogecko*	*meghamalaiensis*	2019	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	36
Gekkonidae	*Dravidogecko*	*septentrionalis*	2019	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	36
Gekkonidae	*Dravidogecko*	*smithi*	2019	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	36
Gekkonidae	*Dravidogecko*	*tholpalli*	2019	WG	Yes	Yes	Yes	No	Yes	No	No	No	No	Yes	36
Gekkonidae	*Hemidactylus*	*chikhaldaraensis*	2019	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	4
Gekkonidae	*Hemidactylus*	*chipkali*	2017	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	106
Gekkonidae	*Hemidactylus*	*flavicaudus*	2020	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	94
Gekkonidae	*Hemidactylus*	*graniticolus*	2011	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	5
Gekkonidae	*Hemidactylus*	*kolliensis*	2019	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	4

Table 1: (continued)

					Molecular Data		SDM- DNA		Morphology						
Taxa	Genus	Species	Year	Region	mttDNA	nucDNA	DM	VM	MDD	SDM	Distribution	ENM	BD	NR	References
Gekkonidae	*Hemidactylus*	*paaragowli*	2018	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	143
Gekkonidae	*Hemidactylus*	*rishivalleyensis*	2020	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	13
Gekkonidae	*Hemidactylus*	*sahgali*	2018	PI	Yes	No	Yes	No	Yes	No	No	No	No	Yes	107
Gekkonidae	*Hemidactylus*	*sankariensis*	2019	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	11
Gekkonidae	*Hemidactylus*	*sirumalaiensis*	2020	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	90
Gekkonidae	*Hemidactylus*	*sushilduttai*	2017	EG	Yes	No	No	No	Yes	No	No	No	No	Yes	69
Gekkonidae	*Hemidactylus*	*vanam*	2018	WG	Yes	Yes	No	No	Yes	No	No	No	No	Yes	37
Gekkonidae	*Hemidactylus*	*varadgirii*	2019	WG	Yes	No	Yes	No	Yes	No	No	No	No	Yes	38
Gekkonidae	*Hemidactylus*	*vijayraghavani*	2018	PI	Yes	No	Yes	No	Yes	No	No	No	No	Yes	105
Gekkonidae	*Hemidactylus*	*whitakeri*	2018	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	107
Gekkonidae	*Hemidactylus*	*xericolus*	2020	PI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	94
Gekkonidae	*Hemiphyllodactylus*	*arakuensis*	2019	EG	Yes	No	No	No	Yes	No	No	No	No	Yes	11
Gekkonidae	*Hemiphyllodactylus*	*jnana*	2019	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	11
Gekkonidae	*Hemiphyllodactylus*	*kolliensis*	2019	PI	Yes	No	No	No	Yes	No	No	No	No	Yes	11
Gekkonidae	*Hemiphyllodactylus*	*minimus*	2020	EG	Yes	No	No	No	Yes	No	No	No	No	Yes	110
Gekkonidae	*Hemiphyllodactylus*	*nilgiriensis*	2020	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	12
Gekkonidae	*Hemiphyllodactylus*	*peninsularis*	2020	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	12
Lacertidae	*Ophisops*	*kutchensis*	2018	NI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	8
Lacertidae	*Ophisops*	*pushkarensis*	2018	NI	Yes	Yes	No	No	Yes	No	No	No	No	Yes	8
Scincidae	*Dasia*	*johnsinghi*	2012	WG	Yes	No	No	No	Yes	No	No	No	No	Yes	72
Scincidae	*Sphenomorphus*	*apalpebratus*	2013	NEI	Yes	No	No	No	Yes	No	No	No	No	Yes	45

Header abbreviations: ***BD*** behavioural (acoustic) data, ***DM*** discovery methods, ***ENM*** ecological (climatic) niche models, ***MDD*** meristic and diagnostic data, ***mtDNA*** mitochondrial DNA, ***NR*** nomenclatural revisions, ***nucDNA*** nuclear DNA, ***SDM*** species delimitation methods, ***VM*** validation methods. Abbreviations and definitions for regions: ***EG*** Eastern Ghats (scattered mountains along east coast north of the Krishna-Godavari basin), ***NEI*** Northeast India (mountains and lowlands east of Sikkim), ***PI*** peninsular India (south of the Tropic of Cancer and exluding EG and the Western Ghats), ***WG*** Western Ghats (mountains along the west coast and associated lowlands), ***WHI*** Western Himalayas (Himalayas west of Nepal)

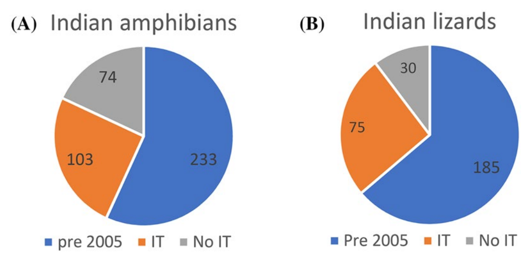

Figure 2: The number of mainland Indian **A** anurans and **B** lizards described before 2005 (blue fill), and since 2005 using integrative taxonomy (IT; orange fill) and not using IT (grey fill)

of integrative taxonomy will contribute significantly to address multiple evolutionary and ecological questions on the species/biodiversity origins which still in its nascent stage in the Indian subcontinent[59,120,119,135]. For example, to assess the geographic mode of speciation (allopatric/sympatric/parapatric), divergences across multiple datasets will indicate traits which may be under selection, identify if there is morphological stasis or convergent evolution[135]: Table 3;[59].

In the following section, we review the literature to understand the state of progress in systematics with respect to integrative taxonomy in the Indian Subcontinent since 2005 (post[46,151]). We build on the recent review of integrative taxonomic studies carried out by Karanth[83] for Indian taxa. We provide an exhaustive list of the species wherein delimitation and formal description were done using an integrative framework across vertebrate and invertebrate groups (Table 1). We list the details on methods and datasets used for each species and also remark on subsequent nomenclatural revisions if they were any. Finally, we illustrate a practical guide on the use of an integrative taxonomic framework with the hope that it will be useful for future systematic studies (Fig. 3). In addition, we use a few Indian examples from multiple vertebrate and invertebrate groups to illustrate the usefulness of integrative taxonomy while discovering and documenting species diversity. We deliberate on how taxonomic and systematic questions were addressed, what data and analytical approach were employed. We also remark on if there were any shortcomings or limitations in these studies. These studies across taxa highlight that invariably when integrative taxonomy is used, it has revealed more species than were previously recognised, as is often the case when molecular sequence data is used. Another interesting point to note is that there is variability among taxa with respect to divergence and/or degree of divergence across datasets, highlighting the importance of integrative taxonomy (Table 1). Towards the end, we argue for the need for a national strategy for taxonomy and systematics research for India with an outline on how to achieve this.

5 Case Studies Using Integrative Taxonomy from the Indian Subcontinent

Google scholar was used to trawl the literature using the following search terms; "new species"+"integrative taxonomy"+"India"; "new species"+"phylogeny"+"India" to collect information on Indian works that used an integrative taxonomic approach among vertebrates and invertebrates. Unfortunately, we could not find a taxonomic or systematic study on angiosperms where an integrative framework was used. Taxon-specific data were collected for select groups of amphibians, lizards, mammals, birds, fishes and invertebrates using specific online resources and Google Scholar for very recent descriptions (Table 1).

In addition, we downloaded species lists for Indian anurans (https://amphibiansoftheworld.amnh.org/ [61]; including the families Bufonidae, Dicroglossidae, Megophryidae, Micrixalidae, Microhylidae, Nyctibatrachidae, Ranidae, Ranixalidae, Rhacophoridae) and lizards (http://reptile-database.reptarium.cz/ [145]) and retained only species from mainland India. We used herpetofauna as an example to understand the rate at which new species are being described and what proportion since 2005 have used an integrative approach. Undoubtedly, a large number of systematic studies have been carried out on herpetofauna which has seen a large number of new species descriptions in the last two decades form the Indian subcontinent (Figs. 1, 2).

Below are four case studies from vertebrates (geckos and amphibians) and invertebrates (centipedes) where integrative taxonomy was used to reconstruct species hypothesis. We hope that these studies and this review provide a framework to assess species hypotheses for many taxa across the subcontinent.

6 Case Study: Six new species of *Dravidogecko* (Squamata: Gekkonidae)[36]

6.1 Diversity and Distribution

The genus *Dravidogecko* is restricted to the southern Western Ghats of peninsular India. It is the sister taxon to the genus *Hemidactylus* which has ~ 165 described species across the tropics,

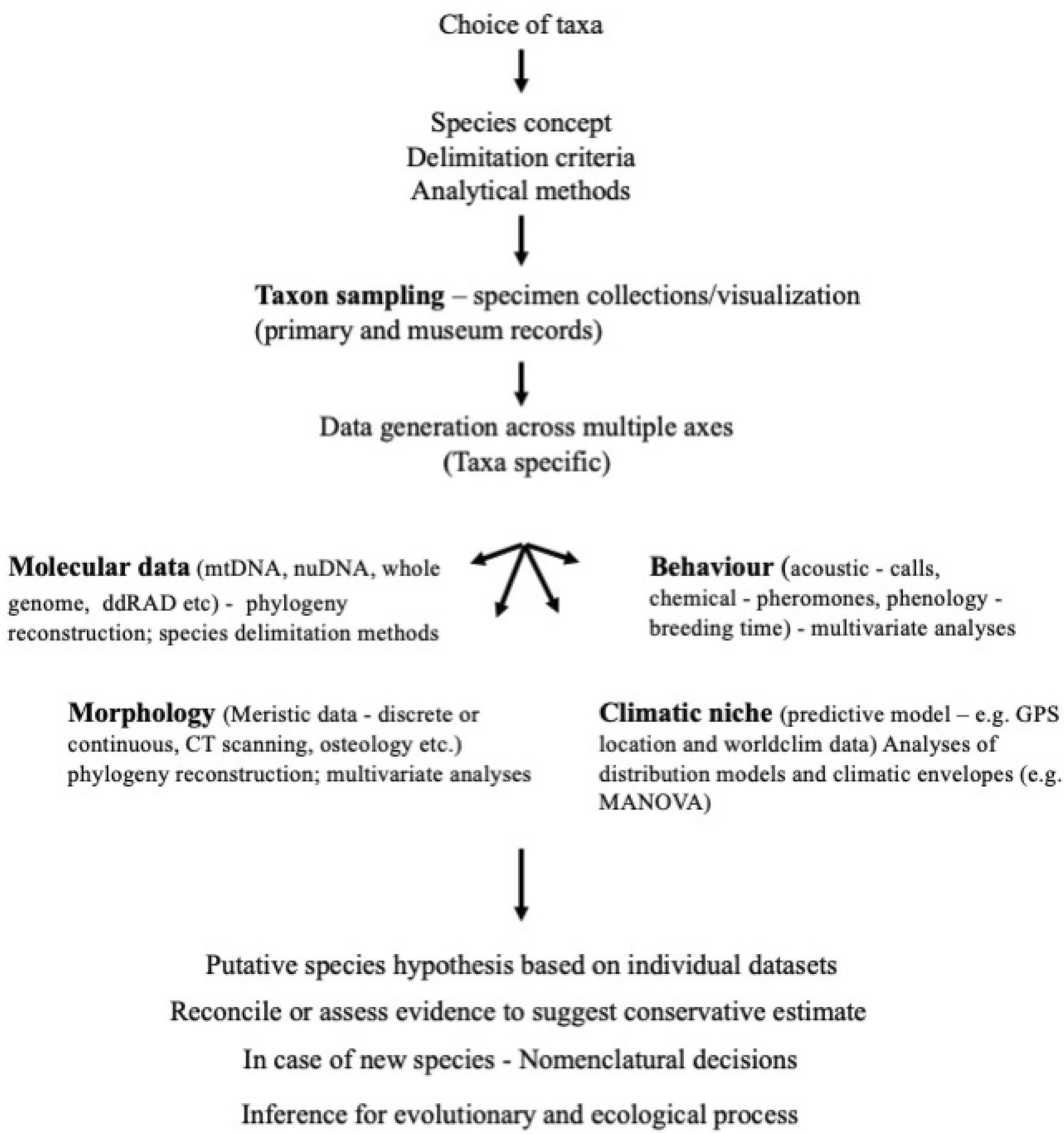

Figure 3: A practical guide to use integrative taxonomy for systematic studies.

and was thought to contain a single species, *D. anamallensis* up until the revision of Chaitanya et al.[36]. *Dravidogecko anamallensis* has been considered a member of *Hemidactylus*[23] but was more recently reassigned to *Dravidogecko*[21].

6.2 Taxonomic History

The single species of the genus, *Dravidogecko anamallensis*, was thought to be a high elevation species with a patchy distribution in the Western Ghats, but there had been no taxonomic assessment of the genus from across its range. Chaitanya et al. [36] carried out a detailed integrative taxonomic review of the genus, describing six new species.

6.3 Methodology

Chaitanya et al.[36] sampled *Dravidogecko* from across its known geographic range as well as additional localities north and east with conducive habitats. A range of commonly used morphological characters were used along with one mitochondrial and two nuclear markers. The authors used species delimitation (GMYC, bPTP;[123,155]) on a single locus mitochondrial phylogeny as a species discovery method, and validated these candidate species using a multi-locus coalescent approach (B,[152]). A subset of phylogenetically informative morphological data was then used to delimit species in morphospace.

6.4 Remarks

The review of Chaitanya et al.[36] included thoughtful geographic sampling and detailed analyses of genetic data. However, the Nilgiris were not sampled and intraspecific genetic sampling was limited to one or a few individuals per species and morphological data was used only in diagnoses and there were no multivariate analyses, perhaps at least in part due to the conserved morphology of the group.

7 Case Study: Three New Species of *Cnemaspis* (Squamata: Gekkonidae)[12]

7.1 Diversity and Distribution

The genus *Cnemaspis* includes three divergent clades, of which the South Asian clade (hereafter SAC) is distributed in peninsular India, Sri Lanka and parts of Southeast Asia. Over 80 species are known from this clade, including 49 species from India, with 100% endemicity. The majority of Indian species are distributed in the Western Ghats, with a few species distributed in southern parts of the peninsula and one species known from the northeast.

7.2 Taxonomic History

This species-rich clade has seen an incredible increase in the number of described species since the revision of Manamendra-Arachchi et al.[100], with 31/49 known Indian species described from 2007 onward. This has been due to a combination of a review of all name-bearing types[100], expanded survey effort and the use of molecular data. Mitochondrial phylogenies for the clade have been recently published, with most named species included[12, 86,134].

7.3 Methodology

Agarwal et al.[14] described three new species of South Asian *Cnemaspis* from granite boulder habitats on the southern edge of the Mysore Plateau. They used a single mitochondrial marker to reconstruct relationships and estimate divergence times for the entire clade. A simple p-distance cut-off was used to flag potentially divergent lineages, and morphological characters were used to diagnose the new species.

7.4 Remarks

The authors did not carry out species delimitation analyses using molecular data and simply used a distance-based cut-off with limited intraspecific sampling, besides lacking nuclear data. Additionally, morphological data were used only in diagnoses and there were no multivariate analyses. Geographic sampling was opportunistic. Further work on the genus needs to include nuclear data as well as more rigorous species discovery and delimitation approaches.

8 Case Study: Nine New Species of *Raorchestes* (Anura: Rhacophoridae)[147]

8.1 Diversity and Distribution

Bush frogs of the genus *Raorchestes* are distributed in peninsular India (mainly the Western Ghats) and Southeast Asia. Members of this genus are unique in that they show direct development, bypassing the tadpole stage. They are small and almost all arboreal with a few canopy-dwelling and terrestrial species.

8.2 Taxonomic History

Indian bush frogs, formerly included in the genus *Philautus*, have seen a resurgence in species descriptions and systematic studies since the turn of the century. The last 20th-century work revision of the group was by Rao[130], and only two species were described in the latter part of the century (SI). Since 2002, there have been a plethora of new species descriptions from peninsular India (mainly from the Western Ghats), with as many as 47/62 known Indian species described during this period.

8.3 Methodology

A range of morphological characters was used along with three mitochondrial markers. The authors used a novel pipeline, which involved screening of pairwise mtDNA divergences and the comparison with 'good' species—sympatric species pairs that show divergence in morphology and calls, followed by separation into different 16 s divergence categories, validated by examination of overlap in geographic range and morphology.

8.4 Remarks

This study had good geographic sampling, especially in southern parts of the Western Ghats, and used a well-thought-out and systematic pipeline for species discovery and validation. Some of the drawbacks of their work include that genetic data was used in a tree-based or distance-based method without species delimitation analyses, that they lacked nuclear data, and finally it is unclear why they chose to not name some of the genetically divergent lineages that met their criteria, and what the implications are for their pipeline. They also chose to use the slower evolving mitochondrial gene to flag preliminary divergence, and it is unclear why one of the quicker evolving genes was not chosen. Additionally, geographic location is argued by some to represent an extrinsic trait of a species[58], and this is of particular significance in the Indian context as many species are known only from the holotype or original description and may not have any or precise locality information.

9 Case Study: Five New Species of *Rhysida* (Chilopoda: Scolopendridae) Wood, 1862 from India[79]

9.1 Diversity and Distribution

The centipede genus *Rhysida* is distributed across South America, Africa, Australia and Asia with ~ 35 species. Most species are restricted to only one continent or biogeographical region. Joshi et al.[79] reported 11 *Rhysida* species from India almost doubling the previously known diversity.

9.2 Taxonomic History

The systematics of the centipede genus *Rhysida* has been a challenge with its pantropical distribution and high diversity. Molecular phylogenetic analysis has indicated that it is a polyphyletic group ([79], Fig. 1). The Indian species form a clade with a few southeast Asian species referred to as Indo-Asian clade[77,79,139]. Joshi et al.[79] revised the Indo-Asian clade in an integrative taxonomic framework where they used molecular, morphological and distributional data. Within the Indo-Asian clade, they identified two distinct clades, *logipes* and *immraginata* with four and and species respectively. They described five new species in peninsular India, one from northeast India, and one subspecies from peninsular India was elevated to species level.

9.3 Methodology

The genus *Rhysida* was well sampled in peninsular India and with opportunistic sampling in northeast India. Molecular phylogenetic analyses were carried out based on two mitochondrial markers (COI and 16S rDNA) and one nuclear marker (28S rDNA). Apart from phylogenetic analyses, the authors used two species delimitation methods (GMYC and mPTP—species discovery methods) based on a single mitochondrial DNA phylogeny. All species including type material were assessed, scored, and described for morphological characters used in Otostigminae systematics. The geographic distribution of each of the species was evaluated based on primary location data and through literature. In a follow-up study, individual species niche models were also assessed (Bharti et al. *in review*). A robust species hypothesis was proposed based on the reconciliation of molecular phylogeny, species delimitation methods, diagnostic morphological characters, and distribution data (Table 2).

9.4 Remarks

No validation method was used for the DNA sequence data such as BPP or *BEAST, which would be ideal to do in future studies. Also, morphological data was used for diagnoses, however, meristic data were also presented in the study. It needs to be further analysed either in a phylogenetic or multivariate framework.

10 A Need for a National Strategy for Taxonomy and Systematic Research

The importance of taxonomy and systematics research in sciences, education and innovation has been argued and highlighted for a long time across the globe[34,39,103]. The political boundaries of mainland India span a large latitudinal and longitudinal gradient, with elevations from sea level to well over 7000 m. This topographic and climatic heterogeneity has given rise to a consequent multitude of habitats including coastal habitats, savannas and grasslands, hot and cold deserts, dry forests to tropical wet evergreen forests, and alpine habitats,with high biodiversity of which a large proportion is endemic. However, there is a deep lack of understanding of this biodiversity—with most data on species diversity and distribution coming from pre-independence colonial studies. Only in the last two decades have concerted efforts begun to inventory biodiversity, resulting in the description of scores of new species across taxa at an unprecedented rate (Fig. 1; Table 1).

It is then clear that India is a hugely biodiverse country, with strong gaps in the understanding of species diversity and distribution. These gaps impact conservation planning, studies in ecology

Table 2: Summary of the multiple lines of evidence used to delimit species in the centipede genus ***Rhysida*** from peninsular India

Species name	Molecular Phylogenetic analysis (mt and nucDNA)	Species delimitation based on the single locus (COI)		Morphological data-meristic and diagnostic characters	Distribution (geographic location data and predicted niche models)
		GMYC	mPTP		
***Longipes* clade**					
R. longipes	Monophyletic	2	1	1	South and SEA
R. konda sp. nov	Monophyletic	1	1	1	Central EG
R. crassispina	Monophyletic	1	1	1	Northern WG
R. pazhuthara sp. nov	Monophyletic	2	1	1	Southern WG
***Immarginata* clade**					
R. trispinosa	monophyletic	7	4	1	Peninsular India
R. lewisi sp. nov	monophyletic	3	1	1	Central WG
R. immarginata	monophyletic	1	1	1	SEA
R. sp1	monophyletic	1	1	1	South WG and Central EG
R. sp2	monophyletic	1	1	1	Northern EG
R. sada sp. nov	monophyletic	1	1	1	Northern WG
R. aspinosa	monophyletic	1	1	1	South WG
R. ikhalama sp. nov	monophyletic	1	1	1	Northeast India

mt and nucDNA mitochondrial and nuclear DNA, ***GMYC*** Generalised Mixed Yule Coalescent, ***mPTP*** multi-rate Poisson Tree Process, ***WG*** Western Ghats, ***EG*** Eastern Ghats, ***SEA*** southeast Asia

Biological collections: "Biological collections typically consist of organisms (specimens) and their associated biological material, such as preserved tissue and DNA, along with data—digital and analogue (such as handwritten field notes)—that are linked to each specimen. Non-living specimens, which include organisms preserved by scientists and naturally preserved remains, such as fossils, are commonly referred to as natural history collections. Living specimens include research and model organisms that are grown and maintained in genetic stock centres, germplasm repositories, or living biodiversity collections. The defining trait of these different types of collections is that they capture aspects of the living world in such a way that it can be intensively studied and understood through time"—National Academies of Sciences, Engineering, and Medicine 2020. Biological Collections: Ensuring Critical Research and Education for the twentyfirst century. Washington, DC: The National Academies Press. https://doi.org/10.17226/25592.

and evolution, agricultural practices, and disease ecology among other fields; and there is a pressing need to develop a detailed and long-term strategy for taxonomy and systematics in India. The field of taxonomy and systematics face a multitude of challenges including lack of infrastructure, modern national history collection facilities, as well as the expertise and investment in training to study biodiversity. The government funding agencies currently do not have dedicated field research grants, reflecting the general lack of emphasis on field surveys which are vital to understanding species numbers and distribution.

In this regard, national strategies have shown to play an important role in advancing science by identifying the knowledge gap, strengthening the operational requirements such as infrastructure, funding and training and also ensuring the future health of the discipline. The UK government and the Natural Environment Research Council (NERC) commissioned a review to come up with a strategic plan for the Taxonomy and Systematics research community in 2000. They focused on three main aspects: (1) current status and trends in the UK taxonomy and systematics sector, funding availability, manpower and training, (2) to produce an assessment of needs for the outputs from taxonomy and systematics activities and research known as 'Next Generation Science for Planet Earth' and lastly, (3) to produce strategic recommendations for the future development of taxonomy and systematics in the UK[34]. This review has helped the growth and advancement in systematic research in the UK as well at a global scale.

One recent assessment in the US focused on exploring the contributions of biological collections in research, education and innovation[111]. In that review, they outlined the critical challenges in maintaining these large biological collections across the USA, how to create new spaces and suggested a long-term strategy for the same. This report has been published along with its recommendations by the National Academies Press and is freely available.

We briefly discuss a few points that could be useful for national-level strategy planning in taxonomy and systematic biology in India.

1. **Need for a national repository:** there is a dire need for a national repository where voucher specimens will be kept, maintained, and will be accessible to all scientists/ taxonomists. The collection facility needs to be modern with infrastructure that allows long term storage of tissue samples for molecu-

lar work, whole specimens for morphology work and should have state of the art imaging and computational facilities. The facilities should also allow long-term data storage, annotation, integration, and facilitating accessibility to a broader range of stakeholders. This may involve restructuring existing facilities but certainly also creating new ones. There is a large existing infrastructure of museums associated with the Zoological Survey of India and Botanical Survey of India; besides the collection of the Bombay Natural History Society, which can potentially be upgraded with the creation of long term tissue storage facilities.

2. **Use of best practices in taxonomy**: this could be achieved through discussions, forming a consortium with both international and national experts to develop the best practices in systematics and describing biodiversity. Indian journals that publish species descriptions, besides dedicated taxonomy and systematics journals should also be involved to encourage the use of best practises, not just in integrative taxonomy but nomenclatural issues as well, to ensure a stable taxonomy.
3. **Teaching and training the next generation**: it is extremely important to train researchers in taxonomy and systematics along with evolutionary biology which is currently lacking in India. There are no courses that offer a holistic view of systematics at either the graduate or postgraduate level. It is a pity that we live in one of the most biodiverse parts of the world but have not invested in training in taxonomy and systematics.
4. **Research and infrastructure funding**: there is a need for dedicated research and infrastructure money allotted given to taxonomy/systematics research community.

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Declaration

Conflict of Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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