Indian Insects:
Diversity and Science
A festschrift for Professor C.A. Viraktamath's 75th birthday

Edited by
S Ramani
Prashanth Mohanraj
H M Yeshwanth

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16 Taxonomy, Systematics, and Biology of Indian Butterflies in the 21st Century

Krushnamegh Kunte, Dipendra Nath Basu, and G. S. Girish Kumar

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INTRODUCTION

India is a large landmass with a unique geological history, which is placed at a critical meeting point of several biogeographic regions and subregions of the world. It provides diverse habitats and environmental gradients in its oceans and mountains, and encompasses some conspicuous biogeographic breaks, which together form complex land- and seascapes that support remarkable biodiversity. Indeed, India is one of the most biodiverse countries of the world, hosting four globally recognized biodiversity hotspots that contribute to the densest cluster of hotspots in the world (Figure 16.1) (Marchese 2015; Myers et al. 2000). As a result, India is one of the most critical centres for the exploration and conservation of tropical biodiversity. Yet, India has not been able to keep pace in documenting species diversity, from the basic taxonomic characterization of species to deeper understanding of their biology, compared to the progress that has been made by foreign researchers in this area. This stunted growth of biological research has especially affected studies of exceptionally biodiverse groups such as insects, plants, and microbes, which still remain poorly inventoried in India's biodiversity hotspots. As India makes progress in building scientific institutions and infrastructure in its ambition of becoming a scientific and technological entity, it is crucial to keep a firm focus on its unique and invaluable biological heritage—its biodiversity—that can place Indian science in a unique leadership.

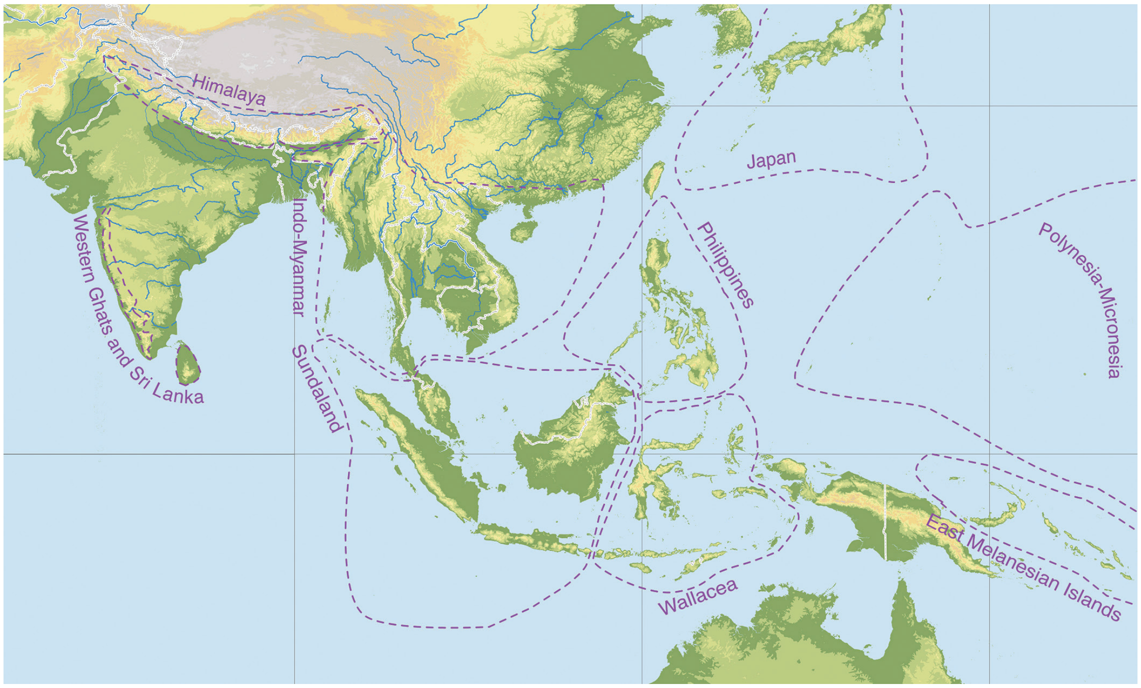


FIGURE 16.1 India's four globally recognized biodiversity hotspots, which are part of the densest cluster of hotspots placed in the Indo-Australian Region. Indian biodiversity needs to be understood in the larger context of biogeography and diversification in the Oriental, Afrotropical, and Palearctic Zones. The map of biodiversity hotspots is based on (Marchese, C., *Glob. Ecol. Conserv*., 3, 297–309, 2015; Myers, N. et al. *Nature*, 403, 853–858, 2000) and the Conservation International map of biodiversity hotspots.

Butterflies are charismatic, so they are often considered to be a flagship group for insect biology and conservation. In India, the state of butterfly biology instead effectively represents the problems that have dogged insect biodiversity research: (a) taxonomy of butterflies is outdated, (b) there is widespread misunderstanding of species and subspecies names, synonyms, and taxonomic rules, (c) competent taxonomists are largely missing, and those who exist largely lack easy access to historically most important European museum collections, (d) knowledge of current distributions and populations was virtually absent until 10 years ago, and it is still sketchy, (e) detailed morphological characterization, which is very important for taxonomic works, has been done poorly, (f) information on basic natural history such as habitat use, early stages, larval host plants, nectar plants, etc., is just beginning to accumulate, and (g) advanced knowledge of population and community ecology, plant-butterfly associations and other inter-species interactions, trait evolution, biogeography, population genetics, speciation patterns, etc., is almost completely lacking. This situation needs to change rapidly.

The primary goals of this chapter are to: (a) provide a historical account of the development of taxonomy and biology of Indian butterflies, including a brief review of trends in taxonomic, natural historic, and scientific research on Indian butterflies, (b) point out recent developments in the fields of evolutionary biology, phylogenetics, molecular systematics, and biogeography, which have a strong bearing on current taxonomic developments and trends, (c) highlight problems with current taxonomic practices in India, and (d) offer a vision for growth of modern taxonomy, systematics, and butterfly biology, in the 21st century India. It is meant to be a primer on historical and modern methods in taxonomy, molecular systematics, and museum sciences in general, for students of entomology, who will benefit from using butterflies as a case study to understand insect systematics and biology. Thus, this chapter will present an array of illustrations and examples that have a special significance in the Indian context.

INDIAN BUTTERFLIES, A TAXONOMIC LEGACY

Historical accounts and literature on Indian butterflies, natural history, and naturalists, are extensive. It is not possible to include an exhaustive account here, although such an account would be an excellent academic pursuit, and it needs to be written for posterity. However, the short account given below will serve as a basic introduction that will get students initiated. It will also highlight some important milestones that will be relevant for the remainder of the chapter.

Indian butterflies started to be systematically studied and formally named with the publication of Carl Linnaeus's *Systema Naturae* in 1758 in which he established the binomial system of naming species. This was a novel way of assigning unique scientific names to any species of organism on earth based on a genus name followed by a species name, which would ease communication among scientists. This proved especially timely since the natural world around Linnaeus was rapidly expanding as European empires reached far corners of the world, bringing in previously unfamiliar species from distant lands. Linnaeus's binomial system was an instant success: tens of thousands of species had been named using this system, and its acceptance spread far and wide in Europe, within decades. The system has subsequently become the core of taxonomic nomenclature for all life on earth. Linnaeus's work was soon followed by two sets of volumes in which dozens more Indian butterfly species were described, one written by Linnaeus's student Johan Christian Fabricius and the other by a Dutch merchant and amateur entomologist, Pieter Cramer. Together, these three taxonomists described nearly 350 butterfly taxa from the Indian region (Figure 16.2). Most of the butterfly type specimens used by Linnaeus, which have been intensively inventoried, are now housed in the Linnean Society of London, Museum Ludovicae Ulricae (Uppsala University), the Clerck and De Geer collections in the Naturhistoriska Riksmuseet (Stockholm), and the James Petiver Collection in the Sir Hans Sloane Collection at The Natural History Museum, London (Honey and Scoble 2001). The Linnean type specimens have also been photographed by The Natural History Museum, London (NHMUK, previously the British Museum of Natural History, or BMNH) (http://www.nhm.ac.uk/research-curation/research/projects/linntypes/), and by the GART project (Globales Ahgister Tagfalter), i.e., The Global Species Register Butterflies (http://www.naturkundemuseum-bw.de/sites/default/files/forschung/user_122/gart_biolog-status_2001.pdf). Many of Cramer's type specimens are also in NHMUK (Chainey 2005). The Fabricius Collection is largely in the Natural History Museum of Denmark in the University of Copenhagen and in the Zoological Museum of the University of Kiel (Germany) (https://samlinger.snm.ku.dk/en/dry-and-wet-collections/zoology/entomology/fabricius-collection/). These are significant type collections since Fabricius alone described nearly 10,000 species of insects, including many butterflies, for which he is considered one of the founders of systematic entomology (see the last link).

This initial flurry of species descriptions was followed by a relative lull in the early 1800s. What might be considered a golden period in the discovery and naming of Indian butterflies started from the 1820s with the publication of Thomas Horsfield and Frederic Moore's *A Catalogue of the Lepidopterous Insects in the Museum of the Honorary East-India Company*. Both Horsfield and Moore had very long careers, and they together covered nearly 90 years of studies of Indian butterflies, describing over 500 taxa. Indeed, Moore holds a record for describing more butterfly taxa from the Indian region than any other butterfly taxonomist in history (Figure 16.2C), although some of his species descriptions were published as collaborations, and therefore their authorships were shared with other taxonomists. The golden period of taxonomic discovery of butterflies on the Indian subcontinent peaked from ca 1840 to 1900, when the majority of the species and subspecies that are currently considered taxonomically valid were described (Figure 16.2B). Apart from Moore, the bulk of this work was done by entomologists of the British Raj, such as Hewitson, Doubleday, Horsfield, Westwood, and de Nicéville, although continental European entomologists such as Kollar, C. Felder, and R. Felder also made important contributions (Figure 16.2). Details of their active periods on Indian butterflies, landmark publications, and the number of taxa described by them from the Indian subcontinent, are given in Figure 16.2B,C. The majority of the type specimens used by these British entomologists are housed in NHMUK, except many of de Nicéville's types that are in the Zoological Survey of India in Kolkata (ZSI-K). Types described by the continental European entomologists are scattered, and some of them have not been properly catalogued and therefore not easily accessible. Many of the Indian butterfly types housed in NHMUK, and the majority of the de Nicéville types in ZSI-K, have recently been photographed by one of us (KK) (e.g., Box 16.1). These are being made publicly available on the Butterflies of India website, at http://www.ifoundbutterflies.org/(Kunte et al. 2018).

The 1880s–1910s saw the publication of two critically important compilations of Indian butterflies. The first was a 3-volume series, *The Butterflies of India, Burmah and Ceylon*, by Marshall and de Nicéville (Marshall and de Nicéville 1882; de Nicéville 1886b, 1890b). The second set was a 10-volume series started by Moore and finished by Swinhoe, called *Lepidoptera Indica* (Moore 1892, 1896, 1899, 1900, 1903, 1905; Swinhoe 1910, 1911, 1912, 1913). Both these sets of volumes compiled all the available information on species descriptions, distributional ranges, and larval host plants. The ten volumes of *Lepidoptera Indica* especially still stand strong in the history of Indian butterfly research as the only set of volumes that extensively reviewed and illustrated every known species known at the time.

The 1890s–1910s also saw two other revolutions in taxonomic practices as applied to Indian butterflies. The first revolution was the application of subspecies names, which led to the trinomial system composed of genus, species, and subspecies names. By this time, there was a widespread recognition that different, often spatially widely separated populations of the same species varied in morphological features such as wing colouration and body size. Biologists had by then realized the importance of such variation in understanding morphological diversification, evolution, and natural selection in isolated populations. This led to the widespread establishment of the subspecies concept, which cast a long shadow on taxonomic practices especially in well-collected and extensively studied groups such as butterflies, birds, and mammals. Thus, both taxonomists and evolutionary biologists embraced the subspecies concept and its use in trinomial names as a means of formally referring to geographically structured, morphologically distinct populations of the same species. Three people led this practice in butterfly taxonomy, especially as relevant to Indian butterflies: Walter Rothschild, Karl Jordan (Mallet 2007; Riley 1960), and Hans Fruhstorfer. Rothschild and Jordan's contributions were particularly valuable because they bolstered the conceptual growth of the subspecies concept and widespread acceptance of trinomial names in butterfly taxonomy. The extensive use of subspecies by Fruhstorfer, and later by W. H. Evans, has survived to this day. The taxonomic and biological implications of this are discussed in later sections of this chapter.

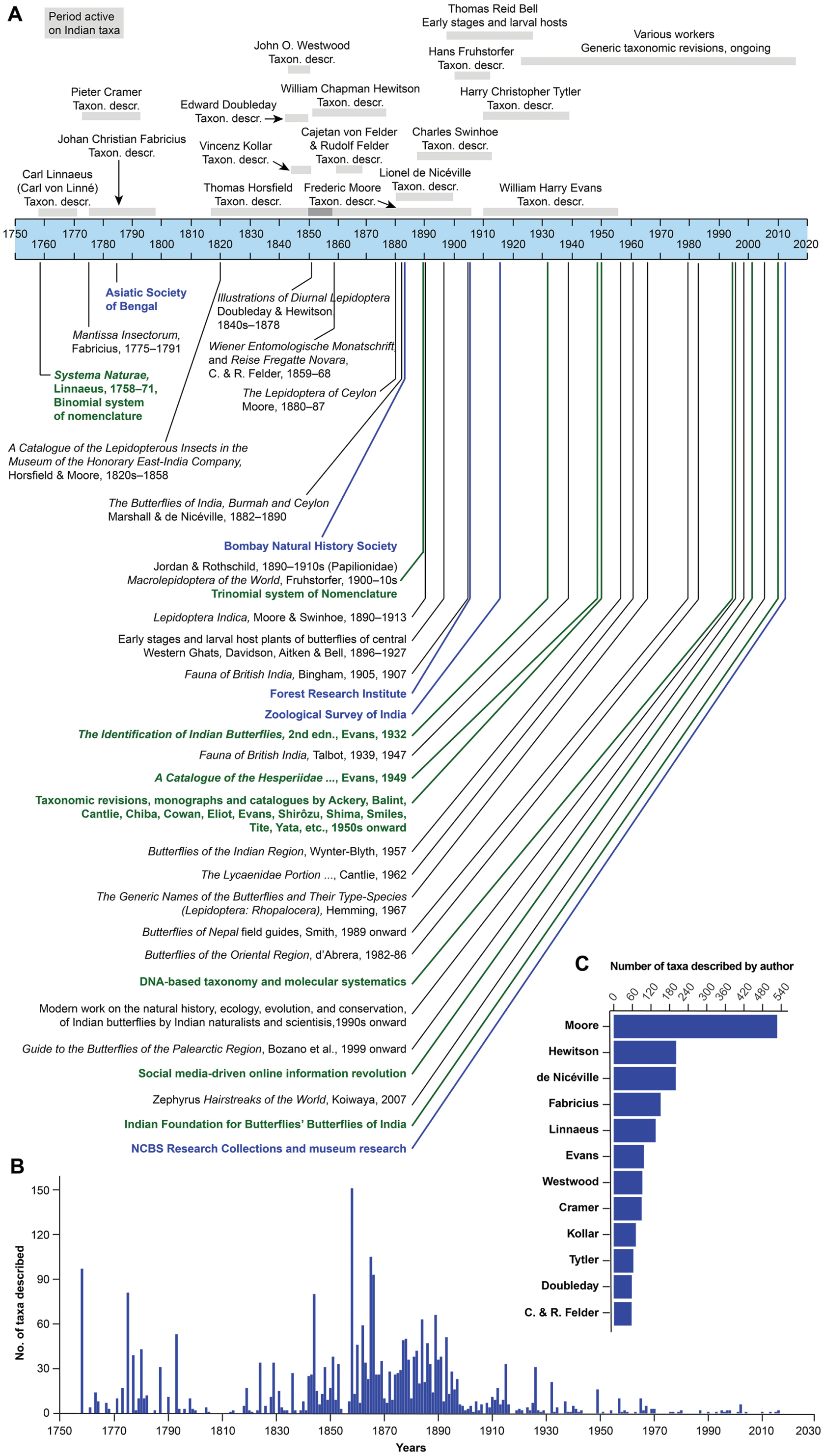


FIGURE 16.2 History of taxonomy and biology of Indian butterflies. **Panel A:** Major milestones and prominent figures along a timeline from Linnaeus's *Systema Naturae* that laid the foundation of modern taxonomy in the mid-1700s to the present time. Entries in green are highlighted milestones that contributed towards the growth of butterfly taxonomy and biology in India. Entries in blue show establishment of major societies, institutions, and infrastructures that have played critical roles in the development of scientific research and publications on Indian butterflies. Names above the timeline represent taxonomists who contributed in major ways to the development of butterfly taxonomy and biology in India, although the list is naturally somewhat selective. Only the years in which these lepidopterists were active on Indian butterflies are marked in this panel. The beginning years of multi-year works are marked on the timeline, the actual ranges in years are given in the text. **Panel B:** A timeline of taxonomic descriptions of valid species and subspecies, as recognized at present, of butterflies of the Indian region. **Panel C:** The number of taxa described by major authors of Indian butterflies, i.e., authors who published over 50 valid taxonomic names (species and subspecies) of butterflies of the Indian region. Based on data from K. Kunte, unpublished.

BOX 16.1 A CLASSIFICATION OF TYPE SPECIMENS USED COMMONLY IN TAXONOMIC LITERATURE

The quoted definitions given below are from the latest (4th) edition of the International Code of Zoological Nomenclature, or "The Code" as it is popularly called, and its latest online version (International Commission on Zoological Nomenclature (ICZN) 1999). Further explanations provided for each definition are also largely based on The Code. ICZN is a world authority on nomenclatural matters of zoological nature, which rules on nomenclatural acts through its bulletin and other publications.

Holotype: "The single specimen (except in the case of a hapantotype, q.v.) designated or otherwise fixed as the name-bearing type of a nominal species or subspecies when the nominal taxon is established" (ICZN 1999). Holotype is thus taxonomically the most important specimen of a species or subspecies. E.g., holotype of *Hypolycaena narada* Kunte, 2015, in National Centre for Biological Sciences (NCBS).

Paratype: "Each specimen of a type series other than the holotype [Recommendation 73D]" (ICZN 1999). Paratypes cannot be treated as syntypes and used for lectotype selection if the holotype is lost or destroyed; however, they are eligible for neotype selection. E.g., paratype of *Hypolycaena narada* Kunte, 2015, in NCBS.

Syntype: "Each specimen of a type series (q.v.) from which neither a holotype nor a lectotype has been designated [Arts. 72.1.2, 73.2, 74]. The syntypes collectively constitute the name-bearing type." (ICZN 1999). For a nominal species-group taxon established before 2000, all the specimens of the type series are treated as syntypes if neither a holotype nor a lectotype had been fixed. E.g., syntype of *Lethe tristigmata* Elwes, 1887, in NHMUK.

Lectotype: "A syntype designated as the single name-bearing type specimen subsequent to the establishment of a nominal species or subspecies [Art. 74]" (ICZN 1999). In taxonomic value, lectotypes are equivalent to holotypes. E.g., lectotype of *Charaxes dolon magniplagus* (Fruhstorfer, 1904), in NHMUK.

(*Continued*)

BOX 16.1 (Continued) A CLASSIFICATION OF TYPE SPECIMENS USED COMMONLY IN TAXONOMIC LITERATURE

Paralectotype: "Each specimen of a former syntype series remaining after the designation of a lectotype [Art. 72.1.3, Recommendation 74F]" (ICZN 1999). In taxonomic value, paralectotypes are equivalent to paratypes. E.g., paralectotype of *Charaxes dolon magniplagus* (Fruhstorfer, 1904), in NHMUK.

Neotype: "The single specimen designated as the name-bearing type of a nominal species or subspecies when there is a need to define the nominal taxon objectively and no name-bearing type is believed to be extant" (ICZN 1999). See under Paratype above.

Cotype: "A term not recognized by The Code, formerly used for either syntype or paratype, but that should not now be used in zoological nomenclature [Recommendation 73E]" (ICZN 1999). E.g., cotype of *Hyponephele (pulchra) astorica* (Tytler, 1926), in NHMUK.

Allotype: "A term, not regulated by The Code, for a designated specimen of opposite sex to the holotype [Recommendation 72A]" (ICZN 1999). For example, if a species is described from a male holotype, then a female type may be designated as an allotype, and vice versa. E.g., allotype (female) of *Chrysozephyrus tytleri tytleri* (Howarth, 1957), in NHMUK.

The second revolution of the very early twentieth century was the use of differences in the male genitalia in making taxonomic decisions. It was realized by then that sister species of insects often have distinctly different male genitalia. With the availability of microscopes, the use of genitalia dissections became a gold standard in taxonomic studies of butterflies. Early studies that described male genitalia of Indian butterflies were performed by Bethune-Baker and Swinhoe (Bethune-Baker 1918; Swinhoe 1910, 1911, 1912, 1913). The structures of male genitalia continue to be used as an important morphological dimension in making taxonomic decisions to this day. The use of female genitalia has also proved useful in resolving species relationships in some genera, although taxonomists have tended to rely on evidence from female genitalia to a lesser degree. Some examples of male and female genitalia will be discussed later in this chapter.

Brigadier William Harry Evans entered the Indian butterfly scene in early 1900s and made a deep impact with his extensive work that spanned nearly seven decades. Evans secured his position in the annals of Indian butterfly taxonomy not only with his dozens of species descriptions, but also with his generic revisions (e.g., Evans 1954, 1957), an influential catalogue and identification key of Hesperiidae of Asia, Europe, and Australia in the BMNH collections (Evans 1949), and an identification key to all the Indian butterfly species and subspecies that were known in his time (Evans 1932), which is followed by butterfly watchers to this day. Evans did some of this work as a serious amateur like so many other British lepidopterists of his generation, while serving as a military engineer. His military postings offered excellent opportunities to collect butterflies far and wide, from Balochistan and Chitral to Simla, Jabalpur and Kodaikanal. Based on this growing experience, he initially made some preliminary attempts to list Indian butterflies (Evans 1912). After World War I, however, Evans started working on a more comprehensive catalogue and identification key to butterflies of the Indian subcontinent, which was published in multiple volumes in the *Journal of the Bombay Natural History Society*. This series later contributed to Evans's most well-known identification guide, *The Identification of Indian Butterflies* (Evans 1932). This book was remarkable in that it provided the first synonymic catalogue of Indian butterflies in a trinomial system, describing several dozen new subspecies in the process. After retirement in 1931, Evans moved to London where he spent the remainder of his life devoted to the taxonomic listings and in-depth studies of butterflies in the BMNH, taking advantage of the millions of butterfly specimens deposited there. He dissected and illustrated male genitalia of thousands of hesperiid and lycaenid butterflies, which informed his taxonomic decisions. A large part of this effort resulted in his most prominent works—catalogues of Hesperiidae of the world, including that of Asia (Evans 1949), and very close to his death in 1956, of *Arhopala* (Lycaenidae) (Evans 1957). In all, Evans published dozens of papers and comprehensive catalogues in what might be considered by any standards a very productive lifetime (Evans and Bellinger 1956; Riley 1956). Evans's specimens were largely deposited in the BMNH, where his study materials of world Hesperiidae and *Arhopala* are maintained separately as reference collections to this day, which one of us (KK) has extensively photographed.

Two of Evans's contemporaries need a particular mention: Harry Christopher Tytler, also a British army officer, and George Talbot. Tytler collected extensively while on duty in Chitral in the western Himalaya and the Naga-Manipur-Chin Hills in north-eastern India and northern Myanmar. He described several dozen new species from this material (e.g., Tytler 1911, 1914, 1915, 1926, 1940) whose type specimens were deposited in the BMNH. Some of his species have not been recorded from India since their descriptions. The areas where Tytler collected are just beginning to be properly explored once again, so many of the butterfly populations that Tytler reported on may be rediscovered in coming years. On the other hand, Talbot's main contribution was not his new taxonomic descriptions, but his extensive notes on original species descriptions, natural history, and distributional ranges of butterflies of the Indian subcontinent that he published in two volumes of the *Fauna of British India* (Talbot 1939, 1947). His *Fauna* volumes also provided illustrations of male genitalia of many species. For these reasons, Talbot's *Fauna* volumes remain among the most comprehensive taxonomic works on Indian butterflies.

Scientific publications on Indian butterflies until the 1880s were largely species descriptions and/or catalogues of specimens in museum and private collections. However, natural history papers with relevance to the then newly minted theory of evolution by natural selection and other papers of interest to modern ecologists and evolutionary biologists started to appear from the 1870s (Aitken 1897; Davidson and Aitken 1890; Dudgeon 1895; Forsayeth 1884; Fryer 1914; Punnett 1908). From the 1880s, comprehensive regional checklists and other compilations of Indian butterflies started to appear since there was so much information and specimens available by then (e.g., Aitken 1886; Betham 1890a, 1890b, 1891, 1894; Cantlie 1952, 1956; de Nicéville 1885a, 1885b, 1886a, 1886b, 1890a, 1890b, 1883; Davidson et al. 1896, 1897; Doherty 1886; Elwes and de Nicéville 1886; Elwes and Möller 1888; Marshall and de Nicéville 1882; Mackinnon 1898; Mackinnon and de Nicéville 1898; Parsons and Cantlie 1948; Swinhoe 1886). Butterfly surveys in the Nilgiris and Palnis in southern Western Ghats, which had been frequented by the British tea planters and missionary school teachers, culminated in a series of papers over several decades, although the efforts still continue (Larsen 1987; Mathew and Kumar 2003; Rufus and Sabarinathan 2007; Wynter-Blyth 1944a, 1944b, 1945, 1947; Yates 1946). Studies of early stages and larval host plants of Indian butterflies received a major uplift with James Davidson, Edward Hamilton Aitken, and Thomas Reid Bell's series of papers on butterflies of the Karwar area (reported as North Kanara in the erstwhile Bombay Presidency) (e.g., Bell 1909, 1927; Davidson et al. 1896). Bell's papers, which were published over nearly 20 years in the *Journal of the Bombay Natural History Society*, offered unmatched detailed descriptions of larval and pupal morphology and behaviour of butterflies of the Western Ghats. Some of this information has subsequently contributed to a deeper understanding of larval host plant specialization that can shed light on speciation and diversification.

Demise of Tytler in the decade preceding India's independence, and that of Bell, Talbot, and Evans in the decade following, drew the direct British engagement in field expeditions and the butterfly taxonomy and biology in the Indian subcontinent more or less to a close. From World War I, attention and priorities of British officers, including that of professional and amateur lepidopterists, had already started to wander elsewhere. Shortly after World War II and India's independence in 1947, the British enterprise of natural historic and taxonomic studies largely wrapped up from the Indian subcontinent. Most of the works published after this period, including last pieces of work by Evans and Talbot, were based exclusively on specimens that had accumulated in BMNH in the preceding 125 years or so. Major highlights and expansive works after independence were few and far in between. Only a few new species have been described from India since independence, almost exclusively from the eastern Himalaya and NE India (e.g., Cantlie 1958; Cantlie and Norman 1959, 1960; Koiwaya 2002; Kunte 2015; Roy 2013). Several more species and subspecies have been described, but their taxonomic validity needs to be verified after making adequate comparisons with related species and improving morphological diagnosis (Kumar et al. 2009; Sharma 2013a, 2013b; Singh 2007; Smetacek 2004, 2011, 2012). Many more species and subspecies have been described from the neighbouring Nepal and Tibet, some of which likely occur in India (Fujioka 1970; Huang 1998, 2000, 2001, 2002, 2003; Huang and Xue 2004). However, the most important taxonomic works on Indian butterflies in the second half of the 20th century involved revisions and catalogues rather than species discovery and descriptions. Apart from Evans's *Hesperiidae Catalogue* (Evans 1949), an updated list and identification key of Indian Lycaenidae was published by Cantlie (1962). An important generic catalogue of the world butterflies that also included all the Indian genera known at the time still remains valuable today (Cowan 1970; Hemming 1967). The bulk of the progress in this area, however, involved a number of tribal and generic revisions and monographs by a large number of taxonomists (Figure 16.2) (e.g., Cowan 1966, 1967, 1974; Chiba 2009; Chiba and Eliot 1991; Chiba and Tsukiyama 1993, 1994; Eliot and Kawazoé 1983; Eliot 1963, 1967, 1969; Eliot 1973, 1986, 1990; Evans 1957; Fan et al. 2010; Howarth 1957; Masui 2004; Shirôzu and Shima 1979; Smiles 1982; Tite 1963, 1966; Tsukiyama and Chiba 1994; Yata 1989, 1991, 1992, 1994, 1995 Yata et al. 2010). A glance at these publications reveals a striking pattern: the racial dominance in taxonomic expertise and scientific output on Indian butterflies has shifted from early to late 1900s from predominantly white Europeans to Japanese Asians. However, Indians continue to be under-represented in biodiversity-related studies—from species discoveries to taxonomic revisions—in the Indian region itself. This has reinforced a "taxonomic impediment" that continues to cause trouble for Indian taxonomy and systematics (see further sections). In any case, it is very likely that traditional taxonomic works will continue in large and historically strong museums abroad with or without Indian participation. However, most of the critically important revisions in the future will be based on molecular phylogenies that are likely to stabilize tribal and generic classification and illuminate species- and subspecies-level relationships of butterflies. This is an area where Indian biologists may perhaps be able to make relatively rapid progress. Several notable recent developments in this area will be reviewed in the section below, "Recent Insights from Molecular Systematic Studies … ."

This historical legacy has had a profound influence on the current state of butterfly taxonomy in India. Before reviewing these influences and current practices, we will briefly review traditional tools of butterfly taxonomy. We will view these in light of some recent trends in evolutionary biology, phylogenetics, and molecular systematics, which form pillars of modern taxonomy. This perspective is critical for the vision of future growth in this field.

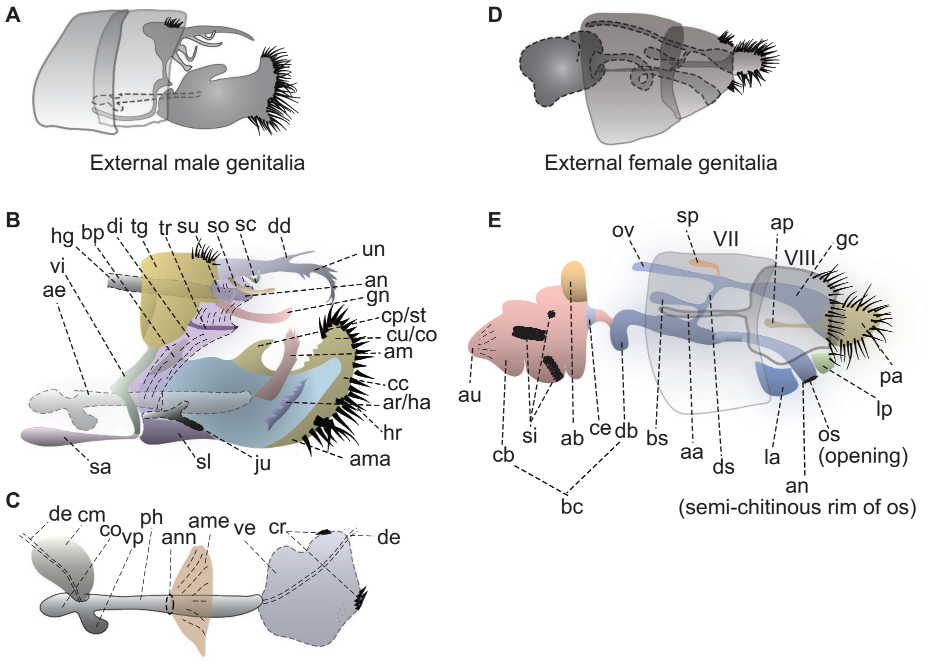
TRADITIONAL TOOLS OF TAXONOMY

Genitalia

From Linnaeus's time, butterfly taxonomists have relied to a great extent on wing colouration to define species. Body form and size, wing shape, structure of legs, labial palpi, structure of scales, etc., have also been used in various species groups, but to a lesser degree. The historical summary of work on Indian butterflies above shows that from the late 1800s, the use of male genitalia became widespread in insect taxonomy. In the case of butterflies, it became particularly common from 1910s onward, and by the 1920s and 1930s, differences in the structures of male genitalia had become one of the most predominant ways in which taxonomists tried to distinguish between closely related species in many difficult species groups. Studies of male genitalia, and in some species groups female genitalia, continue to be one of the prominent axes of evidence on which taxonomic decisions are based. However, the nomenclature of genital parts has changed to a degree in the past century. Comprehensive, well-marked reference diagrams of male and female genitalia are rarely accessible, so we provide detailed diagrams and nomenclature of butterfly genitalia in Figure 16.3. For male genitalia, structures of the uncus, cuiller, clasp, and aedeagus, are considered taxonomically especially important since they often differ prominently even among sister groups. However, not all structures are found in all butterflies, and there is considerable variation in the presence and shapes of different genital components in different groups of butterflies (Figure 16.4). The cartoon shown in Figure 16.3B is more complex than average male genitalia in any species because this is a composite of various structures that may be found in different butterfly groups and have therefore been shown together for reference. For female genitalia, structures of signum and bursa copulatrix are considered taxonomically important, although they are less frequently used for species delineation compared to structures of the male genitalia. The illustrations in Figure 16.3 are based on (Cordero and Baixeras 2015; Evans 1949; Mehta 1933).

Wing Venation

Wings of butterflies and moths are transparent, membranous structures that are crossed by veins through which haemolymph, which is somewhat equivalent to vertebrate blood, is circulated (see below for scales and colouration).


External male genitalia

External female genitalia

FIGURE 16.3 Idealized structures of the male and female genitalia of butterflies, which have been used extensively in the past for taxonomic studies. **Panel A:** External male genitalia, including the last two abdominal segments that envelop the genitalia. **Panel B:** Detailed structures of the male genitalia, excluding the aedeagus (see Panel C). **ae** aedeagus, **am** ampullary process, **an** anal opening, **ama** anal margin, **ar/ha** ampullary ridge/harpe, **bp** basal process, **cc** cucculus, **cp/st** costal process/style, **cu/co** cuiller/corona, **dd** dorsal dentate process, **di** diaphragma, **gn** gnathos, **hg** hind-gut, **hr** hairy sensilla, **ju** juxta, **sa** saccus, **sc** scaphium, **sl** sacculus, **so** socius, **su** subuncus, **tg** tegumen, **tr** transtilla, **un** uncus, and **vi** vinculum. Among these, ama, ar/ha, am, bp, cc, cp, cu/co, hr, and sl, together form the clasps or valvae (singular "valve"), with which male butterflies hold females during copulation. **Panel C:** Structure of aedeagus: **ann** annulus, **ame** annular membrane, **cm** coecal membrane, **co** coecum, **cr** cornuti, **de** ductus ejaculatorius, **ph** phallus, **ve** vesica, and **vp** ventral process. **Panel D:** External female genitalia, including the last two abdominal segments that envelop the genitalia. **Panel E:** Female genitalia: **aa** apophysis anterior, **ab** accessory bursa, **an** antrum, **ap** apophysis posterior, **au** appendix bursa, **bc** bursa copulatrix, **bs** bulla seminalis, **cb** corpus bursa, **ce** cervix, **db** ductus bursa, **ds** ductus seminalis, **gc** genital chamber, **la** lamella antevaginalis, **lp** lamella postvaginalis, **os** ostium, **ov** oviduct, **pa** anal papilla, **si** signum, and **sp** spermatheca.

Veins are stiff, and stronger than wing membranes, giving the wings sufficiently strong support that they sustain sometimes extremely high-speed, strenuous flights. Thus, veins are prominent wing structures that also have group-specific spatial arrangements. Therefore, venation is widely used in defining genera and other higher taxonomic categories of butterflies, although there may sometimes be differences even between sister species. For these reasons, wing venation has been characterized in a broad range of butterflies. Specific veins may be missing, distinctly arranged, or prominently modified, in some butterfly families, subfamilies, or tribes. Additionally, wing colour patterns develop during late larval and pupal development in relation to veins, so veins typically define boundaries between various colour patches, spots, and bands on butterfly wings (Nijhout 1991). These colour markings are commonly used in identification keys (see the next section). Thus, wing venation has great utility in studying butterflies whether from a taxonomic or developmental perspective.

Wing venation of butterflies is described with two commonly used systems (Figure 16.5). The Comstock-Needham system (Figure 16.5A) is universal, i.e., it describes wing venation across insects, because it relies on the origins of veins in relation to the cells (cell is an area of the wing that is enclosed by veins on all sides. However, open cells, i.e., cells that are not enclosed on all sides by veins, are also known in some butterflies, e.g., groups of nymphalids). This system is commonly used all over the world in entomological and other scientific literature.

The numerical system simply numbers veins from 1a through 12 on the forewing, and 1a through 8 on the hindwing, of butterflies and moths (Figure 16.5B). It is popular because of the simplicity of numbering veins. It is commonly used in identification keys of Asian butterflies, including in the extensive keys developed by Evans (see above for Evans's works) and used subsequently. In both the systems, wing areas between the numbered veins are also numbered. These numbered areas are often used to localize spots, bands, and other colour markings, as well as brands, specialized scales, and other distinctive features, while describing butterflies. Thus, it is important to familiarize oneself with wing venation before diving into serious

FIGURE 16.4 Diversity and variation in male genitalia across butterflies. Note that the male genitalia for each species are usually simpler than the cartoon shown in Figure 16.3. Also note that genitalia structures in Lycaenidae are fused in some groups. All genitalia dissections are of specimens deposited in the NCBS Research Collections.

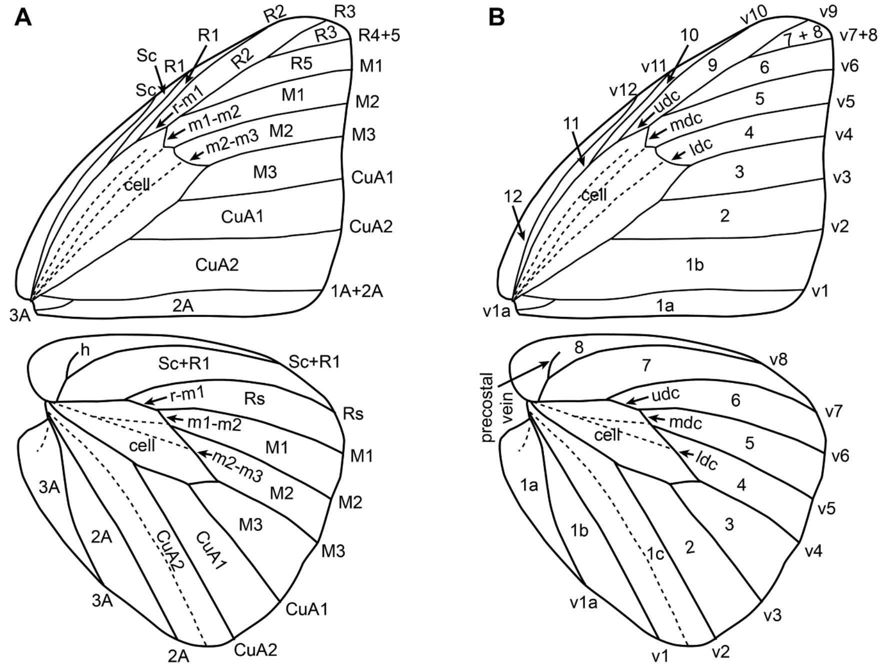


FIGURE 16.5 Wing venation of *Appias paulina* (Pieridae) as a representative butterfly species, with the relationship shown between the two most commonly used systems of classifying veins. **Panel A:** The Comstock-Needham system is universal, i.e., used across insects, because it relies on the origins of veins in relation to the cells. **Sc** subcosta (see costa, the leading edge of the wings, in Fig. 16.6), **R** radius, **M** media (middle), **CuA** as **Cu** cubitus (elbow), **A** anal veins (indicating their position near dorsum, the trailing edge of the wings, see Fig. 16.6), and **h** precostal. Some of these veins are linked with cross-veins, which are named after the veins that they link. **Panel B:** The numerical system simply numbers veins from dorsum to costa. Cross-veins in the numerical system are named after **dc** discocellular veins, as **udc** (upper discocellular vein), **mdc** (middle discocellular vein), and **ldc** (lower discocellular vein). In both panels, wing vein numbers are shown at the ends of the veins, i.e., outside the wings, except in case of veins around the cells. Numbers on the wings represent wing areas defined in relation to veins. Based and redrawn from (Sondhi, S. and Kunte, K., *Butterflies and Moths of Pakke Tiger Reserve,* 2nd edn., Titli Trust (Dehradun), National Centre for Biological Sciences (Bengaluru), and Indian Foundation for Butterflies (Bengaluru), India, p. 242, 2018, with information based on Yata, O. et al., *Syst. Entomol*., 35, 764–800, 2010; Miller, L.D., *J. Res. Lepidoptera*., 8, 37–48, 1970.)

butterfly literature, including identification keys. Further details of venation systems, and conversions between the Comstock-Needham and numerical systems, may be found in a number of scientific papers (e.g., de Jong 2004; Miller 1970; Yata et al. 2010).

COLOUR PATTERNS

Both wing surfaces of butterflies and moths are covered with rows of scales, which are dead cells. This has earned their order the scientific name Lepidoptera, which means “scale-winged.” Scales are often pigmented, which give them colour, and some have characteristic hollow spaces and nanostructures that give them other spectral properties such as iridescence and fluorescence. Butterflies that have mostly transparent wings (e.g., some Neotropical ithomiine and *Cithaeria* butterflies), or transparent wing patches (e.g., Indian *Kallima*), are still covered by scale cells that may be highly underdeveloped, differently shaped, and/or sparsely placed, on the wing membranes.

Many butterflies are incredibly colourful and prominently patterned. Since even closely related species have distinct colour patterns, however subtly different, wing colour patterns of butterflies are commonly used to distinguish between species. One must closely inspect spots, bands, and other colour patches in relation to wing venation and wing areas (Figure 16.5) to distinguish between closely related and subtly different species. For this purpose, different wing margins and areas have been defined in detail, although their names are the same on forewing and hindwing (Figure 16.6). The leading edge of the wing is called costa, the outer edge is termen, and the trailing edge is dorsum. The wing tip is called apex, and the lower corner of the wing between termen and dorsum is called tornus. The area immediately beyond the cell is called discal area, the area just inside of the wing edge is called marginal, and before that, sub-marginal. Various colour patches and markings on butterfly wings are defined in relation to these wing margins and areas (Figure 16.6B) (Kunte and Tiple 2009).

Butterflies have also been classified based on other morphological characters such as legs, labial palpi, and mouthparts (Chapman 1982).

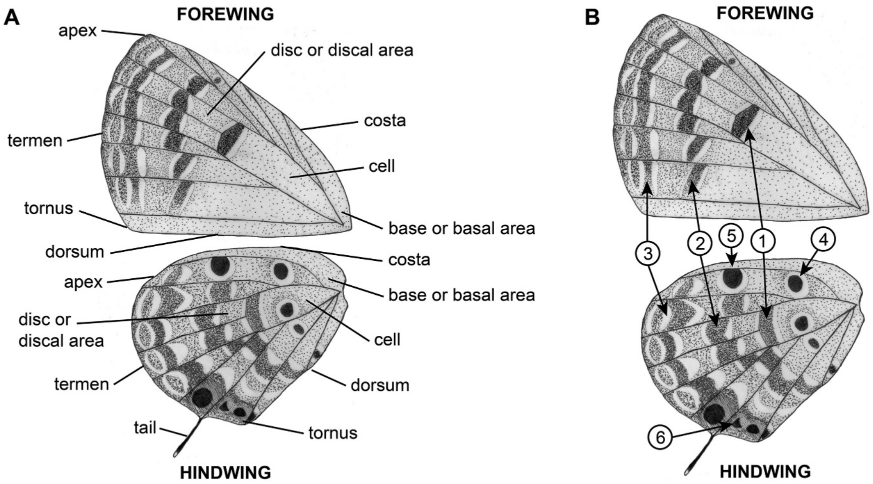


FIGURE 16.6 Wing areas of butterflies, which feature prominently in identification keys of butterflies in conjunction with wing venation (**FIGURE 16.5**), as illustrated from the wing pattern of *Chilades pandava* (Lycaenidae). **Panel A:** Nomenclature of wing margins and areas used to describe markings on butterfly wings. **Panel B:** Nomenclature of markings used commonly to describe wing colour patterns of butterflies. (1) cell-end bars, (2) discal bands, (3) sub-marginal bands, (4) sub-basal spot in space 7, followed by three sub-basal spots in the cell and spaces 1c and 1a, (5) sub-costal spot in space 7, and (6) tornal orange-crowned black spots. (Based on Kunte, K. and Tiple, A., *News Lepid. Soc.*, 51, 86–88, 109, 2009; Sondhi, S. and Kunte, K., *Butterflies and Moths of Pakke Tiger Reserve,* 2nd edn., Titli Trust (Dehradun), National Centre for Biological Sciences (Bengaluru), and Indian Foundation for Butterflies (Bengaluru), India, p. 242, 2018.)

EVOLUTIONARY BIOLOGY, PHYLOGENETICS, AND MOLECULAR SYSTEMATICS AS PILLARS OF MODERN TAXONOMY

Taxonomy and evolutionary biology grew in large part as distinct, independent fields with no academic connections between them. Linnaeus believed in a world created by a divine power, and he invented the binomial system of naming species simply as a formal way to give unique names to each species to facilitate scientific communication. The practice of binomial classification flourished in the entire century prior to the Darwin-Wallace theory of evolution by natural selection. On his part, although Darwin wrote extensively about evolutionary divergence and speciation, he did not define species in an evolutionary sense, and he was largely silent on applying evolutionary thinking to the science of recognizing and naming species (Darwin 1859). Evolutionary biology, the concept of species, and the practice of systematics grew somewhat in parallel in the decades following (Mallet 2004, 2007). Eventually, building up from a number of significant works by German systematists, Willi Hennig's efforts and influential book, *Phylogenetic Systematics*, brought a fundamental shift in integrating evolutionary biology and phylogenetics with taxonomy (Hennig 1966) (this book was first published in German in 1950). Conceptual, computational, and empirical developments in phylogenetic systematics have since made these three areas inseparable. The processes of population divergence, sub-speciation, and speciation have been intensively studied in the past few decades using rigorous mathematical models and computer simulations. As a result, there is a general consensus about the conceptual framework to think about these evolutionary processes. These developments have provided clear directions for systematic studies and taxonomic practices. This has already resulted in significant advances in the higher classification of butterflies and other organisms (see below). Students are encouraged to refer to recent excellent books on systematics and phylogenetics to gain a deeper understanding of the issues discussed below. However, the following briefs (based on Hennig 1966; Wiley and Lieberman 2011) will suffice for the objectives of this chapter. The concepts of species and subspecies will be briefly reviewed before discussing phylogenetic principles that are useful to understand Indian butterflies in the historical and current context. This will also establish some definitions and concepts that are used in the discussion towards the end of this chapter.

WHAT ARE SPECIES?

Species are considered fundamental units in biology. However, opinions on the matter of species are diverse in terms of philosophy (what constitutes a species; are species real entities; and are they kinds, sets, or individuals?) as well as practice (how to delimit and distinguish between species?). Thus, dealing with species is more complicated than an average non-biologist might expect. For practical reasons, most biologists work with the assumption that species are real, identifiable biological entities. However, which species concepts they use in practice varies considerably (Box 16.2). While the biological species concept has been adopted very widely in principle, in practice, its use is limited because of the lack of knowledge about reproductive isolation. Phylogenetic species concept is increasingly more popular because of a flood of phylogenetic studies and phylogeny-based species delimitation algorithms that

BOX 16.2 SPECIES CONCEPTS IN BIOLOGY

Given below are definitions and brief notes about the most popular species concepts. See the main text for further discussion.

Biological Species Concept: "… groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1965, quoting earlier work). This is by far the most popular species definition, and it has been used widely. However, it cannot be used for asexually reproducing plants, bacteria, and many other groups of organisms and under varied ecological circumstances. The issues of reproductive isolation, allopatry, etc., can also be problematic under this definition.

Phylogenetic Species Concept: "… the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals..." (Nixon and Wheeler 1990). This definition has gained substantial popularity in recent literature on phylogenetics and systematics. This definition is also practical in the sense that it may be used to delineate species even when there is no relevant information on reproductive isolation, which is the case for most species. The widespread use of phylogenetic inference has also contributed to its recent popularity.

Evolutionary Species Concept: "… a species is a lineage of ancestral descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1978). This definition combines several useful elements of the above two species concepts, for which it has become well-known among evolutionary biologists.

Genealogical Species Concept: Genealogical species are "… basal, exclusive groups of organisms, where exclusive groups are ones whose members are all more closely related to each other than to any organisms outside the group" (Baum and Shaw 1995).

Unified Species Concept: This concept interprets "… the common fundamental idea of being a separately evolving lineage segment as the only necessary property of species and viewing the various secondary properties either as lines of evidence relevant to assessing lineage separation or as properties that define different subcategories of the species category (e.g., reproductively isolated species, monophyletic species, diagnosable species)" (de Queiroz 2005a). This species concept has recently been discussed extensively because it argues for integrating various kinds of evidence—from natural history to genetic to phylogenetic—in defining species. This approach is likely to gain greater favour in the future as more information accumulates on the biology of species and their phylogenetic relationships, without necessarily relying directly or exclusively on the knowledge of reproductive isolation.

depend on extensive molecular evidence. Molecular datasets and phylogenetic studies have rapidly outpaced the generation of knowledge about the biology and reproductive isolation among species. For the discussion below, species are treated as a unified concept, i.e., species are separately evolving lineages with diagnosable characters and distinctive biology, whose reproductive isolation from related lineages may be inferred from a phylogenetically cohesive population structure (de Queiroz 1998, 2005a, 2005b, 2007). In practice, in the absence of data on reproductive isolation, species biology, or phylogenetic cohesiveness, most taxonomists treat species as diagnosable entities that appear different along several morphological, ecological, and behavioural trait axes. For butterflies, differences in morphology may include traits such as wing patterns, genitalia, venation, labial palps, tibial claws, and larval and pupal characters. Ecological and behavioural traits may include the use of larval host plants/habitats, flight periods, and mating preferences.

Species can either be sympatric (i.e., existing in the same area, or in other words, with overlapping distributions), parapatric (occurring in neighbouring regions with little distributional overlap), or allopatric (existing in different areas, with widely non-overlapping distributions) (Figure 16.7). If populations are allopatric, then the amount of morphological and ecological/behavioural differences between them, along with the nature of geographical separation between them with respect to well-known biogeographical breaks, may be particularly important

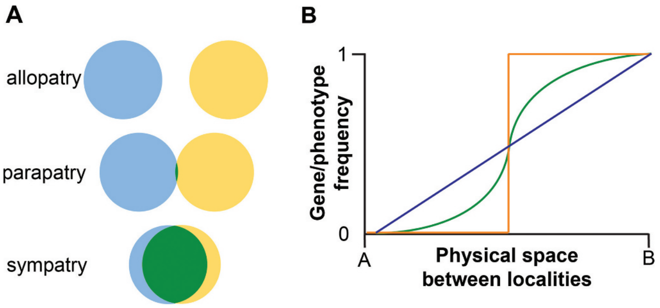


FIGURE 16.7 Evolutionary aspects of species, speciation, and population divergence that affect taxonomic interpretation and application of names to taxa. **Panel A:** Three common kinds of distributions that determine the degree to which populations may be isolated in space. Yellow and blue circles represent two populations, and green areas represent geographical overlap between the populations. **Panel B:** Different types of clines. Gene/phenotype frequencies may change in space linearly (dark blue) or in a step-like manner (green and orange).

in determining their species status (see Sections 'What are Subspecies?', and 'When are Subspecies Names Inappropriate?'). However, classifying populations as sympatric, parapatric, or allopatric may not always be easy: how much geographical separation is enough separation (Figure 16.7A)? One solution to this problem is to focus on gene flow between the populations rather than geographical distance, since the amount of gene flow is more directly relevant to reproductive isolation. This, however, is by no means easy to measure, although modern sequencing technologies have made this feasible.

What Are Subspecies?

As mentioned above, by the mid-1800s, many naturalists and collectors had started to appreciate the value of recognizing geographically structured variations within species of well-collected groups such as butterflies, birds, and mammals. Before the concept of subspecies was formalized, these geographical variations were often referred to as varieties or local forms. Taxonomists of the time dealt with the problem of distinguishing between species and subspecies (varieties) thus: "… we have a definition [of species] which will compel us to neglect altogether the *amount* of difference between any two forms, and to consider only whether the differences that present themselves are *permanent*. The rule, therefore, I have endeavoured to adopt is, that when the difference between two forms inhabiting separate areas seems quite constant, when it can be defined in words, and when it is not confined to a single peculiarity only, I have considered such forms to be species. When, however, the individuals of each locality vary among themselves, so as to cause the distinctions between the two forms to become inconsiderable and indefinite, or where the differences, though constant, are confined to one particular only, such as size, tint, or a single point of difference in marking or in outline, I class one of the forms as a variety of the other" (Wallace 1865). This reasonable practice has changed little in the past over 150 years. Only recently have phylogenetic methods and molecular datasets begun to address the problem of distinguishing between species and subspecies. The solution is to sample molecular variation in multiple individuals from several populations of each putative species. The general expectation is that the genetic (and morphological) divergence within interbreeding populations/subspecies of the same species will be relatively smaller than divergence across reproductively isolated sister species. Thus, populations/subspecies of the same species should form a cohesive phylogenetic cluster that is separated from other cohesive clusters that represent related species. Cohesive clusters thus obtained may form an objective basis for delineating species and subspecies.

In addition to considering how to distinguish between species and subspecies, it is important to understand why and how populations diverge and subsequently form subspecies and species. A tremendous amount of scientific literature exists on the subject (Coyne and Orr 2004; Dobzhansky 1951; Futuyma 1998; Howard and Berlocher 1998; Mayr 1942, 1965, 1982; Nosil 2012; Simpson 1961). The following is a very brief, simplified summary of the general understanding of population divergence from this evolutionary biology literature.

Populations have a tendency to diverge in space over time. This may be because space is not uniform: abiotic (e.g., climate and soil) and biotic factors (e.g., intra- and interspecific interactions) may vary even over short distances. Thus, geographically isolated or separated populations may be under ecological selection for local adaptation. For example, in butterflies: (a) body size and the amount of wing melanization may change in response to thermal envelopes across elevational gradients, and (b) ovipositing females, and subsequently caterpillars, may prefer or avoid certain host plants based on locally variable secondary compounds in plants or pressure from competing species, predators, and parasitoids. Such local adaptation will cause inter-populational divergence in relevant morphological and behavioural characters. However, populations will diverge even in absence of any local adaptation if they are isolated for a sufficiently long time. In isolated populations, phenotypes and/or genotypes will diverge even under neutral processes such as random genetic drift. Many isolated butterfly populations (e.g., island populations) show differences in the intensity or hue of wing colours, or the presence/absence/extent of spots, bands, and other colour patches. The functional significance of such visual differences are largely unknown at present, but many may involve random genetic drift. Thus, over a sufficiently large number of generations, geographically structured populations with little gene flow between them will diverge in their phenotypic and genotypic composition because of ecological selection or genetic drift. Such geographically structured variations among populations may be formally described at the subspecies level.

Based on this summary, one might ask whether subspecies are on their way to becoming species, which appears to be a popular belief. If populations have a tendency to diverge and they have accumulated many phenotypic and genetic differences (enough to be recognized as subspecies), then it is possible that they will continue to diverge and, given sufficient amount of time, turn into reproductively isolated species. However, this is only one of the expected evolutionary outcomes. It is also possible that slightly diverged populations/subspecies may homogenize once again if gene flow increases. It is also possible that some of the populations/subspecies will go extinct. These three outcomes might occur because of changes in ecological selection, changes in distributional ranges, and breakdown of geographical barriers, among a number of reasons (Mayr 1942; Simpson 1961). The taxonomic and evolutionary value of named subspecies must be judged with these outcomes in mind.

WHEN ARE SUBSPECIES NAMES INAPPROPRIATE?

It is taxonomically inappropriate to name all variations within a species at subspecies level. Two common cases where this applies are considered below.

Linear Clinal Variation

Spatial divergence across populations might take place along elevational, temperature, rainfall, and other environmental and resource gradients such as those found across the Himalaya and the Western Ghats. As a result, the mean of a character and/or allele frequency gradually change across a geographic transect (Figure 16.7). This is called a cline (Futuyma 1998; Huxley 1939; Simpson 1961). The ends of a gradual, linear cline may appear distinct, but they are connected by intermediate variations across adjacent populations. Hence, gradual, linear clinal variations should not be given separate subspecies names, they should really be recognized as a cline (Huxley 1939; Simpson 1961). It is interesting to note that a population may belong to several distinct clines going in different directions and along multiple phenotypic axes, but it can only get a single subspecies name; hence, taxonomists should avoid assigning subspecific names to such clinal variations (Huxley 1939; Mayr 1942; Simpson 1961). Clinal variations must abound in the Indian region because of large gradients in elevation, temperature, rainfall, forest types, and other climatic and biotic regimes in the hills and the plains. It is known that size and colouration of organisms varies with rainfall, e.g., individuals occurring in wetter areas tend to be darker than individuals occurring in drier areas. The Western Ghats-endemic *Idea malabarica* provides a good example of clinal variation across the south-north rainfall gradient. There is a prominent decline in rainfall from the southern to northern Western Ghats, so forests in the south are much wetter overall. Southern populations associated with wetter forests (e.g., Shendurney WLS, Kerala) are darker and larger, whereas populations from the drier north (e.g., Goa and Maharashtra) are brighter white and smaller. Although these south and north ends of the cline are easily distinguished, darkness and size of butterflies is quite variable from the Nilgiris to the Karwar-Goa border depending on the season and wetness of forests. Because of these rainfall gradient-associated darkness and size clines, the two described subspecies of *Idea malabarica*—the darker-larger *malabarica* and the paler-smaller *kanarensis*—should really be considered infrasubspecific, clinal variations. Similarly, western Himalayan populations of many butterflies are paler compared to their eastern Himalayan darker counterparts. Since the amount of rainfall declines from the east to the west, it is natural that butterfly populations in the drier western Himalaya are paler compared to butterfly populations in the wetter eastern Himalaya, but one also expects to find intermediate, more or less continuously variable forms in areas between. Such gradual, nearly continuously varying clinal variations have been given subspecies names in the Indian region. These subspecific names will need to be synonymized as evolutionary biologists and taxonomists gain greater insights into clines that are relevant for Indian butterflies.

On the other hand, sharp step clines (Figure 16.7B) may form based on the nature of the environmental gradient, the nature of selection, and any developmental genetic thresholds that may alter phenotypes non-linearly. Following Wallace's logic, if a sharp step cline occurs along a single phenotype/genotype axis, then the resultant variations may be treated as subspecies. If sharp step clines overlap along a number of independent phenotype/genotype axes such that the populations on two sides of the step differ sharply by sets of independent characters, then these populations likely represent distinct, parapatric species.

The nature and distribution of clines need to be carefully studied because of the geological and climatic heterogeneity apparent in the Indian subcontinent and because of the implications of clinal variation for taxonomy and biology of species. However, clines are greatly understudied, and indeed neglected by Indian taxonomists and other biologists.

Phenotypic Plasticity

Inter-population phenotypic differences are not exclusively controlled by genotypic variation, they may also be environmentally induced and occur in absence of genetic differentiation. Indeed, phenotypic differences are often a product of interaction between the genotype and the environment. Two classic examples illustrate this point. First, many butterfly species show seasonally changing forms, often called dry or wet season forms, spring or summer forms, etc., that are produced with the same genomic information, but in different environments (Nijhout 1991). Switches between seasonal forms are caused by non-genetic, external factors such as climatic parameters, food resources, and substrate texture. Second, many insects in colder areas have dark stripes and patches on wings, which help them warm up faster in cold climates (Clusella Trullas et al. 2007). This thermal melanism is in many cases purely environmentally induced and produced during development because of differential gene expression profiles rather than due to gene sequence variation. Similarly, animals in colder climates tend to be larger in size (Bergmann's rule) (Futuyma 1998). If inter-population differences are purely because of environment-induced phenotypic plasticity, then it is inappropriate to name subspecies based on these differences. In this case, populations may have morphological differences, but they are *not constant*, e.g., when early stages are raised under different climatic conditions.

RECONSTRUCTING AND INTERPRETING PHYLOGENIES FOR SYSTEMATIC AND TAXONOMIC STUDIES

All life on earth has descended from a common ancestor, and all the species—from bacteria and viruses to highly multicellular and complex eukaryotes—are a product of evolutionary processes involving ancestor-descendant relationships between species. A natural extension of this understanding is

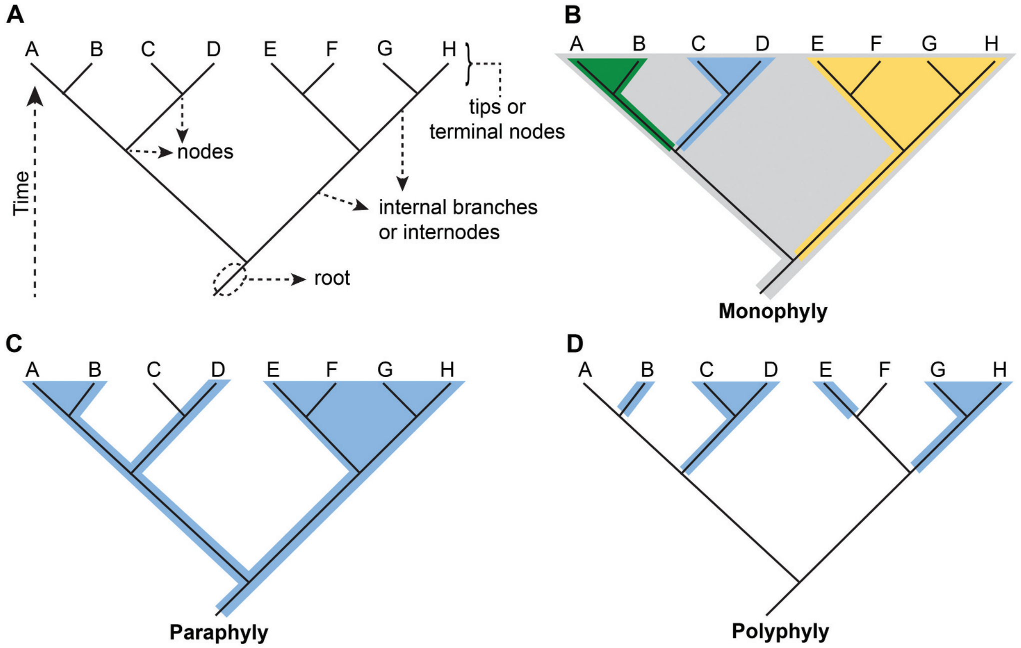


FIGURE 16.8 A simplified cartoon of a phylogeny (in this case, a species tree) on which phylogenetic concepts of monophyly, paraphyly, and polyphyly, which affect taxonomic grouping from subspecies and species to family level and above, are illustrated. **Panel A:** Terminology used in describing various components of a phylogeny. Terminal nodes A to H represent eight extant species with phylogenetic relationships as illustrated. **Panels B–D:** Representation of monophyly, paraphyly, and polyphyly. In each panel, similarly coloured species with their common ancestors represent distinct taxonomic rankings that might have been in use. See Section 'Reconstructing and Interpreting Phylogenies ...' for further details.

that species show evolutionary relationships with each other, which may be represented as a species tree with a root, stems, and branches (Figure 16.8). Such a tree is called a species phylogeny, in which the most recent common ancestor (MRCA) of all the species in the phylogeny is represented as a root (Figure 16.8A). Branching events, when one ancestral species splits into two descendent species, are represented by nodes. Branches between the nodes are called internal branches or internodes, which represent ancestral species. The tips of the species tree, also called terminal nodes, represent extant species. Phylogenies are reconstructed in reverse, i.e., data from extant species are tested against models of character evolution to reconstruct a relative topology of ancestral nodes. For example, variation in molecular sequences of sampled genes and/or morphological characters of a group of extant species can be used to reconstruct relationships between those species through to the phylogenetic root. The following ideas are fundamental to interpreting and using phylogenies.

A primary motive behind reconstructing phylogenies is to discover monophyletic groups. Monophyly, in which all the extant species along with all their ancestors down to their MRCA are included, defines a clade. Such monophyletic groups or clades is an inclusive, taxonomically desirable arrangement. However, monophyly can be applied at different levels, so exactly where a clade is delineated may depend on accessory information and/or preference of a taxonomist. For example, in Figure 16.8B, species A-B and their MRCA (green) represent a monophyletic group or a clade, as do species C-D and their MRCA (blue), species E-F and their MRCA (not shown), species G-H and their MRCA (not shown), species A-D and their MRCA (not shown), species E-H and their MRCA (dark yellow), or species A-H and their MRCA (grey). A genus may be defined at any of these levels. Many of the currently accepted genera of world butterflies are likely monophyletic. However, this hypothesis needs to be rigorously tested in a molecular phylogenetic framework before genus- and species-level arrangements of butterflies become stabilized.

A paraphyletic group includes most of the species and their MRCA, but some embedded groups are excluded (Figure 16.8C). The clade (species A-H) is said to be paraphyletic with respect to species C, which is excluded from the group in a taxonomic arrangement. One of the most well-regarded examples of paraphyly is a clade that includes turtles, crocodilians, dinosaurs, and related reptiles, from which birds are excluded and classified into their own class. Thus, Class Reptilia is paraphyletic with respect to Class Aves. An example from Lepidoptera will be explained below.

A polyphyletic group is composed of species that are not related to each other through a common ancestor, but which are classified into a single taxonomic unit (Figure 16.8D). Species B, C, D, E, G, and H in Figure 16.8D, if classified as a single genus, will represent a polyphyletic group. Paraphyly and polyphyly are taxonomically undesirable outcomes as they are not inclusive groups in a phylogenetic sense. The idea that taxonomic groups must represent clades, and therefore classification of organisms should reflect their evolutionary relationships, was one of the most critical contributions of Henning to the field of systematics.

Identification of monophyletic groups across the tree of life will stabilize classification and nomenclature in the long term. Detailed discussions may be found elsewhere (Futuyma 1998; Hennig 1966; Wiley and Lieberman 2011).

RECENT INSIGHTS FROM MOLECULAR SYSTEMATIC STUDIES INTO THE EVOLUTION AND HIGHER CLASSIFICATION OF BUTTERFLIES

Since the 1990s, there has been a strong emphasis on using molecular data and phylogenetic methods to gain insights into organic evolution and to resolve taxonomic problems, in a field that is now known as molecular systematics. Several studies have emphasized the importance of combining morphological and molecular data in resolving issues in Lepidoptera classification and taxonomy (Aduse-Poku et al. 2016; Huang et al. 2018; Wahlberg et al. 2005). This was especially important when a small number of molecular markers was used in generating phylogenies. However, modern, cheap sequencing and phylogenomic methods have now nearly obviated a need for using more labour intensive but limited morphological data into phylogenetic analysis. Standardized, large molecular (nuclear) marker sets ranging from ca 10 to over 400 genes have now been developed that are being used in most large-scale butterfly taxonomic studies (Espeland et al. 2018; Kawahara et al. 2018; Wahlberg and Wheat 2008). Such a large molecular marker set promises to offer a robust phylogenetic framework that was nearly inaccessible using morphological data. Indeed, most recent butterfly phylogenies are reconstructed exclusively using molecular phylogenetic approaches (see below). These molecular phylogenetic analyses have fundamentally changed the understanding of butterfly evolution and higher classification, as summarized below.

Butterflies Are Moths, Butterfly-Moths Are Butterflies, Swallowtails Are Older than Skippers, and Other Startling Observations

For a long time, butterflies have been assumed to be sister to, but somewhat distinct from moths. Indeed, this thinking has pervaded popular understanding of butterflies to the extent that a chart of differences between moths and butterflies is included in nearly every book and article introducing butterflies. However, butterflies have been classified in several taxonomic categories that are no longer tenable as a result of insights provided by recent molecular phylogenetic studies. One of the most startling findings is that butterflies are indeed moths. It has now been established from robust molecular phylogenetic analyses that the superfamily Papilionoidea that encompasses all butterflies (see below) is monophyletic, but completely embedded among other moth superfamilies (Figure 16.9) (Kawahara and Breinholt

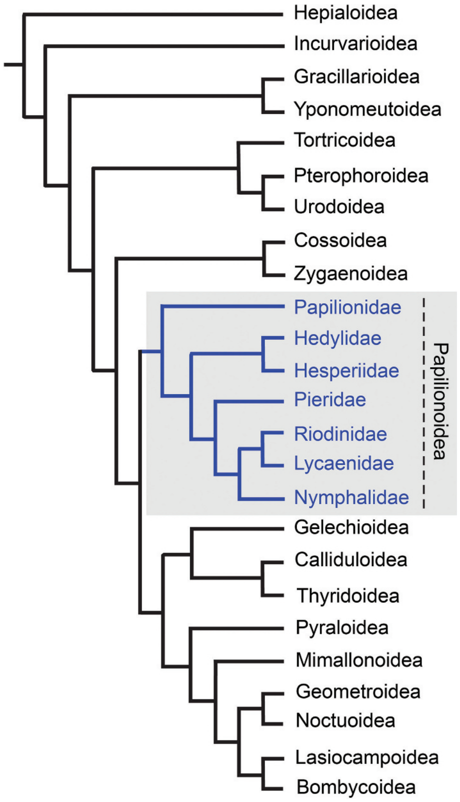


FIGURE 16.9 Lepidoptera phylogeny showing relationships of superfamilies of moths that are closely related to the butterfly superfamily, Papilionoidea. Note that: (a) butterflies are a monophyletic group (i.e., a clade), but it includes Hedylidae ("butterfly- moths"), (b) Papilionidae is the most basal family of butterflies, not Hesperiidae, as is still widely believed among Indian lepidopterists. Hedylidae and Hesperiidae are sister families. Superfamily and family relationships are redrawn from (Kawahara, A.Y. et al. *Mol. Phylogenet. Evol.*, 127, 600–605, 2018; Kawahara, A.Y. and Breinholt, J.W., *Proc. R. Soc. Lond. B Biol. Sci.*, 281, 20140970, 2014; Mutanen, M. et al. *Proc. R Soc. B*, 277, 2839–2848, 2010).

2014; Mutanen et al. 2010). Thus, moths are paraphyletic with respect to butterflies, if one wants to treat butterflies and moths as somehow different. In other words, butterflies are specialized and monophyletic, but they are only a subgroup of moths, without any exclusive morphological characters that distinguish all butterflies from all the other moths.

Another startling finding is that in spite of a long-held belief, Papilionidae (swallowtails) are the most basal, i.e., the oldest, butterflies, not Hesperiidae (skippers) (Figure 16.9) (Espeland et al. 2018; Heikkilä et al. 2012). Additionally, the South American Hedylidae (butterfly-moths; earlier classified under superfamily Hedyloidea) are sister to Hesperiidae (earlier classified under superfamily Hesperioidea), and both are embedded within true butterflies (superfamily Papilionoidea) (Figure 16.9) (Espeland et al. 2018; Heikkilä et al. 2012). Thus, superfamilies Hedyloidea and Hesperioidea are synonymized with superfamily Papilionoidea. According to this recent, but broadly accepted classification, the monophyletic butterfly superfamily Papilionoidea contains seven families: Papilionidae (swallowtail butterflies), Hesperiidae (skippers), Hedylidae (butterfly-moths), Pieridae (whites and yellows), Lycaenidae (blues, hairstreaks), Riodinidae (metalmark butterflies), and Nymphalidae (brush-footed butterflies), with the family-level phylogenetic relationships as given in Figure 16.9.

Family- and Subfamily-Level Changes

Molecular systematic findings are shaking other long-held taxonomic frameworks as well. For example, family Lycaenidae has long been classified among two large subfamilies: Theclinae ("Strong Blues") and Polyommatinae ("Weak Blues"), among a host of other smaller subfamilies. Although recent phylogenetic work supports monophyly of the smaller subfamilies, it shows Theclinae to be paraphyletic with respect to Polyommatinae, i.e., Polyommatinae is embedded within Theclinae (Espeland et al. 2018). This finding, which is complicated by the fact that Polyommatinae is an older name compared to Theclinae, prompts a reclassification of a significant fraction of the tribes and a major subfamily under Lycaenidae. Another finding that prompts a subfamily-level synonymy is that Neotropical Ithomiinae is embedded within Danainae, and must therefore be subsumed as a tribe under Danainae (Espeland et al. 2018). This has long-reaching implications for our understanding of the evolution and biology of Danainae. On the other hand, Riodinidae is now normally treated as a sister family of Lycaenidae, rather than its subfamily, an arrangement that is phylogenetically well supported (Espeland et al. 2015, 2018; Wahlberg et al. 2005). Similar re-examinations of higher classification of butterflies are likely in the next decade or two as molecular systematics advances significantly and as a large fraction of butterfly species are sequenced and put in a phylogenetic context.

Resolutions at Generic and Species Levels

The standardized nuclear and mitochondrial markers that are now commonly used in butterfly phylogenetics also provide resolution at genus and species levels. After preliminary phylogenetic analysis (Kodandaramaiah et al. 2010), recent comprehensive studies split the nymphalid genus *Heteropsis* in three well-supported and geographically subdivided genera: Asian *Telinga*, Malagasy *Heteropsis*, and African *Brakefieldia* (Aduse-Poku et al. 2016). Another recent molecular phylogenetic analysis found many of the genera under the tribe Aeromachini (Hesperiidae) to be either paraphyletic, prompting synonymy of some genera, or polyphyletic, prompting description of two new genera and significant movement of species across the newly delineated genera in that tribe (Huang et al. 2019). As the world's butterflies are sequenced and analysed in coming years, generic placements of many butterflies will alter and species-level classifications will undergo prominent changes. These taxonomic changes will be especially prominent in the Asian, African, and American tropics as cryptic species are discovered and specific relationships are clarified (Hebert et al. 2004; Huang et al. 2018; Kawahara 2013; Kawahara et al. 2018; Toussaint et al. 2015; Yata et al. 2010). In the Asian context, this will certainly affect a considerable number of genera under Nymphalidae, Lycaenidae, and Hesperiidae, which have historically been created with poor taxonomic characterization, and they continue to be commonly used without sufficient modern scientific investigations and revisions, e.g., the *Euthalia-Bassarona-Tanaecia-Dophla-Symphaedra* group (Nymphalidae), the *Zephyrus* hairstreaks, and many other genera under the traditional subfamilies Theclinae and Polyommatinae (Lycaenidae), and genera under the tribes Tagiadini, Aeromachini, and Baorini (Hesperiidae).

Genomic sequencing has become reasonably cheap and widely accessible even in developing tropical countries such as India. The next-generation sequencing platforms are providing large amounts of molecular data that have the power to reveal cryptic genetic variation and reproductive isolation that was difficult to decipher using traditional morphological data. Rapidly growing computational infrastructures and establishment of research groups in developing countries themselves are also likely to drive taxonomic discovery and resolution in the world's super-biodiverse tropics in the next few decades. Since taxonomic studies have hardly taken place in India in the past few decades, Indian butterfly taxonomy will no doubt see a flood of taxonomic rearrangements and other kinds of updates based on molecular systematic studies.

INDIAN BUTTERFLIES, A TAXONOMIC IMPEDIMENT

In Section "Indian butterflies, a taxonomic legacy", a glimpse was offered into how taxonomic studies on Indian butterflies have progressed through time, and how this field has historically been dominated by non-native taxonomic experts. At the same time, natural history museums and museum-based sciences have been neglected in India. Indeed, historically significant collections in India's natural history museums have hardly grown in the past few decades, with the museums, research staff, and field surveys grossly under-funded. The quality of academic training leaves much room for improvement. There are very few large-scale international collaborations, which has bred a culture of insularity. Naturally, the volume of work produced from India has been very small and the quality alarmingly poor. Restrictive laws and permitting procedures have also burdened taxonomic studies (Prathapan et al. 2006, 2008). Along with taxonomy, complimentary fields such as natural history, ecology, evolutionary biology, systematics and phylogenetics, and biogeography, which generate information on species that is critical in advancing taxonomic studies, have also been neglected. The lack of native expertise and uninterrupted taxonomic works has had a profound impact on the scientific development and current practices in this field. One of the unfortunate consequences of this stunted growth is that taxonomists working on Indian taxa continue to rely on outdated taxonomic arrangements generated at the time when concepts of species and subspecies were not properly elucidated in systematics and evolutionary biology, and in a phylogenetic context. In many cases, evidence exists that contradicts old arrangements and current practices. Some of these problems are easily addressed if taxonomists consulted extensive type collections, museum specimens, catalogues, and records in European research collections, where most of the type specimens of Indian species are deposited. It is true that these museums openly welcome foreign and especially native scientists from countries where the type specimens were collected a long time ago. However, funding for scientists from developing countries to make such research visits is scarce at a time when visiting these European countries is prohibitively expensive for most practicing taxonomists. Therefore, most of the collections are practically inaccessible, especially to Indian taxonomists. Nonetheless, several attempts have recently been made to update the taxonomy of Indian butterflies (Varshney 1993, 2010; Varshney and Smetacek 2015). Although these compilations are useful in the overall vacuum that exists in India, their scientific value is compromised because of: (a) inadequate notes and annotations, (b) glaring omissions resulting from neglect of recent taxonomic and phylogenetic literature, (c) lack of museum work especially including inspection of type and other specimens as well as genitalia dissections, (d) a critical review and reassessment of available evidence, (e) heavy reliance on old Indian literature that is vastly outdated, and (f) poor understanding of modern trends in taxonomy and systematics. This has given rise to an alarmingly flawed culture of "copy-and-paste," where successive generations have carried taxonomic arrangements forward even as the academic landscape in systematics and taxonomy was transformed elsewhere in the world. The specific examples given below and illustrated in Figures 16.10 through 16.12 offer detailed case studies of taxonomic problems pertaining to Indian butterflies.

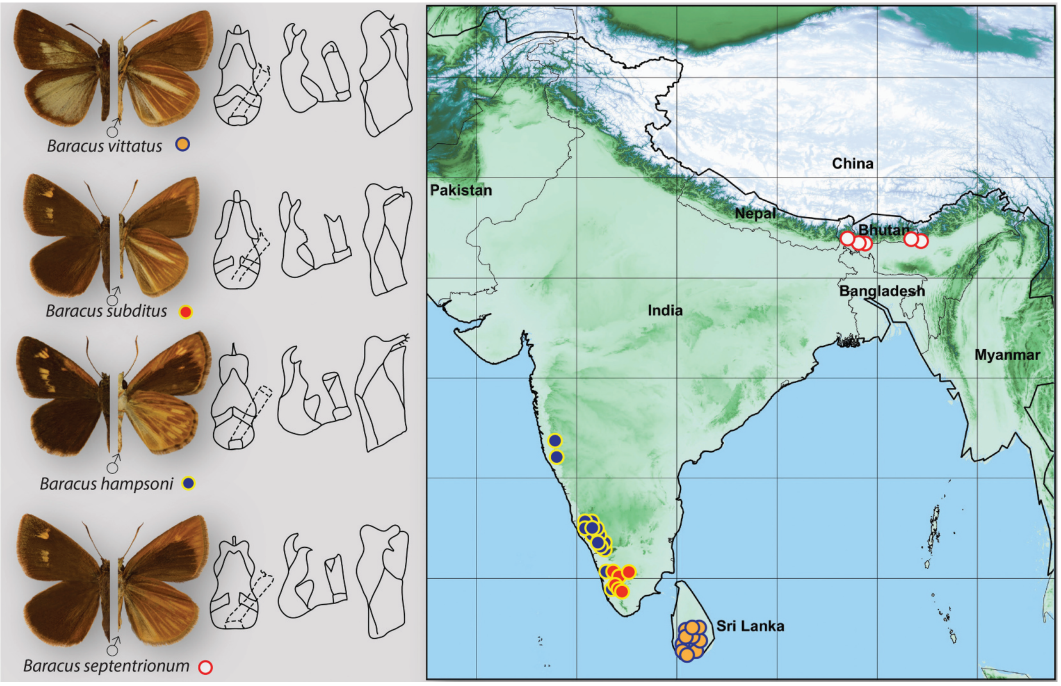


FIGURE 16.10 Wing phenotypes, male genital morphology, and distributional ranges of Indian *Baracus* (Hesperiidae). For each species, images of adult butterflies show dorsal (left) and ventral (right) views, and drawings of the male genitalia illustrate ventral view of uncus (left), lateral view of uncus with aedeagus (centre), and inside of valve with distal end facing up (right). Illustrations of male genitalia are redrawn from (Evans 1949). Distributional maps are generated from published spot records (Evans 1949; van der Poorten and van der Poorten 2016), museum records from NHMUK and NCBS (K. Kunte, unpublished data), and spot records on the *Butterflies of India* website (From Kunte, K. et al. *Butterflies India*, v. 2.56, 2018.)

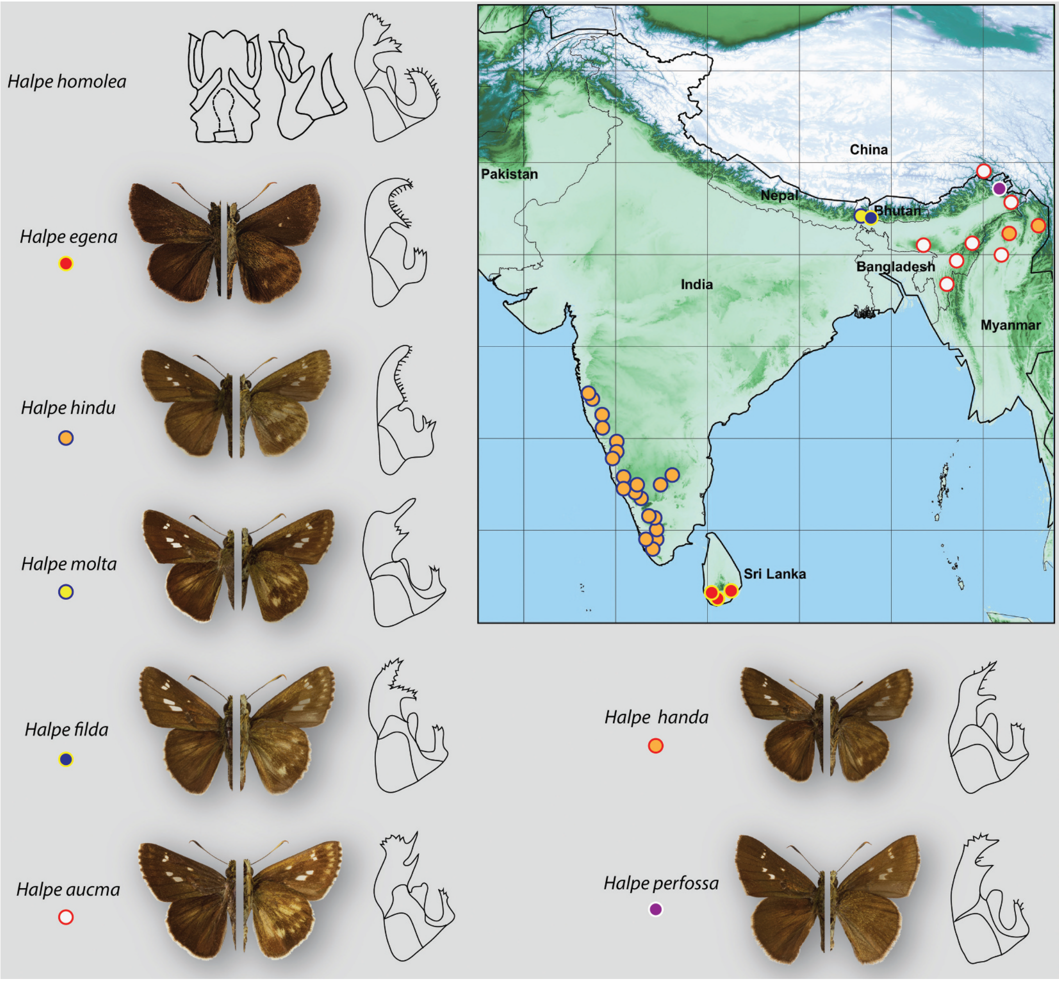


FIGURE 16.11 Wing phenotypes, male genital morphology, and distributional ranges of S. Asian *Halpe* (Hesperiidae). For *Halpe homolea*, ventral view of uncus (left), lateral view of uncus with aedeagus (centre), and inside of valve with distal end facing up (right) are illustrated. For all other *Halpe*, only the inside of valve, which is characteristic, with distal end facing up is illustrated. Illustrations of male genitalia are redrawn from Evans, W.H., *A Catalogue of the Hesperiidae from Europe, Asia and Australia in the British Museum (Natural History)*, British Museum (Natural History), London, UK, p. 502, 1949. See a note about distributional maps in the legend of Figure 16.10.

The Genus *Baracus*

Evans listed two species under the hesperiid genus *Baracus*: (a) *vittatus* from Sri Lanka and India, including four subspecies: *vittatus*, *hampsoni*, *subditus*, and *septentrionum* (Figure 16.10), and (b) *plumbeola* from Luzon, the Philippines (Evans 1932). Later, he moved *plumbeola* under the genus *Aeromachus*, treating *Baracus* as a monobasic genus (Evans 1949). He continued to treat the four Sri Lankan and Indian taxa as subspecies of *vittatus* and described one more subspecies, *gotha*, from the Anaimalai (Evans 1949) that appears to be an aberration and has not been seen since the description. His treatment of the Sri Lankan and Indian taxa as subspecies of *vittatus* was surprising given that his genitalia dissections showed these four taxa to have distinct structures (specifically, clasps or valvae; Figure 16.10) (Evans 1949). This evidence should have prompted their treatment as allopatric species by Evans himself. Recent, presumably updated checklists have continued to treat these taxa as subspecies following Evans (Varshney 2010; Varshney and Smetacek 2015), without reassessing available evidence and its current taxonomic implications.

The *homolea* Species-Group of *Halpe*

Another glaring example of taxonomic lumping by Evans and subsequent authors is the *homolea* species-group of South Asian *Halpe* (Hesperiidae). In this species-group, Evans once again found considerable differences in the structure of clasps or valvae of the male genitalia (Figure 16.11), but he still listed all the S. Asian, S. Chinese, and Indo-Chinese taxa as subspecies of the Singaporean *H. homolea* (Evans 1949). The differences in the male genitalia are so prominent that any modern taxonomist who sees this evidence would treat these taxa as distinct species. Indeed, the S. Chinese and Indo-Chinese species have recently been treated as distinct species (Huang 2003; Inayoshi 2018). However, Indian taxa that were not reassessed by these authors have been continued

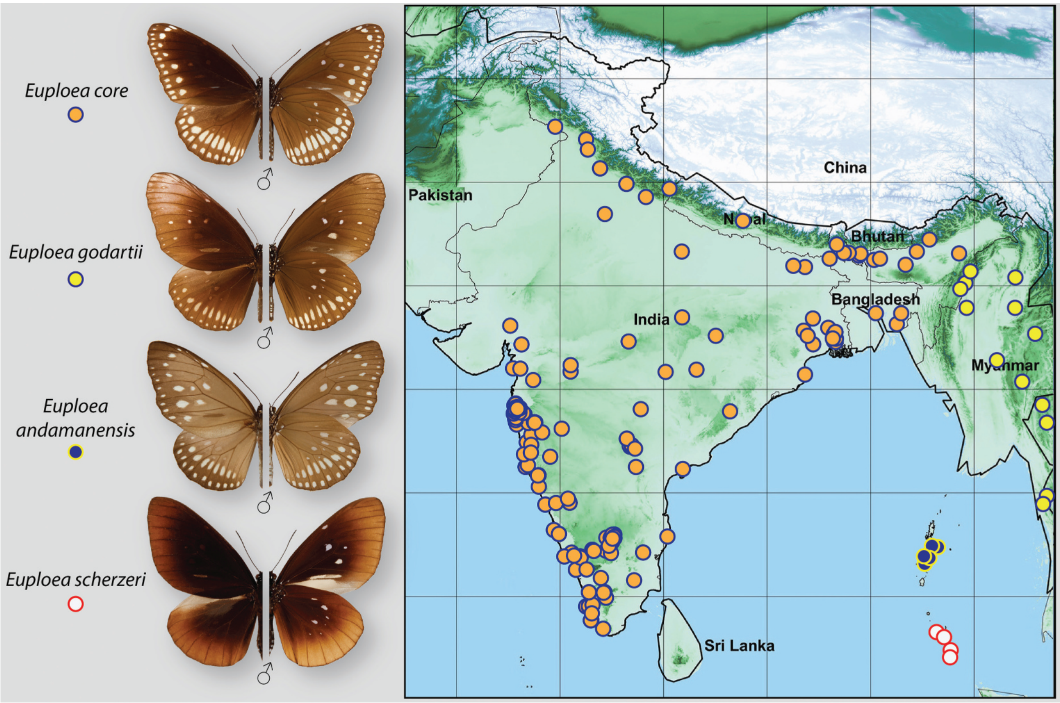


FIGURE 16.12 Wing morphology, sex-brands, and distributional ranges of some Indian *Euploea* (Nymphalidae). *godartii*, *andamanensis,* and *scherzeri* have for a long time been treated as subspecies of *Euploea core*, although each has characteristic androconia (sex-brands) on forewing and hindwing, and a distinctive forewing shape. Distributional maps are generated from museum records from NHMUK, NCBS, and ZSI Port Blair (K. Kunte, unpublished data), and spot records on the *Butterflies of India* website. (From Kunte, K. et al. *Butterflies of India*, v. 2.56, 2018.)

to be treated as subspecies of *H. homolea* by Indian authors. This has led to completely untenable biogeographic and taxonomic arrangements: the Singaporean *homolea* is replaced in Indo-China and S. China by various species (Huang 2003; Inayoshi 2018), but it is supposed to reappear in NE India, Western Ghats, and Sri Lanka in several subspecific forms—each with highly distinctive male genitalia (Figure 16.11)—according to recent Indian authors (Varshney 2010; Varshney and Smetacek 2015). Considering the available evidence of prominent differences in the male genitalia, all these *Halpe* should really be considered distinct species, some as allopatric (e.g., Sri Lankan *egena* and the Western Ghats *hindu*) and others as sympatric (e.g., *aucma*, *perfossa,* and *handa* in NE India and northern Myanmar; Figure 16.11).

The examples of *Baracus* and the *homolea* species-group of *Halpe* suffice to illustrate that in spite of his stellar work and a highly productive career, Evans had a flawed understanding of subspecies. This compelled him to treat many good species as subspecies, even though the evidence from genitalia structures indicated otherwise. Looking back, it is perhaps easy to see the roots of this error: most of Evans's work on Indian butterflies took place prior to 1950, just as the concepts of species and subspecies were being clarified in evolutionary and systematic literature. Evans certainly did not appear to have been cognizant of these developments based on his writings and taxonomic treatments. In any case, he misapplied the concept of subspecies far and wide, creating dozens of cases where taxa were inaccurately treated as subspecies. Many of his generic placements were also flawed. Some of these errors have been corrected in other parts of the world, but they are largely carried forward in India from the very old literature.

The *Euploea core* Species-Group

Euploea core is a complex species-group which has been taxonomically tossed around for a long time. Evans treated *core*, *godartii,* and *andamanensis* as distinct species and *scherzeri* as a subspecies of *climena* (Evans 1932). Without any justification, Talbot lumped all these taxa as subspecies of *core* (Talbot 1947). Talbot's arrangement was followed by Ackery and Vane-Wright, again without giving justification for the lumping (Ackery and Vane-Wright 1984). Vane-Wright, however, later realized that there are differences in the male genitalia and androconia that show these taxa (except *godartii*, which he did not consider) to belong to potentially different species-groups and revised their taxonomic status to be semispecies (Vane-Wright 1993). However, the presence and/or size of androconia (also known as sex-brands) on both the wings, and the forewing shape, of males of all these taxa are distinctly different (Figure 16.12). Given that the scent produced by androconia is one of the most important sexual traits that strongly influence chemical communication and mate preference in the Danaini (Ackery and Vane-Wright 1984), and the fact that the male genitalia as well as androconia of these taxa are different (Vane-Wright 1993), these taxa are reasonably treated as distinct species that have parapatric and allopatric distributions. In summary, there is no justification for lumping these taxa as subspecies of *core*, but the available evidence supports treating them as distinct species. And yet, Indians continue to treat them as subspecies of *core* without any justification (Varshney and Smetacek 2015), and most seem unaware of the available literature on this matter.

More Examples

Apart from the three examples just discussed in some detail and illustrated in Figures 16.10 through 16.12, dozens more taxonomic treatments of Indian butterflies readily point to the neglect of taxonomic works in India, to the culture of "copy-and-paste" that is evident in the Indian literature, and the lack of new, scholarly works that are required to truly update the taxonomy of Indian butterflies. Indeed, the culture of academic insularity in India has long affected access to scientific literature and international collaborative networks and research projects. As a result, Indian taxonomists, ecologists, and naturalists seem to frequently miss developments in scientific research and publications. For example, the following three findings affect taxonomic treatments and names of Indian butterflies, but they are largely neglected in India, as judged from lack of citation to the recent research papers as well as continued use of older arrangements in recent Indian literature. First, the southern Indian *lepitoides* has since the 1930s been listed as a subspecies of either *Libythea lepita* or *L. celtis* (d'Abrera 1985; Evans 1932). A recent monograph of Libytheinae moved it under *Libythea laius* (Kawahara 2013). Second, *galba* has historically been listed as a subspecies of *Appias nero* (d'Abrera 1982; Evans 1932; Talbot 1939), but was recently shown to be a distinct species (Yata et al. 2010). Third, a subclade of Indian Mycalesina is now placed in the resurrected genus, *Telinga* (Aduse-Poku et al. 2016), which affects name combinations of approx. 10 Indian species.

Many of the problems highlighted above appear to stem from inaccessibility of resources in India, whether scientific literature or museum resources, and inadequate training. It is important to sort out these taxonomic problems not only for academic reasons (e.g., an enriched understanding of diversity of life on the planet), but also for practical reasons. National legislation such as the Wildlife (Protection) Act (WPA) and National Biodiversity Act depend on reliable and updated biological information. Many butterflies are protected in India either at subspecies or species levels under various Schedules of Wildlife (Protection) Act. There should be periodic taxonomic updates and reassessments of these scheduled species, but the lists of scheduled butterflies have never been properly reassessed. It is unfortunate that such an important piece of conservation legislation continues to rely on woefully inadequate biological information and reassessment framework. The biological information is critical in other ways, too. While conservationists may want to protect every population, it may be feasible to protect only a subset of populations. Under these circumstances, taxonomically distinctive, phylogenetically unique, and biologically specialized species may be given greater priority over some populations that show minor phenotypic and genetic differences. Thus, addressing the taxonomic impediment is one of the most significant challenges while rejuvenating taxonomic and systematic studies in India, which will have wide-ranging practical outcomes as well.

A MODERN *MANTRA* FOR BUTTERFLY BIOLOGY IN THE 21ST CENTURY INDIA

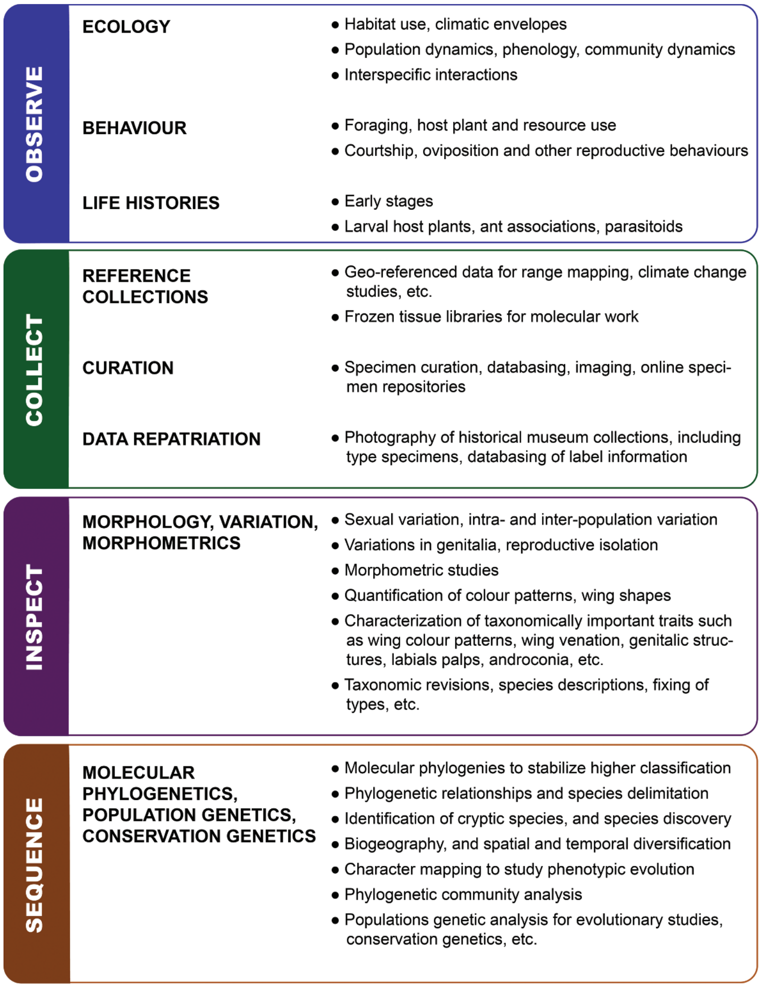
Biodiversity sciences are undergoing a long-awaited renaissance due to a strong and very broad interest in exploring and conserving biodiversity that is increasingly threatened with habitat loss and climate change, among other threats. Scientific discovery of species and their biology is no longer an arcane activity only for taxonomists in the world's museums, but it is a central goal for any modern evolutionary biologists, ecologists, systematists, conservation biologists, and even citizen scientists. In India, amateur and professional scientists are increasingly forming closely knit teams to discover and describe new species as well as study natural history (Karmakar et al. 2018; Kunte et al. 2012, 2018; Nitin et al. 2018; Rai et al. 2012; Sondhi et al. 2016; Sondhi and Kunte 2016). It is widely recognized that organismal biology and taxonomy have to grow side-by-side. Integrative taxonomy indeed relies on a deep understanding of ecology, behaviour, and morphological diversity of butterfly populations and species, that is used in conjunction with application of concepts and methods of species delimitation, biogeography, and molecular systematics (de Queiroz 2005a, 2005b). These modern scientific explorations critically depend on museums that hold deep-frozen tissue libraries and georeferenced data that can assist in understanding the evolutionary history of species and their potential for future survival in a changing world under the influence of climate change and other human impacts on climate and habitats. In this context, Indian scientific community needs to step up in several major ways (Figure 16.13).

Collection of Field Data

Very little is known about the natural history of Indian butterflies. Extensive field observations are needed to study climatic envelopes in which species occur, seasonal population dynamics and phenology, community dynamics and inter-specific interactions, foraging and host use, reproductive behaviour and early stages, host plant use, etc. (Figure 16.13). Although some good natural history publications exist on these subjects [see Section 'Scientific Research' below], very few scientific, high-quality studies have emerged on species biology from India. Any other work on Indian butterflies needs a solid foundation of the fundamental understanding of butterfly biology.

Developing Museum Resources

The Natural History Museum, London, has an estimated 11 million Lepidoptera specimens (Geoff Martin and Blanca Huertas, personal communication with KK), along with many



OBSERVE	**ECOLOGY**	• Habitat use, climatic envelopes • Population dynamics, phenology, community dynamics • Interspecific interactions
	BEHAVIOUR	• Foraging, host plant and resource use • Courtship, oviposition and other reproductive behaviours
	LIFE HISTORIES	• Early stages • Larval host plants, ant associations, parasitoids
COLLECT	**REFERENCE COLLECTIONS**	• Geo-referenced data for range mapping, climate change studies, etc. • Frozen tissue libraries for molecular work
	CURATION	• Specimen curation, databasing, imaging, online specimen repositories
	DATA REPATRIATION	• Photography of historical museum collections, including type specimens, databasing of label information
INSPECT	**MORPHOLOGY, VARIATION, MORPHOMETRICS**	• Sexual variation, intra- and inter-population variation • Variations in genitalia, reproductive isolation • Morphometric studies • Quantification of colour patterns, wing shapes • Characterization of taxonomically important traits such as wing colour patterns, wing venation, genitalic structures, labials palps, androconia, etc. • Taxonomic revisions, species descriptions, fixing of types, etc.
SEQUENCE	**MOLECULAR PHYLOGENETICS, POPULATION GENETICS, CONSERVATION GENETICS**	• Molecular phylogenies to stabilize higher classification • Phylogenetic relationships and species delimitation • Identification of cryptic species, and species discovery • Biogeography, and spatial and temporal diversification • Character mapping to study phenotypic evolution • Phylogenetic community analysis • Populations genetic analysis for evolutionary studies, conservation genetics, etc.

FIGURE 16.13 A roadmap for making progress on the taxonomy, systematics, and biology of Indian butterflies in a truly integrative manner. The modern *mantra* of "Observe-Collect-Inspect-Sequence" depends on intensive field work, strong academic institutions, rich museum resources, and joint efforts by professional and amateur scientists.

more million specimens in dozens of other museums in Europe and North America. These collections are at the heart of hundreds of scientific publications every year by taxonomists and butterfly/moth biologists from all over the world. The largest Lepidoptera collections in India are in the Zoological Survey of India among its various regional centres and the head office in Kolkata, and the Forest Research Institute in Dehradun, among dozens of collections spread in smaller institutions all over the country. However, the museum resources in India are tiny by any comparison. Only a strong culture of museum-based research will build strengths in species discovery and systematic revisions that are necessary to advance the understanding of Indian butterflies. Note that almost every leading university and research centre in the world engaged in research on organismal biology has an entomological collection. Therefore, Indian institutions and researchers need to start building significant research collections with modern strengths: geo-referenced data, deep-frozen tissue libraries, online or otherwise electronic databases, and high-throughput sequencing facilities. Specimen curation should include high-quality imaging and online image repositories. At the same time, we should recognize that most of the type specimens of currently known Indian species are in European museums. It is unlikely that these specimens will be repatriated to countries of origin, but it should be easy to repatriate label data and high-quality images of type specimens. Fixing of type specimens (Box 16.2) is also important because of its implications for taxonomic stability. Such museum-based research alone will facilitate a large number of studies of Indian butterflies. This work has already been initiated at NCBS, with imaging of nearly 15,000 butterfly specimens, including dozens of type specimens, completed in major international museums and other repositories. The NCBS research collections are also making a significant impact on the availability of modern infrastructures for taxonomic, systematic, evolutionary and conservation studies by providing state-of-the-art museum facilities.

SCIENTIFIC RESEARCH

Although taxonomic discovery of Indian butterflies has slowed down, natural historic, evolutionary ecological, biogeographic, and phylogenetic information has grown in leaps and bounds in the past two decades. Modern Indian naturalists, entomologists, and biologists are better trained to do natural history and scientific studies, and they are also better provisioned. Many Indians have received training in biology in some of the best research institutions and museums in the world. Their return to India to take up academic positions, in what might be termed "reverse brain-drain," has made a deep impact on the direction of scientific research in India. The rise of institution-building in the era of reverse brain-drain and citizen science has also increased the pace at which new discoveries are made and published. Numerous checklists and other records of butterflies from the Garo Hills, Eastern Himalaya, Assam Valley, and NE India, have reported many species rediscoveries as well as species new to India (e.g., Balaji et al. 2018; Gogoi 2012, 2013, 2015; Karimbumkara et al. 2016; Kunte 2009, 2010; Kunte et al. 2012; Rai et al. 2012; ; Sondhi and Kunte 2016). Since Bell's time, early stages and larval host plants have been reported to some extent (e.g., Kalesh and Prakash 2007; Karmakar et al. 2018; Kunte 2006; Kunte et al. 2018; Nitin et al. 2018; Pant and Chatterjee 1949; Sevastopulo 1973), although rigorous scientific studies are still lacking. Recent studies have investigated microbial associations of adult butterflies and caterpillars, effect of host plants and environmental factors on pupal polymorphism, and diversification of butterflies following host shifts (Ankola et al. 2012; Mayekar and Kodandaramaiah 2017; Phalnikar et al. 2018; Sahoo et al. 2017; Sahoo and Kodandaramaiah 2018). There is considerable promise in similar studies in the Indian context because of the rich diversity of butterflies, plants, and microbial communities. Building up on historic work, the southern Indian butterfly migrations are being studied (e.g., Bharos 2000; Bhaumik and Kunte 2017; Briscoe 1952; Chaturvedi and Satheesan 1979; Chaturvedi 1992; French 1943; Kunte 2005; Larsen 1978; Williams 1938). Flight morphology and other aspects have provided interesting insights into dispersal (Sekar 2012; Sekar and Karanth 2013, 2015). Recent work on mimicry has provided insights into morphological evolution and community assembly (Joshi et al. 2017; Su et al. 2015). Some preliminary work on population dynamics has also been published (Tiple et al. 2009). Taxonomy, phylogenetic relationships, biogeography, and related fields are gaining greater ground (Aduse-Poku et al. 2016; Huang et al. 2019; Kunte 2015; Sahoo et al. 2016, 2018; Toussaint et al. 2015). The overall picture that emerges from this summary is that butterfly biology is growing strong in India. This growth will be stronger in the future if long-term research programmes are built by specific labs and research centres around themes of particular significance for Indian butterfly biology and conservation.

There are other promising developments that will facilitate rapid growth of butterfly biology in India. The information age, the internet, and social media, have given easy access to vast literature, museum resources, and a globally interactive pool of subject experts whether they are amateur or professional. Butterfly-watching has become popular, with parallel growth in the volume of photographic records of Indian butterflies. At the same time, several citizen science projects have taken off, which are accumulating an unparalleled amount of data on the natural history and biology of Indian butterflies. The most successful citizen science project on Indian butterflies is *Butterflies of India* (http://www.ifoundbutterflies.org/), which has created a powerful online platform for aggregating spot records and reference images of butterflies (Kunte et al. 2018). These records are largely contributed by amateur butterfly-watchers and peer-reviewed before publication by advanced amateurs and professional biologists. Thus, this is one of the best-integrated professional-amateur scientific communities that aggregates big data on Indian butterfly diversity with the goal of studying ecological trends. This web-project has already accumulated over 55,000 reference images representing detailed distributional ranges, seasonal occurrence, early stages, and larval and nectar plants of Indian butterflies. It has also resulted in over a dozen scientific publications. Similar citizen science projects have a tremendous potential for future growth.

The modern mantra of "Observe-Collect-Inspect-Sequence" has significant potential to impact the growth of systematics and biology of butterflies in India. Figure 16.13 illustrates a roadmap for future growth.

CONCLUSION

India faces a major taxonomic impediment due to many decades of neglect of modern systematic research, the inaccessibility of reference materials of taxonomic importance, and a culture of academic isolation that has led to scarcity of in-house taxonomic expertise. This is compounded by a lack of vision that taxonomic advancement is central to understanding basic evolutionary and ecological processes. In this chapter, it was shown how these four problems have impeded scientific growth in India, specifically as applied to the taxonomy, systematics, biogeography, evolution, and ecology of butterflies. It was also shown that butterfly taxonomy currently used in India largely dates back to the early and mid-1900s, before the concepts of species and subspecies were clarified. This was also a time when the importance of biogeographic barriers, allopatry, vicariance, and dispersal in (sub)speciation process was just beginning to be explored in evolutionary biology. As a result, our understanding of Indian butterflies is vastly incomplete and to a large degree outdated. It is common to see the use of species and subspecies concepts/delimitations that confuse between clinal variation, environmentally induced variation, individual variation, and distinct geographic variation as applied to subspecies. Misapplications of the concepts of sympatry and parapatry to define species are also commonly observed. On the whole, the taxonomy and systematics of Indian butterflies has largely lagged behind the work on other Asian butterflies. These various problems were outlined in this chapter with examples. As a way forward, a roadmap was proposed to modernize taxonomy and species discovery of Indian butterflies. This should be put in the larger context of Asian butterflies and Oriental biogeography, with a combination of: (a) intensive taxonomic work with types and other important specimens housed in the research collections of European museums and, more recently, Japanese collections, (b) collecting new geo-referenced specimens, especially around critical climatic transitions and biogeographic barriers that have influenced diversification and endemism in the Oriental Region, and (c) using morphometric, molecular, and phylogenetic methods to distinguish between polymorphisms, subspecific, and specific variations to define taxa in modern evolutionary and phylogenetic frameworks with a strong emphasis on systematics (Figure 16.13). This will require considerable new work in the field and also substantial collaborations across museums, universities, and governments; leading to a truly international scientific enterprise.

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