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BURROWER BUGS. Members of the family Cydnidae (order Hemiptera). See also, BUGS.

BURROWING WATER BEETLES. Members of the family Noteridae (order Coleoptera). See also, BEETLES.

BURSA COPULATRIX. A sac-like modification of the oviduct, or copulatory chamber, that receives the male aedeagus.

See also, REPRODUCTION.

BURSICON. A neuropeptide hormone produced by the neurosecretory cells of the brain that controls sclerotization (tanning) and cuticle expansion.

BUSH CRICKETS. A subfamily of crickets (Eneopterinae) in the order Orthoptera: Gryllidae. See also, GRASSHOPPERS, KATYDIDS AND CRICKETS.

BRUSH-FOOTED BUTTERFLIES (LEPIDOPTERA: NYMPHALIDAE). The Nymphalidae is one of five families in the superfamily Papilionoidea (true butterflies) of the order Lepidoptera (moths and butterflies). Although a number of lineages within the family are well circumscribed and have been recognized since the 1800s, the taxonomic rank which such lineages should be accorded and how they should be subdivided remains contentious. A number of currently recognized subfamilies, and even some tribes, have been considered distinct families by some authors. However, continuing morphological and especially molecular research now provides real hope of a stable higher classification in the future. Ten subfamilies are currently recognized, including:

Order: Lepidoptera
  Superfamily: Papilionoidea
    Family: Nymphalidae
      Subfamily: Libytheinae
      Subfamily: Calinaginae
      Subfamily: Morphinae
      Subfamily: Satyrinae
      Subfamily: Charaxinae
      Subfamily: Apaturinae
      Subfamily: Nymphalinae
      Subfamily: Danainae
      Subfamily: Heliconiinae
      Subfamily: Biblidinae

Distinguishing characteristics and relationships

One distinctive and unambiguous character is unique to the Nymphalidae: the ventromesial surface of the antenna has three longitudinal ridges (termed carinae, meaning 'keel'; the antenna is hence 'tricarinate'), one lying either side and one separating two shallow longitudinal grooves. Two further characters may be the presence of a distinctive structure, von Siebold's organ, in the female genitalia, and a filiform seta in the mature larva that is absent in other papilionoid families.

The sister taxon (most closely related group) to the Nymphalidae is thought to be the Lycaenidae plus Riodinidae, which share several thoracic and musculature characters with the family. More obvious characters are provided by the foreleg, which is reduced in adults of most male Lycaenidae plus Riodinidae, and in male and female Nymphalidae (only in male Libytheinae). The male foreleg in

all three families lacks tarsal claws and has the original five tarsal segments (tarsomeres) reduced in number through fusion, with the latter feature also occurring in some female Nymphalidae. In male Riodinidae, and both sexes of most Nymphalidae, only four legs are used for walking, and in male Nymphalidae the forelegs are clothed in hair-like scales, inspiring the common familial name 'brush-footed butterflies'.

All nymphalid subfamilies, except for Libytheinae, are further grouped by the loss of use of the foreleg in the female. Relationships between other nymphalid subfamilies remain obscure, although certain relationships are often found and seem plausible, such as Morphinae plus Satyrinae. While most subfamilies are probably natural (monophyletic) groups, the Nymphalinae, Biblidinae, and Satyrinae have no convincing autapomorphies (uniquely derived characteristics). They will almost certainly be subdivided or merged with other subfamilies as our knowledge of nymphalid phylogeny increases.

Morphology

Adult. Nymphalid butterflies range from tiny melitaeines (Nymphalinae), the size of a fingernail, to giant *Caligo* (Morphinae), the size of dinner-plates. The wings may be rounded, elongate (e.g., Heliconiinae, Ithomiini), scalloped (e.g., *Cethosia*), or with long hindwing tails (e.g., *Marpesia*). The simplest nymphalid wing patterns consist of a series of dark lines and ocelli (eyespots, a common feature) on a pale background, which are variably modified through loss, expansion or fusion into a fantastic array of patterns.

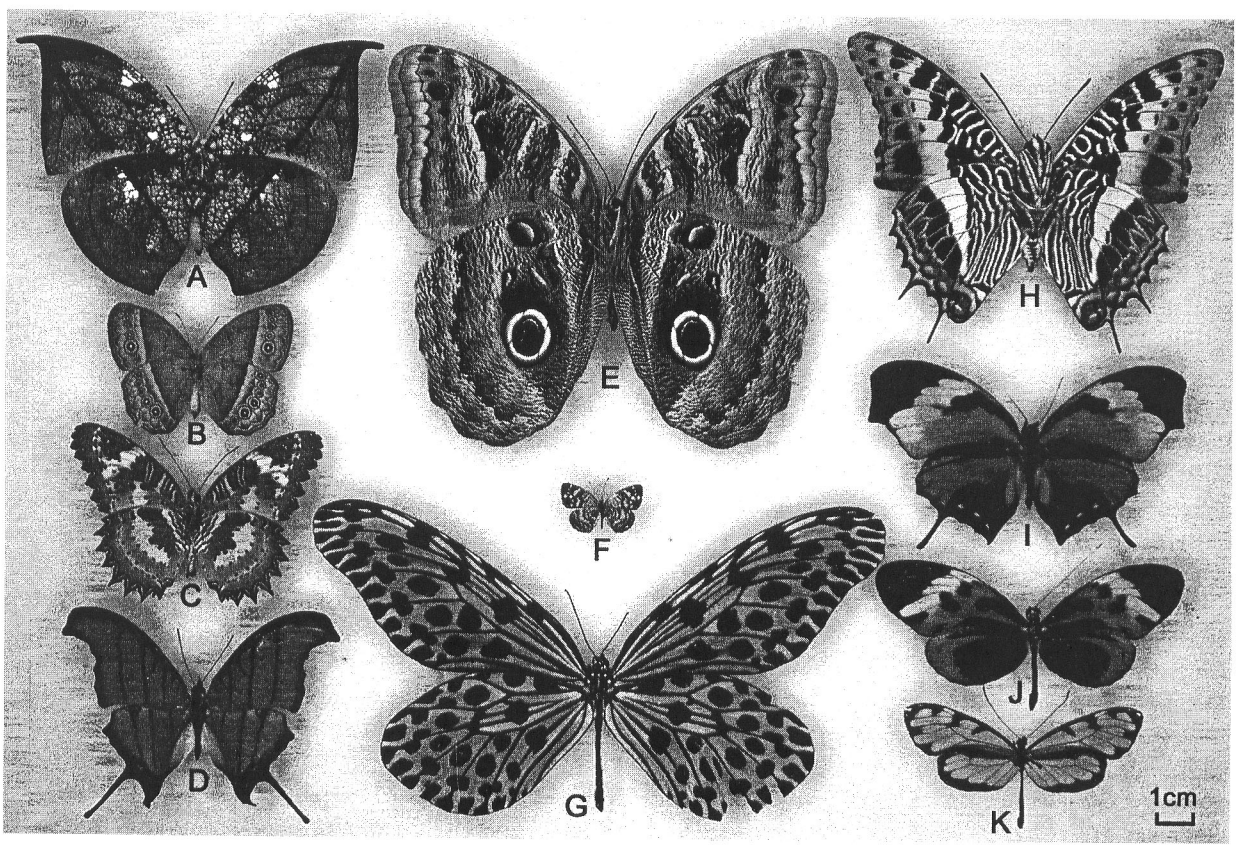

Fig. 133 Representative nymphalid butterflies. A, *Coenophlebia archidona* (Charaxinae), Ecuador; B, *Mycalesis orseis* (Satyrinae), Malaysia; C, *Cethosia penthesilea* (Heliconiinae), Malaysia; D, *Marpesia petreus* (Biblidinae), Ecuador; E, *Caligo ilioneus* (Brassolinae), Ecuador; F, *Phystis simois* (Nymphalinae), Ecuador; G, *Idea lynceus* (Danainae), Malaysia; H, *Charaxes castor* (Charaxinae), Kenya; I, *Consul fabius* (Charaxinae), Ecuador; J, *Heliconius numata* (Heliconiinae), Ecuador; K, *Oleria baizana* (Danainae), Ecuador.

These patterns range from almost entirely transparent and colorless in ithomiine danaines to the extremely complex patterns of certain *Charaxes* species (Charaxinae), to the brilliant iridescent blue that makes *Morpho* butterflies visible from low-flying aircraft. Many insights into the developmental genetics and evolution of lepidopteran wing patterns have been gained from comparative study of nymphalid wing patterns.

Wing color pattern signalling functions include crypsis (e.g., the extraordinary leaf-like *Kallima* and *Coenophlebia*; transparent-winged forest understorey satyrines and ithomiines), startle or deflective coloration (e.g., the eyespots of *Caligo* and Satyrinae), interspecific recognition (e.g., *Nessaea*, *Catonephele*), and both Batesian (e.g., certain Nymphalinae and Charaxinae) and Müllerian (e.g., Heliconiinae, Danainae) mimetic warning coloration. Color pattern variation includes seasonal polymorphism (e.g., *Junonia*), local genetic polymorphisms (e.g., *Heliconius*, *Hypolimnas*), and often remarkable geographic racial polymorphism (e.g., Danainae, *Heliconius*).

The external morphology is rather uniform, being responsible, at least in part, for the poorly resolved high-level classification of the family. Variation in wing venation, thoracic exoskeletal, leg and labial palpal morphology provides the foundation for the current subfamilial classification. In certain species the veins and basal wing sclerites on either fore or hindwing may be modified to form a tympanal organ (e.g., *Heliconius*, Satyrinae), though its function is poorly understood. At the subtribal, generic and species level genitalic morphology, especially male, has been used extensively, although there is often no variation between closely related species.

The Nymphalidae exhibit a rich diversity of secondary sexual structures. Most commonly these are modified scales with glandular bases, typically confined to the male sex, termed 'androconia'. Androconial scales usually form patches, fringes, tufts or pockets, and may be flattened or elongate, but often are hair-like and erectile (e.g., Satyrinae, Danainae). Alar androconia are often associated with wing veins, and occur commonly in the Satyrinae and Danainae. Abdominal androconia may be located on eversible glands (e.g., *Vila*) or contained within a membranous sheath that can be everted through an increase in haemolymph pressure (e.g., the coremata that characterize the Danaini). Especially complex androconial systems, such as those in the Danaini, involve abdominal brushes that are remote from glandular alar areas but make contact with them immediately before scent dispersal. Secondary sexual structures also are known for females of some taxa, most notably in some members of the Heliconiinae, which possess a dorsal abdominal gland and associated lateral club-like structures termed stink-clubs or clavatia.

Immature stages. Nymphalid immature stages are morphologically extremely diverse, and although comparative study is in relative infancy compared to adult morphology, immature stage characters may still provide very significant information for the higher level classification of the family.

The eggs are typically spherical, ovoid, or flattened domes, and almost smooth (e.g., Satyrinae), ribbed (e.g., Danainae), or faceted with interstitial spines (Limenitidini). Larvae may be smooth (e.g., some Danainae), covered with small granulations (e.g., Satyrinae), or decorated with fleshy tubercles (e.g., Danainae), dense spines (e.g., Nymphalinae) that may be modified into highly elongate and branched scoli (some Biblidinae), or hair tufts (e.g., some Brassolinae). In later instars of some neotropical Charaxinae the third thoracic and first abdominal segments also may be expanded to form dorsal or dorso-lateral humps. The head capsule may be striped or colored, and may be smooth (e.g., Danainae), or ornamented with chalazae (raised wart-like processes, frequently bearing setae), that often form elaborate dorsal and subdorsal head horns. The ninth abdominal segment is often bifid, forming 'tails' (e.g., Satyrinae, Charaxinae, Morphinae). Larvae may be cryptically colored (most Satyrinae, Limenitidini) or black with bright orange, white or yellow markings that suggest warning coloration.

Except for a few satyrines that pupate terrestrially, the pupa is suspended by the cremaster and never has a girdle. Pupae may be smooth, elongate ovoids (e.g., some Satyrinae and Danainae), or highly ornamented with various spines, flanges, and elongate projections (e.g., some Biblidinae). The pupal color pattern ranges from highly cryptic, mottled brown or green, to bright colors that may be aposematic, and many other species are notable for their brilliant opalescent or metallic coloration (e.g., Limenitidini, Danainae).

Diversity, distribution and biogeography

The family includes approximately 6,000 to 7,000 species and 350 to 400 genera. The largest subfamily

is the Satyrinae with some 2,500 species, many of which remain undescribed. In contrast, the Calinaginae contains only a single genus of about eight species and the Libytheinae only two genera with 12 species.

The majority of the subfamilies are cosmopolitan, although the Calinaginae are confined to the Sino-Himalayan region and the Morphinae are entirely tropical. However, at the tribal level endemism is much higher, with large tribes confined to or overwhelmingly more diverse in single regions. Notable examples include the Brassolini, Morphini and Ithomiini, restricted to the Neotropics; the Amathusiini, occurring only in the Oriental region; the Acraeini, with its spectacular radiation in the Afrotropical region; and the Danaini, largely confined to the Old World.

Species diversity increases steeply from temperate to tropical regions, reaching a peak in the Neotropical region which contains perhaps 40% of the family. Community species richness is also greatest in the Neotropics, in the foothills of the eastern Andes, where lowland tropical rainforest may contain over 450 species, about a quarter of the butterfly fauna. Species richness decreases with elevation, though richness peaks may occur from 500 to 1,000 m above sea-level, due to overlap of lowland and sub-montane faunas.

The variation in dispersal ability within the Nymphalidae is perhaps more extreme than in any other butterfly family. Certain nymphalids are renowned as great wanderers: the famed Monarch (*Danaus plexippus*, Danainae) occurs throughout much of the globe, even on Hawaii, while the nymphaline *Hypolimnas misippus* is almost as widely distributed. However, the vast majority of species occur only within a single biogeographic region, and a number of species have much more restricted ranges, sometimes down to the level of a single mountain range. Distribution patterns in neotropical montane satyrines (tribe Pronophilini) and the nymphaline genus *Hypanartia* have been used to examine geographic modes of speciation in montane habitats. Ithomiine danaines and heliconiines have featured prominently in studies of the historical biogeography of the Amazon basin.

Habitats

Nymphalid butterflies occur in almost all terrestrial ecosystems. They are found in deserts, grasslands (especially Satyrinae), temperate and tropical lowland and montane forests, ranging from sea-level to over 5,000 m in high ice-fields of the Himalayas and the Andes. They are found in all stages of habitat succession, from primary forest to arid scrub, with varying ecological fidelity.

Ecology

Immature stages. All nymphalid larvae are phytophagous, with the vast majority concentrating on about 100 families of flowering plants, in addition to a few groups on Cycadaceae (cycads), Selaginellaceae (club-mosses) and Neckeraceae (mosses). The Satyrinae and Morphinae feed largely on monocotyledons, as do a few Charaxinae, with the remainder almost exclusively on dicotyledons.

Eggs may be laid in clusters or singly, varying between species, and on or off the foodplant, or, in some satyrines, be dropped from the air. Larvae of a number of species are gregarious and aposematic, suggesting unpalatability (e.g., Heliconiinae), while others adopt a variety of defensive strategies. These include camouflage through decoration of the early instars with frass pellets (stercophory), maintenance and extension of the leaf mid-rib with frass to form a perch (common in Biblidinae), and construction of a mass of frass and leaf material at the base of the leaf mid-rib to provide additional camouflage, which may be elaborated further into an apparent decoy larva-shaped mass (Limenitidini). Spinose larvae may react violently to disturbance, swinging the body and head (e.g., Biblidini), or curl into a defensive posture with the spines directed outwards (e.g., Limenitidini), while smooth-bodied satyrine larvae may simply drop from the plant into the ground litter. A number of nymphalid larvae hibernate in shelters made from cut and sewn leaves, and in some species (e.g., *Adelpha*), this behavior apparently has been co-opted for protection.

Pupation takes place on or off the foodplant, and some satyrines form a weak cocoon on the ground in which they pupate.

Adults. Nymphalids exhibit a broad range of behavior. Unpalatable groups, such as Danainae and Heliconiinae, have a typically slow and even flight, while palatable species in the Apaturinae and Charaxinae are some of the fastest and most agile butterflies. They may be found in open areas (e.g., Satyrinae, Nymphalinae), in shady forest understorey (e.g., Satyrinae, Morphinae, Danainae), and at various

levels within forest subcanopy and canopy (e.g., Heliconiinae, Biblidinae, Charaxinae). Throughout the day a succession of different groups becomes active, with the fastest-flying species being active only during the hotter hours of the day.

Adult nymphalids feed on various food substrates including flower nectar, pollen, rotting fruit, carrion, and damp sand. Flower nectar and rotting fruits provide the carbohydrates that power flight, while pollen is used by *Heliconius* butterflies to provide nutrients for egg production. Damp sand and carrion are thought to provide sodium ions, important for neuromuscular activity, which are typically in low concentration in larval foodplants. These last two sources may also provide amino acids that are used in manufacturing body proteins. To some extent the preferred food source may be dependent on habitat, with open-country species seeking flowers and damp sand, and forest species feeding on rotting fruit and carrion.

A variety of strategies protect nymphalid butterflies from predators, particularly birds. Many species have cryptic underside markings, especially in the Satyrinae and Morphinae, while bright dorsal coloration in the same species probably confuses predators. Most Biblidinae and Charaxinae probably rely on fast flight to evade predators.

Warningly colored ithomiine danaines and heliconiines were instrumental in the formulation of mimicry theory, providing some of the most outstanding examples of this phenomenon in the animal kingdom. Unpalatable danaines and heliconiines are the basis for numerous Müllerian mimicry rings, in which other nymphalids (e.g., Charaxainae, Nymphalinae), as well as other butterflies and moths, participate as probable Batesian (palatable) mimics.

Unpalatable nymphalids obtain protective chemicals by several means. They may sequester secondary chemicals from larval feeding, such as the cardiac glycosides obtained by Danaini from their apocynaceous foodplants. Alternatively, protective compounds, such as the cyanogenic glucosides in *Heliconius*, may be synthesized from amino acids in the larval or adult food. More complex precursors also may be stored from the larval stage, or obtained through adult pharmacophagy (literally, 'chemical feeding'). Adult danaines obtain dehydropyrrolizidine alkaloids by feeding on Asteraceae flowers (sometimes Boraginaceae), or dried or withered Boraginaceae plants (sometimes Asteraceae). In ithomiine danaines, it is predominantly males which exploit these alkaloid sources, transferring the compounds to females in the spermatophore during mating.

Nymphalids generally seek females for mating by 'patrolling' appropriate areas of habitat (e.g., *Morpho* butterflies may patrol several kilometers along rivers or roads), or by 'perching'. Perching nymphalids wait for passing females in species-specific locations, such as a forest light-gap or edge, hilltop, riverside, or prominent patch of vegetation, usually at a characteristic height above ground and at a particular time of day. Many satyrines and brassoline morphines are crepuscular, actively perching or patrolling only at dusk and dawn. Ithomiine danaines perch most actively in the middle to late afternoon, while fast-flying forest canopy species, such as the Charaxinae, are active in the middle of the day. The same perching location may be maintained for years. Perching males are territorial and pugnacious, swiftly engaging in high spiralling flights with intruding conspecific males, with the resident male typically winning the encounter to return to the perching site. Some *Charaxes* butterflies have serrate forewing costal margins, which are reported to be used in male-male interactions. Certain species in the genus *Hamadryas* (Biblidinae) are notable for loud crackling sounds that are emitted by perching males in flight, by percussion of the forewings.

Male ithomiine danaines are remarkable in forming dense aggregations, or leks, of up to 20 to 30 species, which may last several months. Pheromones released through the hindwing hair-pencil androconia attract both sexes, including those of non-conspecific but co-mimetic species, thus providing increased protection from predation and providing a mating place that can be more easily located through the concentrated odor. Aggregations of similar origin and function also are reported in some danaines (*Euploea*).

Males of certain species of *Heliconius* patrol foodplants and mate with females before eclosion from the pupa, thus avoiding courtship. In those species where courtship has been studied in some detail (Satyrinae, Danainae, Heliconiinae), the importance of androconially disseminated pheromones in achieving successful courtship has been demonstrated. In the Danainae, sex pheromones like danaidone (Danaini) are manufactured from pyrrolizidine alkaloids that also confer protection from predators.

Economic importance

With the exception of *Brassolis* and *Caligo* (Brassolinae) which may be pests on coconut palm and

banana plantations, respectively, and certain Heliconiinae which attack passion fruit plants, few other nymphalid butterflies cause any serious damage to crops. Nymphalid butterflies, however, do have a positive economic value. Nymphalid butterflies are an important component of the dead butterfly specimen trade (e.g., *Agrias*, *Charaxes*), the trade in specimens for education (e.g., the Monarch), and are widely used in butterfly houses in temperate countries (e.g., *Heliconius*, *Caligo*). Butterfly houses import much livestock from butterfly farms in tropical countries, providing an alternative source of income in rural areas.

Conservation

Because of their aesthetic appeal, butterflies may be used as flagship taxa for conservation. Attempts to preserve the spectacular over-wintering colonies of the Monarch butterfly in Mexico have raised awareness of conservation in that region. Butterfly diversity and abundance are increasingly being used at the habitat scale as indicators of disturbance and its effects on biodiversity. Nymphalidae are diverse, one of the easiest groups to identify, and many respond to baited traps, and are thus a principal group in such studies. At the biogeographic scale, the Ithomiini have been proposed as an indicator taxon for neotropical lowland forest butterfly diversity, because of their ease of sampling and apparent close correlation with overall butterfly diversity. Finally, recent shifts in geographic range limits of butterflies, especially nymphalids, have been used as evidence for global climate change.

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BUTTERFLIES (LEPIDOPTERA: RHOPALOCERA). Among the insect order Lepidoptera, butterflies comprise about 9% of the order worldwide, totaling about 20,400 described species (moths represent the other 91% of all lepidopterans). There are perhaps another 3,500 butterfly species awaiting discovery and naming, mostly from tropical regions of the world, and especially among the smaller species such as skippers (family Hesperiidae) and blues (family Lycaenidae). The Nymphalidae are the largest butterfly family, with about 7,080 known species worldwide; second largest is Lycaenidae with 5,955 known species. Although the name Rhopalocera is not used in modern classification of Lepidoptera, the name can be used to refer to all the butterflies (Heterocera is used as the name for all moths). While most moths are nocturnal (with many exceptions), most all butterflies are diurnal, although some are known to be crepuscular (especially a few tropical skippers).

Out of the total of 125 families of Lepidoptera, there are seven families of butterflies, although many specialists continue to place snout butterflies (family Libytheidae, only 12 known species) among the Nymphalidae and thus have only six families. Likewise, there is controversy about whether skippers (family Hesperiidae) should be in their own superfamily, Hesperioidea, or together with other butterflies in a single superfamily Papilionoidea. One solution to this controversy is to use a subclassification below the superfamily level, thus the series Hesperiiformes and series Papilioniformes are used. The main true butterfly families are Papilionidae (swallowtail butterflies), Pieridae (yellow-white butterflies), Lycaenidae (gossamer-winged butterflies), Riodinidae (metalmark butterflies), Libytheidae (snout butterflies), and Nymphalidae (brush-footed butterflies). Some specialists combine Riodinidae with Lycaenidae. Contrarily, most of the subfamilies in Nymphalidae in the past often have been separated as their own families, like Satyridae, Charaxidae, Morphidae, Amathusidae, Danaidae, Heliconiidae, etc. Butterflies now are thought to be a lineage from