mance liquid chromatography (radio-HPLC) and radio-gas chromatography (radio-GC) are widely used to provide a preliminary identification of the intermediates and end products of the biosynthetic process under study. Final identification and structure assignment require the use of more sophisticated techniques such as capillary gas chromatography-mass spectrometry (CGC/MS), HPLC/MS, and nuclear magnetic resonance (NMR). Enzyme studies might be carried out employing appropriate label tracers and/or by spectrophotometric measurements for preliminary characterization. Studies on enzyme location, purification, cofactors required, kinetic parameters and, regulation are carried out by more complex studies including HPLC purification, molecular mass determination, amino acid sequence, electronic microscopy, immunofluorescent assays, protein purification and characterization in addition to the previously mentioned techniques. Furthermore, if isolation of genes encoding the target enzyme and insertion in an appropriate vector are feasible, the overexpression of such enzyme in an appropriate system can increase the quantity of intermediate precursors, i.e., very long chain fatty acids, and thus increase the substrates available to study wax formation.

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METALLIC WOOD-BORING BEETLES. Members of the family Buprestidae (order Coleoptera). See also, BEETLES.

METALLYTICIDAE. A family of praying mantids (Mantodea). See also, PRAYING MANTIDS.

METALMARK BUTTERFLIES (LEPIDOPTERA: RIODINIDAE). This is one of the five families of 'true' butterflies (in the superfamily Papilionoidea). Recent morphological and molecular evidence, for the first time based on sufficient taxon sampling, indicates the Riodinidae to be the sister group to the Lycaenidae (blues, coppers and hairstreaks). Based on the only confirmed riodinid fossils, of Napaeina and *Nymphidiini* species in Dominican amber, the family is at least 25 million years old. The higher classification of the Riodinidae is now relatively well resolved, and the group is currently divided into three subfamilies, twelve tribes and six subtribes, with only one *incertae sedis* section of unplaced riodinine genera still remaining. However, intertribal relationships in the largest subfamily, the Riodininae, are poorly understood.

Order: Lepidoptera
Superfamily: Papilionoidea

Family: Riodinidae Grote

Subfamily: Nemeobiinae Bates
  Nemeobiini Bates
  Zemerini Stichel
  Abisarini Stichel

Subfamily: Euselasiinae Kirby
  Corrachiini Stichel
  Euselasiini Kirby

Subfamily: Riodininae Grote

  Mesosemiini Bates
    Mesosemiina Bates
    Napaeina Hall
  Eurybiini Reuter
  Riodinini Grote

Stalachtini Bates
Helicopini
Symmachiini
incertae sedis of Harvey
Nymphidiini Bates
Aricorina Hall & Harvey
Lemoniadina Kirby
Theopeina Clench
Nymphidiina Bates

Morphology

The Riodinidae present perhaps the most kaleidoscopic array of colors, patterns, shapes and sizes of any butterfly family. Many have metallic silver or gold markings, hence their common name of metalmarks. They are generally rather small and range in size from about 12 mm to 60 mm. The only distinguishing characteristic of the Riodinidae that is visible to the naked eye is their greatly shortened male forelegs, which are no longer used for walking. Although the Nymphalidae share this character, Riodinidae additionally have a coxa on the male foreleg that extends as a spine-like projection below the trochanter (a character only weakly developed in the two species of Corrachiini, and also quite well developed in various poritiine and curetine lycaenids), trichoid sensilla on the female foretarsal segments that are clustered into single instead of medially divided patches, and no posterior apophyses extending anteriorly from the ovipositor lobes of the female genitalia.

Although their external morphology is comparatively uniform, the male and female genitalia exhibit a remarkable diversity of form given the relatively small size of the family. The most comprehensive set of drawings of venation, palpi, legs and genitalia is still that of Stichel (1910–11). Although androconia, specialized male secondary-sexual scales, have historically been thought to be rare in the Riodinidae, especially, for example, compared to the Lycaenidae, a recent comprehensive study found that at least 25% of riodinid species possess a wide morphological array of them. Because the Riodinidae are now known to have abdominal coremata (similar to those of danaine nymphalids), concealed internal and visible external abdominal androconia, genital brush organs and hind leg hairpencils (unique within the Papilionoidea), as well as the more obvious alar organs, the family can reasonably be described as exhibiting among the greatest morphological diversity of androconial organs in the butterflies.

Diversity and biogeography

The Riodinidae contain about 1,350 species, only a few of which remain undescribed. The family has a worldwide distribution, but it is unique among the butterflies in being almost exclusively confined to a

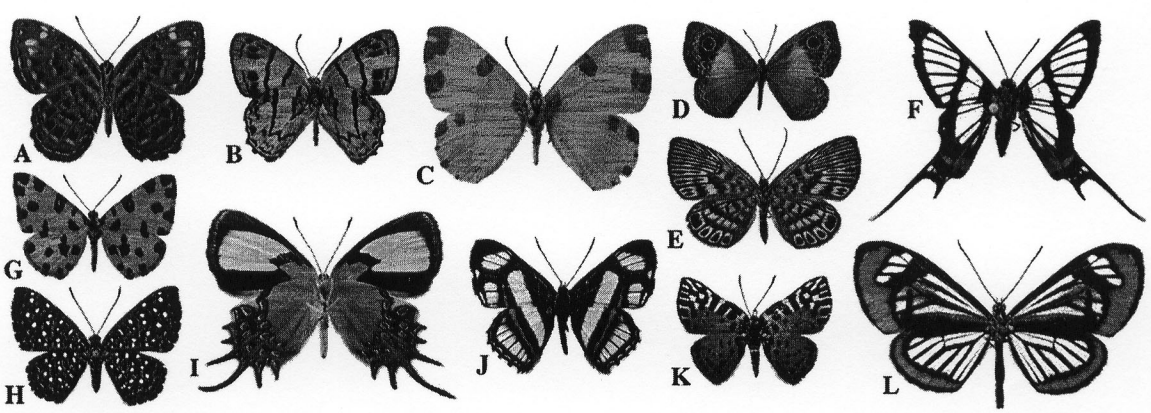

Fig. 627 Adult riodinids. A. *Neotaxila thuisto* ♂ Hewitson (Nemeobiinae, Nemeobiini). B. *Euselasia labdacus* Stoll (Euselasiinae, Euselasiini). C. *Hermathena candidata* Hewitson (Riodininae, Mesosemiini, Napaeina). D. *Perophthalma lasus* ♂ Westwood (Riodininae, Mesosemiini, Mesosemiina). E. *Alesa amesis* ♂ Cramer (Riodininae, Eurybiini). F. *Chorinea batesii* Saunders (Riodininae, Riodinini). G. *Baeotis sulphurea* R. Felder (Riodininae, Riodinini). H. *Calydna calamisa* ♂ Hewitson (Riodininae, *incertae sedis* of Harvey). I. *Helicopis gnidus* Fabricius (Riodininae, Helicopini). J. *Synargis fenestrella* Lathy (Riodininae, Nymphidiini.) K. *Symmachia suevia* Hewitson (Riodininae, Symmachiini). L. *Stalachtis phaedusa* Hübner (Riodininae, Stalachtini).

single biogeographic region, the Neotropics, where approximately 95% of the familial diversity occurs. Riodinid diversity peaks in the lowlands of the Amazon basin, where as many as 400 species can be found in a single heterogeneous locality, constituting more than 20 percent of the local butterfly fauna (including Hesperiidae). Species richness in Central America is roughly half that of Amazonia, and only two dozen species extend northwards into North America. Species richness also tapers off gradually with increasing elevation, and very few species occur above 2000 meters.

On average, riodinids have smaller geographic ranges than their close relatives the lycaenids, and this makes them ideal subjects for biogeographic study. *Detritivora* Hall & Harvey, a genus of small, drab, forest-dwelling riodinines, provides perhaps the most extreme example in the Lepidoptera of a continuously distributed lowland group with highly fragmented species ranges. The *D. cleonus* group is divided into an incredible nineteen parapatrically distributed species across Amazonia, each occupying a variably small area of endemism. A cladogram of these riodinids, superimposed over a map of their distributions, led to the most detailed hypothesis yet of Amazonian area relationships.

Adult ecology

Riodinids are found in a wide variety of primary and secondary habitats, from dry *Acacia* scrub to pluvial forest, but most are exclusive denizens of primary rainforest. Most species are very localized in time and space. Years of observations in an area usually result in finding only one or two places where a particular species occurs and even then the species will most likely only be present for a couple of hours a day, and perhaps only during certain months of the year. It is not surprising then that so many riodinids are very rare in collections. Intergeneric and interspecific differences in male riodinid perching behavior, involving variably sized groups of males resting at characteristic sites and investigating passing butterflies in search of conspecific females, can be explained these differences in the context of premating isolating mechanisms. Such perching behavior, better known in birds, is known as lekking, a word derived from the Swedish verb ''leka'', meaning ''to play''. Male riodinids most frequently lek along forest edges, streamsides, and especially on ridgetops and hilltops, where they may use the same patch of vegetation year after year, arriving from the surrounding forest and departing at roughly the same time every day, and always resting on leaves or tree trunks at about the same height above the ground.

Mimicry is perhaps more rampant in the Riodinidae, especially in females, than in any other butterfly family in terms of the diversity of taxa that its species mimic. There are tiger striped riodinids that resemble papilionids, pierids and various nymphalid subfamilies, clear-winged species that seem to mimic ithomiine nymphalids and dioptine and arctiine moths, and gaudy blue, red, orange, or yellow patterned species that seem to be mimicking dioptine, arctiine, geometrid and tortricid moths. Such riodinids also mimic the same flight behavior of the presumed model(s), often even holding the antennae at the same angle. Most of these mimetic relationships are probably Batesian, with moths generally being the unpalatable models, but we know essentially nothing about the palatability of mimetic riodinids.

Like other butterflies, riodinids can be found feeding on flowers, or imbibing nutrients and ions from damp sand or mud (known as puddling). However, carrion is the most frequently recorded food source, both in terms of number of individuals and taxa. This behavior is common elsewhere in butterflies only in certain subfamilies of the Nymphalidae and Lycaenidae. There is also a correlation between food substrate choice and wing area to thoracic volume ratio in male riodinids, with puddlers and carrion feeders having lower such ratios (i.e., relatively larger thoraces for their overall size). These feeding behaviors are believed to supplement nutrient stores from larval feeding to increase reproductive success and provide the necessary nutrients to maintain high metabolic rates during rapid flight.

Immature stages and myrmecophily

The early stages of the Riodinidae remain probably the most poorly known of all the butterfly families and only a small fraction of the genera have been reared, making the immatures a fertile field for further study. Riodinid eggs are generally laid singly, but in certain groups, such as the Euselasiinae, they are often laid in clusters, resulting in gregarious groups of often aposematic larvae. Riodinid eggs are remarkably diverse in form compared to those of the Lycaenidae, in anthropomorphic terms resembling crowns, pies, cakes, cones, footballs, automobile tires and more. Those larvae that have

symbiotic relationships with ants tend to be smooth, whereas those that are non-myrmecophilous are generally hairy. Riodinid pupae are generally smoothly cylindrical, girdled, and best distinguished from those of other butterflies by their broadly flattened cremaster. Some pupae have spines, others are moth-like cocoons made from the shed larval setae, and those of *Eurybia* Illiger are extraordinary in having an elongate spine-like posterior projection almost as long as the remainder of the pupa to enclose the very long proboscis.

Myrmecophily, or the ability of butterfly caterpillars to form symbioses with ants by providing food secretions in exchange primarily for protection from arthropod predators, is almost entirely confined to the Lycaenidae and Riodinidae. Although this phenomenon is very widespread in the Lycaenidae, only about one quarter of the Riodinidae are myrmecophilous, encompassing the tribes Eurybiini and Nymphidiini. Myrmecophilous larvae possess a suite of 'ant-organs' that facilitate their interactions with ants. Tube-like paired tentacle nectary organs (TNOs) on abdominal segment eight, which secrete nutritionally rich droplets to be harvested by ants, are present in both tribes, but a further two 'ant-organs' are restricted to the Nymphidiini. Setose paired anterior tentacle organs (ATOs) on thoracic segment three appear to influence ant behavior through the use of semiochemicals, and a pair of stridulatory rod-like appendages on the first thoracic segment, termed vibratory papillae, grate against granulations on the head as it moves in and out to produce an acoustical call that is thought to function in attracting ants. The function of bladder or balloon setae, a corona of inflated setae on the first thoracic segment which also occur in the non-myrmecophilous Helicopini and *incertae sedis* section, is still unclear, but, at least in the Nymphidiini, they may release an ant alarm pheromone analogue, when squeezed by an ant, to confer protection on the caterpillar.

Riodinids are known to feed on over forty families of flowering plants, using leaves, extrafloral nectaries and, more rarely, flower parts, but are of little economic importance. Certain members of the Euselasiinae feed on harvested myrtaceous plants such as guava, and some Napaeina species can be pests on ornamental Neotropical bromeliads and orchids. Aphytophagy, or feeding on non-plant material such as ants or their regurgitations, or on hemipterans and their secretions, is rare in the Lepidoptera and in butterflies also present only in the Lycaenidae (e.g., Liphyrinae, Polyommatinae and Miletinae) and ''Riodinidae (Eurybiini and Nymphidiini). Although aphytophagy has only been unequivocally documented for two riodinid species, there is evidence to suggest that this phenomenon is significantly more common in the family.

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METALMARK MOTHS (LEPIDOPTERA: CHOREUTIDAE). Metalmark moths, family Choreutidae, comprise 418 species worldwide, in three subfamilies (in the past incorrectly included in Glyphipterigidae); actual world fauna probably exceeds 800 species. There are three subfamilies: Millieriinae, Brenthiinae, and Choreutinae. The family is in the superfamily Sesioidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Adults small (7 to 24 mm wingspan), with head mostly smooth-scaled; haustellum scaled; labial palpi often with a scale tuft on second segment; maxillary palpi 1 to 2-segmented. Forewings somewhat elongate or more triangular. Maculation variable but usually with brilliant metallic-iridescent spots or marks; sometimes more colorful markings, or subdued in a few species. Hindwings colorful or dark, and often with a light band near termen; sometimes