

Taxonomic Studies in New Guinea and Solomons Nymphalidae (Lepidoptera: Rhopalocera), and Discovery of Abdominal Scent Organs in the Females of Various Nymphalinae Genera

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ABSTRACT

The New Guinean mainland montane genus *Pieridopsis* is synonymized with *Erycinidia* (Satyriinae). A new genus, *Algiachroa* (Nymphalinae), is erected for the endemic Solomon Islands species, previously known as *Cupha woodfordi*, and its relationships within the subfamily Nymphalinae are discussed. A key to *Algiachroa* and related genera is provided. The New Guinean mainland taxa *felderi* and *mimicus*, previously placed in *Cirrochroa*, are combined under *Algia*. The *A. woodfordi* female (like those of several other related genera) was found to bear paired club-like organs laterally below the tip of the abdomen. These are considered to be androconial in function and to be analogous to those of Neotropical *Heliconius* (Nymphalinae). Each organ of the pair in *A. woodfordi* is given here the name *clavatum* (plural: *clavatia*). Their discovery in *Algiachroa*, and in certain other related nymphaline genera, may provide a particularly useful character for defining the tribal relationships of these nymphalids as discussed.

INTRODUCTION

The following account is part of an ongoing taxonomic study in preparation for the forthcoming monograph entitled *Butterflies of Papua New Guinea* (Parsons, in prep.). Papers in this series include Parsons (1984a, b; 1986a, b; 1989). General information on the taxonomy of New Guinea butterflies will be found in the introductions to these papers.

A complete revisionary classification of the family, and especially the subfamily Nymphalinae, is still wanting. Ehrlich (1958) stated that Nymphalinae was in more need of thorough generic work than any other subfamily of the Nymphalidae. This view was endorsed by Scott (1985) who suggested that the structure of the larvae and pupae would provide useful characters for analysis. Ackery & Vane-Wright (1984) maintained that the higher classification of the family is, at present, in a "totally unsatisfactory state." This view was upheld by De Vries et al. (1985) who used mainly larval characters in a cladistic study of one particular group of nymphalids. The cladograms obtained by studying also several outgroups were surprisingly different from those suggested by existing systematic hypotheses. According to R. Vane-Wright (pers. comm. 1986), the study was the first of a series of intermittent papers that should greatly rectify the present state of confusion regarding nymphalid classification.

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As with the Lycaenidae, the task of systematically arranging the numerous and often very different-looking nymphalid species demands careful study and access to much material. De Vries et al. (1985) suggested that early stages would be particularly important in future systematic studies of the Nymphalidae, and this suggestion is endorsed here. Many nymphalid systematists have been greatly biased by the large number of specialized adult characters exhibited by the family and so have divided it unnecessarily or irregularly. De Vries et al. (1985) have shown that Nymphalinae (*sensu* Ehrlich), like Satyrinae, is probably polyphyletic. It remains to be seen, therefore, what "final" arrangement a refining of nymphaline classification will produce.

***Erycinidia* Rothschild & Jordan**

Erycinidia Rothschild & Jordan, 1905 Novit. Zool. 12: 457. Type species fixed by authors: *Erycinidia gracilis* Rothschild & Jordan, 1905, Novit. Zool. 12: 457.

Pieridopsis Rothschild & Jordan, 1905, Novit. Zool. 12: 457. Type species fixed by authors: *Pieridopsis virgo* Rothschild & Jordan, 1905, Novit. Zool. 12: 457 **New synonymy.**

Erycinidia Rothschild & Jordan and *Pieridopsis* Rothschild & Jordan: Miller 1968, Mem. Amer. Ent. Soc. No. 24: 80.

The taxon represented by the nominal species *Pieridopsis virgo* Rothschild & Jordan is here treated subjectively as being congeneric with that represented by *Erycinidia gracilis* Rothschild & Jordan, 1905. *E. gracilis* is the type species of *Erycinidia* Rothschild & Jordan, 1905, of which therefore *Pieridopsis* is a junior subjective synonym.

Thus, the genus *Erycinidia* now contains the following taxa previously placed in *Pieridopsis*: *virgo* (Rothschild & Jordan, 1905) **n. comb.**, and *ducis* (Jordan, 1930) **n. comb.** It also comprises: *gracilis* Rothschild & Jordan, 1905; *tenera* Jordan, 1930; *hemileuca* Jordan, 1930.

Remarks. Miller (1968) revised the satyrine nymphalids (according them family rank) and accepted *Pieridopsis* and *Erycinidia* as distinct. However, the genus *Pieridopsis* is treated here as a synonym of *Erycinidia* because the characters by which it supposedly differs from *Erycinidia* are now known to be inconsistent, and the 2 taxa share important morphological features (see below). At the time of their descriptions by Rothschild & Jordan (1905), only 1 species from each genus was available. This overemphasized their supposed differences. *Erycinidia* has page position priority over *Pieridopsis*. Jordan (1924: 286) was the first to point out the possibility of the synonymy of the 2 taxa when he noted that "the discovery of *E. maudei* renders it probable that the slight difference between the two genera will be entirely wiped out by further new forms." However, he made no attempt to synonymize the 2 taxa when he later described 2 further species under each genus (Jordan 1930). A. Sibatani (pers. comm. 1986) had independently reached the same conclusion as the present author regarding the synonymy of *Erycinidia* and *Pieridopsis*.

The original statement by Rothschild & Jordan (1905) that *Pieridopsis* is "allied to *Erycinidia*, but easily distinguished by the short discoidal cell of the hindwing" is incorrect. Jordan (1924) defined the character in another way: "cell of [*Pieridopsis*] hindwing only as long as R₃ [M₃], i.e. somewhat shorter than in *Erycinidia*." This is the only character by which the 2 taxa are supposedly separable. However, a detailed study using accurate measurements of the hindwing venation of all taxa has shown that the character is incorrectly stated. In fact, the concave to convex profile of the hindwing termen, which is anyway somewhat individually variable, has a direct bearing on the length of vein M₃, and this, therefore, varies between all species (Figs. 1-4). It is notable that the venation, coloration, and male genitalia of *Erycinidia maudei* and "*Pieridopsis*" *ducis* are very similar. Holloway (1974: 93) pointed out: "In *Dodonidia* [from New Zealand], *Erycinidia* and *Pieridopsis* the ductus bursae [of the female genitalia] has its exterior

opening in a sclerotised plate; these three genera are also characterised by a developed juxta in the male and similarity of wing shape and banded markings.”

***Algiachroa* Parsons, new genus**

Figs. 8–10, 14–16

Type species. *Cupha woodfordi* Godman & Salvin, 1888: 97.

Diagnosis. A monotypic genus of the Nymphalidae, endemic to the Solomons (including Bougainville, North Solomons Province, which is politically part of PNG, but faunistically part of the Solomons). Average forewing length/wingspan: ♂ 37/64, ♀ 39/68. Closely allied to *Cirrochroa* Doubleday, 1847, and *Algia* Herrich-Schäffer, 1864, with the following combination of characters:

Description. Antenna slightly under ½ length of forewing costa, club narrow and tapering, barely broader than shaft. Eye smooth. Labial palpus (Fig. 9) erect, terminal segment short and pointed. Legs typically nymphalid, male forelegs slightly more modified than in female. Forewing costa convex, inner margin slightly concave, termen convex and weakly scalloped; hindwing tornus slightly pronounced, inner margin very slightly concave between anal veins, termen evenly scalloped; wing cilia short. Venation (Fig. 8); forewing cell approximately ⅓ length of costa, apex rather narrowly rounded at origins of veins R_2 , R_3 , and M_1 , which are closely and approximately parallel, origins of Sc and M_2 more widely separate, but approximately equidistant from either side of cell apex, R_5 arises from middle of R_3 , R_4 from subbasal region of R_5 , lower discocellular long ($\frac{2}{3}$ width of distal end of cell), concave above cubitus, and very narrow. Coloration of male dorsally predominantly dark brown, a broad oblique white band covering central ¼ of forewing, from tornus to mid-costa, subtornally enclosing a large dark brown spot, hindwing with a complete postmedian row of large black spots, broadly ringed with orange, a scalloped pale mauve subterminal line and a more diffuse pale brown terminal line; ventrally similar to dorsally, but ground color much paler, especially pale gray-brown from median to basal regions of wings. Slightly dimorphic with some males lacking a strong mauve sheen. Female similar to this male form but lacking sex-brands.

Male genitalia and androconia (Fig. 10). Uncus simple, beak-like, lacks gnathos, apex slightly hooked, basally waisted in dorsal profile; valvae simple, distally ovate, proximally truncate, ventrally extended into a short, blunt process, inner lamina with a short, proximally hooked, sclerotized ridge; juxta simple, V-shaped; aedeagus simple, short, distally flared, with a short coecum, aperture bearing short, distally directed external cornuti. Forewing dorsally with an elongate ovate orange-brown sex-brand subbasally on vein M_2 , and a similar brand slightly more proximally positioned on M_1 (Fig. 8).

Female genitalia and androconia (Figs. 14–16). Genital aperture wide; antevaginal region of ostium bursae weakly sclerotized with an irregular median sinus and a pair of weakly sclerotized lateral stays; ductus bursae short, broad, narrowing slightly before opening into a short elongate-ovate corpus without signa; papillae anales normal, hirsute; clavatum (see below), apically scaled with fairly loose androconial scales, these spatulate, elongate-subtriangular, crenulate, and with a deeply serrate distal margin (Fig. 16).

Remarks. Godman & Salvin (1888) first described *woodfordi* under the genus *Messaras* Doubleday, 1848, which according to Hemming (1967) is a synonym of *Cupha* Billberg, 1820, as Doubleday designated the same type species, *erymanthis* (Drury, 1773), for *Messaras*. Godman & Salvin (and subsequent authors) failed to note that the *woodfordi* male bears a pair of small, elongate, forewing upperside sex-brands at the bases of veins M_2 and M_1 , otherwise they might have realized that the true affinities of the taxon lie closer to *Cirrochroa* and *Algia* than to *Cupha*. They merely stated that “though evidently a member of this genus [*Messaras*], the colouration of the wings renders it at once easy of recognition.” Ribbe (1898) did point out that *woodfordi*

does not fly in open forest glades as *Cupha* species do but instead in the shade, and that it is a notably slow flier. In a study of *Cupha* Fruhstorfer (1899) merely mentioned that *woodfordi*, treated at the end of his checklist, is the largest and most handsome species of the genus. Van Eecke (1915) maintained that the 10 species of *Cupha* listed in Seitz all belong to *C. lampetia* (Linnaeus, 1764) as their male genitalia vary only slightly and inconsistently. However, he failed to include *woodfordi* in his studies.

The taxon *woodfordi* warrants a new genus because it clearly does not belong in any of its most closely related genera. It differs in several respects: size, being larger than *Algia* and *Cupha*, and of a size similar to smaller species of Oriental *Cirrochroa*; wing shape (compare figures 5–8), the forewings being especially broad and apically rounded, and never as falcate as is usual in *Cirrochroa*; its broad pure white forewing band, not present in any members of *Cirrochroa*, *Algia*, or *Cupha*; the configuration of its forewing cell venation (compare figures 5–8); the configuration of its male sex-brands (compare figures 5, 7, and 8), brands being absent in *Cupha* (figure 6); the morphology of its male genitalia (compare figures 10–13), which are most similar to those of *Cirrochroa*, but differ mainly in the lack of the prominent harpe present on the inner lamina of the *Cirrochroa* valva; and the morphology of its female genitalia and clavatia (compare figures 14–20), notably the corpus bursae being longer and more ovate than in *Algia*, and lacking the double-chamber of the proportionately larger *Cirrochroa* corpus bursae. Other differences include the *Algiachroa* female foreleg tarsus, which is slightly more inflated ventrally (“clubbed”) at its apex than in *Cirrochroa* and more so than in *Algia* or *Cupha* (in which it is somewhat tapered). Otherwise the legs of the sexes of all these genera are similar. They all bear smooth eyes. In *Algiachroa*, *Algia*, and *Cirrochroa*, all male androconia hardly differ from normal scales except in color and their usually more deeply serrate distal margins.

Most of the above-mentioned facies place *woodfordi* in a well-defined group of genera that includes *Algiachroa*, *Algia*, and *Cirrochroa*. It is considered here that the following are apomorphic (i.e., derived or specialized) characters in *Algiachroa* at the level of its generic group: well-rounded forewing cell apex; male dimorphism; broad white forewing upperside band; presence in male of only forewing upperside sex-brands, and absence of hindwing brands; elongate-ovate, non-double-chambered female corpus bursae; and weakly sclerotized ostium bursae antevaginal region with irregular median sinus and a pair of weakly sclerotized lateral stays.

The following adult facies in *Cupha* show that the genus belongs in a separate, well-defined group of 3 genera that also includes *Phalanta* Horsfield, 1829, and *Vagrans* Hemming, 1934: the extremely narrow and elongate female corpus bursae, being as long as the abdomen in *Vagrans* (Figs. 23 and 24); the tubular, not distally flared, male aedeagus that bears 2 groups of densely packed cornuti in the vesica; the whip-like, irregularly dentate dorsal appendage to valva (Fig. 13), which Roepke (1938) figured for *Vagrans*, and which he termed a “flagellum”; the simple, rather spatulate female androconial organs (Figs. 23 and 24; see below); the origin of vein R_2 from vein R_5 (as opposed to directly from the cell in nearly all other Nymphalid genera); the connection of discocellular M_2 – M_3 with the cubitus at, or slightly distally to, base of vein CuA_1 ; and the lack of male sex-brands. Like *Algiachroa*, *Vagrans* is monobasic.

The following key is provided to assist in the identification of the above-mentioned genera. Members of *Vindula* Hemming, 1934, and some of *Cethosia* Fabricius, 1807 (both Indo-Australian genera), are superficially similar to many Oriental *Cirrochroa* (in general wing shape and mainly orange coloration), so they are included. However, the resemblance is likely the result of mimicry of *Vindula* and *Cethosia* by *Cirrochroa*. This is because all *Vindula* and *Cethosia* are *Passiflora*-feeders as larvae, and this genus of plants, as far as is known, confers toxicity (or at least a distastefulness to predators) on its Neotropical heliconiine herbivores (Brower et al. 1963), whereas *Cirrochroa*, *Cupha*, *Vagrans*, and *Phalanta* utilize predominantly flacourtiaceous foodplants not known to contain noxious secondary plant compounds. Apart from the different

foodplant relations of *Vindula* and *Cethosia*, their adult characters and the morphology of their early stages show that they belong in a group distinct from the *Cirrochroa* and *Cupha* groups.

Key to Genera of *Cirrochroa* and *Cupha* Groups and Similar Genera

1. Termens of both wings, especially HW, prominently dentate, accentuated on underside by a single, distinct, zigzagged, white or cream submarginal line ***Cethosia*** (10 species)
Wing termens smoothly and shallowly dentate, or almost rounded, not marked as above 2
- 2(1). HW with short triangular tail at vein M_3 3
HW without short triangular tail at vein M_3 4
- 3(2). HW with a distinct pair of white-pupiled postmedian eye-spots (sometimes with additional vestigial satellite eye-spots) ***Vindula*** (4 species)
HW with a postmedian row of small black spots ***Vagrans*** (1 species)
- 4(2). FW discocellular M_2 - M_3 connects with cubitus at, or slightly distally to, base of vein CuA_1 (Fig. 6) 5
FW discocellular M_2 - M_3 connects with cubitus between bases of veins CuA_1 and CuA_2 (Figs. 5, 7, and 8) 7
- 5(4). FW cell apex acutely pointed (Figs. 5 and 7) 6
FW cell apex well-rounded (Fig. 8) ***Algiachroa***, n. gen. (1 species)
- 6(5). HW upperside with discrete 1-4 mm wide cream or yellow submedian band . ***Algia*** (3 species)
HW upperside not marked as above ***Cirrochroa*** (16 species)
- 7(4). FW termen straight or concave, wing apex acute ***Phalanta*** (4 species)
FW termen notably convex, wing apex broad and/or well-rounded (Fig. 6)
. ***Cupha*** (9 species)

Genus *Algia* Herrich-Schäffer

Algia Herrich-Schäffer, 1864, Correspbl. zool. min. ver Regensburg 18: 125 repaged offprint as Prodrumus 1. 1: 27. Type species by subsequent designation by Hemming (1964, Annot. Lepid. [4]: 124): *Cirrochroa satyrina* C. & R. Felder, [1867] Reise Fregatte "Novara," Lep.-Rhop. (3): 389.

Paduca Moore, 1886, J. Linn. Soc. Lond., Zool. 21: 34. Type species by original designation: *Atella fasciata* C. & R. Felder, 1860, Wein. ent. Monats. 4: 236.

Ducapa Moore, 1900, Lep. Ind. 4 (47): 209. Type species through Section (i) (replacement names) of Article 67: *Atella fasciata* C. & R. Felder, 1860, Wein. ent. Monats. 4: 236.

D' Abrera (1971, 1978) treated the New Guinea species, *felderi* Kirsch, 1877, in the genus in which it was first described, *Cirrochroa*, but later (D' Abrera 1985) employed the generic name *Paduca* for its Oriental Region relatives. However, Corbet & Pendlebury (1978) pointed out—undoubtedly with reference to *felderi* and also based on Moore (1900), who placed the species under *Ducapa*—that *Paduca* (i.e., *Algia*) has a single representative in New Guinea. They noted that the genus is structurally close to *Cirrochroa*, but that *Algia* adults are smaller in size and differ also in appearance and habits (*A. fasciata* being "feeble in flight and frequents shaded forest paths on the plains"). They pointed out that, in the *Algia* male, forewing veins M_2 and M_1 , and hindwing veins M_1 and Rs , are comparatively broadly margined with buff-brown specialized scales. As in the similar scales of *Cirrochroa*, these are apparently androconial in function.

Hemming (1964, 1967) showed that *Paduca* and *Ducapa* are synonyms of *Algia*. However, Cowan (1968) stated that it was wrong to treat *Paduca* as not in current use because it ranked as a perfect example of a *nomen oblitum* when, according to him, a century after its introduction, Hemming (1964) improperly reviewed the genus. Cowan stated that this act contravened Article 23b of the Code in that Hemming did not refer it to the Commission to be placed on the appropriate Official Index of Rejected Names. He maintained that the continued use of *Paduca*, and the rejection of *Algia*, would best serve stability and universality, and proposed to submit this to the Commission. However, Cowan (1970), without giving reasons, stated that

his proposed 1968 23b application had not been carried out. He believed that *Algia* and *Paduca* both remained valid, their synonymy being purely subjective, and maintained that the respective type species, *satyrina* and *fasciata*, are "remarkably different in appearance and there is even some structural difference between them." However, as shown by the present study, this is incorrect, and Hemming (1964) was correct in his original synonymy.

As the taxon *felderi* has all the features characteristic of the genus *Algia* (Figs. 7, 12, 17, and 18) it is now formally placed in that genus. Therefore, besides the type species *satyrina* and the species *fasciata*, *Algia* contains the following nominal PNG taxa, previously placed in *Cirrochroa*:

felderi (Kirsch, 1877), **n. comb.**

mimicus (Rothschild, 1904), **n. syn.**

The taxon *Messararas mimicus* Rothschild, 1904, is synonymized here with *felderi*. Study of various series of topotypical specimens of the 2 taxa (including Kirsch's original figures of *felderi* from Nappan, southwest coast of the Geelvink Bay, Irian Jaya, and the *mimicus* holotype from the Upper Aroa River, Central Province, Papua New Guinea housed in the British Museum of Natural History [London]) has shown that there are no differences by which *mimicus* can be distinguished. Rothschild (1904) was apparently unaware of Kirsch's (1877) publication of *felderi* and erroneously described *mimicus* as a new species from only a single male.

Nymphalinae Female Scent Organs

A survey of the female genital structure of all related Indo-Australian genera was carried out when it was found that the *Algiachroa woodfordi* female bore a pair of club-like organs (Figs. 14–16), almost certainly androconial in function, and apparently analogous to those present in Neotropical Region *Heliconius* (Fig. 25) of the subfamily Nymphalinae. Similar organs were then found to be present in *Algia* and *Cirrochroa* (Figs. 17–20). Even more specialized organs were observed in *Terinos* Boisduval, 1836, and the African genus *Lachnoptera* Doubleday, 1848 (Figs. 21 and 22)—these 2 genera being studied because they were mentioned by various authors to be related to *Phalanta*, *Algia*, and/or *Cirrochroa*. Simple organs were located in *Phalanta*, *Cupha*, and *Vagrans* (Figs. 23 and 24), with a reduction in their structure across the genera in this order, those of *Vagrans* (not illustrated) apparently being vestigial, merely raised irregular humps in the positions where the organs should be. The genera *Cethosia* and *Vindula*, unexpectedly, were found to lack androconial clubs (as they have been assumed to be Old World representatives of the tribe Heliconiini, e.g., by Clark [1927], Eliot in Corbet & Pendlebury [1978], and Brown [1981]).

Algiachroa, *Algia*, and *Cirrochroa* club-like female abdominal androconial organs are most similar in structure to the apparently homologous organs of *Heliconius*. In *Phalanta*, *Cupha*, and *Vagrans* the lateral organs are simple and spatulate, being almost absent in the latter 2 genera, and with minute androconia visible along the dorsal margin of the organ only in *Phalanta*. In *Terinos* and *Lachnoptera* the organs are more impressive club-like structures, those of *Terinos* being very strongly sclerotized, long, inwardly curved and prominently knobbed. In *Lachnoptera* the organ is strongly sclerotized with a broad spatulate apex bearing a deep median sinus. Its spatulate androconia are obviously designed, like those of *Heliconius*, to interact with a dorsal gland. However, the *Lachnoptera* dorsal gland, positioned on the smooth membrane between the 8th and 9th tergites, is interesting because it bears a covering of setose androconia, whereas that of *Heliconius*, despite deep reticulate convolutions, is naked.

The *Clavatium*

There has not yet been a formal scientific naming of any Nymphalinae female organs in the literature (see below), and a concise and descriptive term is wanting to replace word pairs or phrases used in describing the organs noted above. Therefore, the name *clavatium*, derived from the Latin *clava*, meaning club (plural: *clavatia*), is given here to the organs of *Algiachroa woodfordi*

(Figs. 14–16). These are a pair of simple, posteriorly directed, club-like processes, laterally, 1 each side of the abdomen, each of which arises near the distal margin of the 8th sternite and bears an array of spatulate androconial scales, the distal margins of which are deeply serrate. The clavata are recessed in lateral “pockets” formed by the overlap of the 8th tergite. Their apices are drawn out and exposed as the abdomen tip is curved downwards.

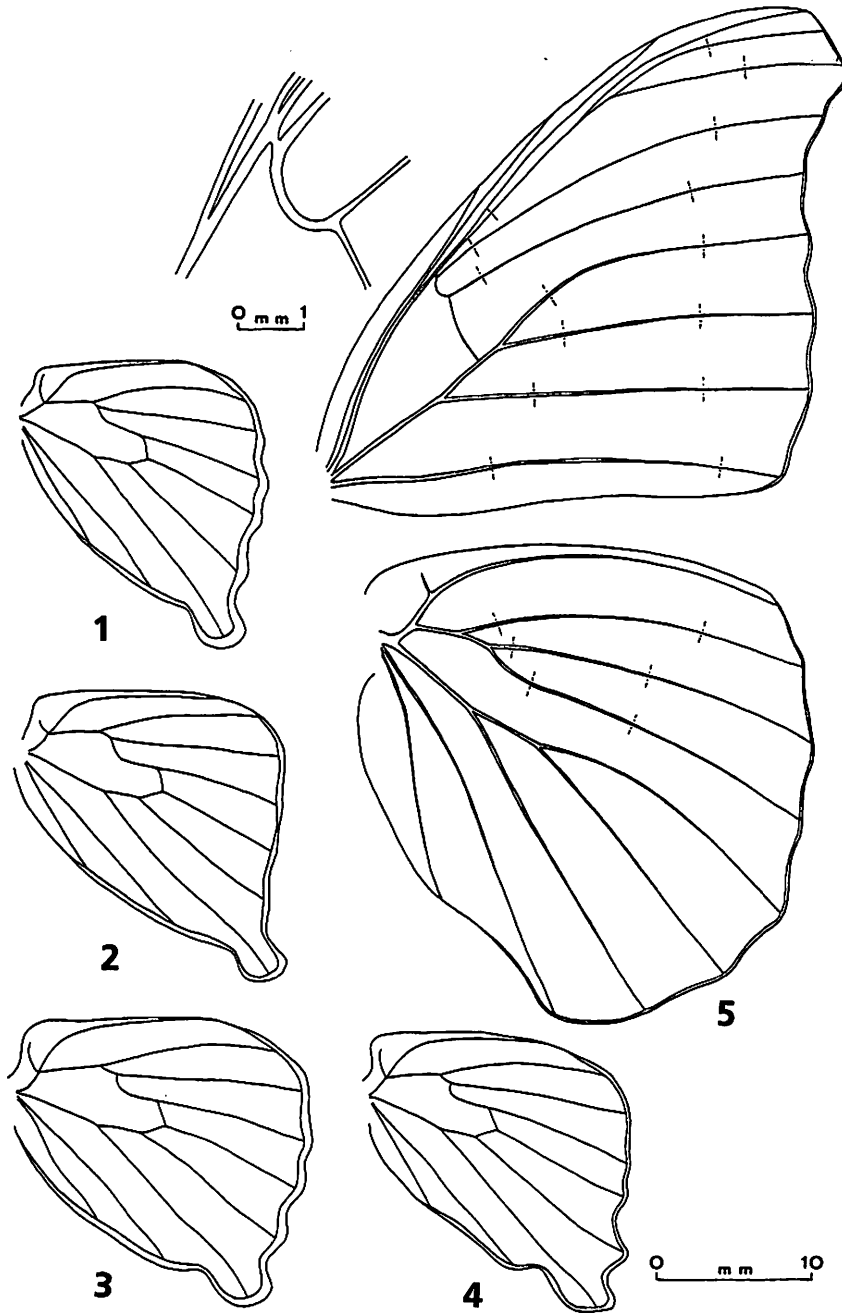
This new term also applies to the similar structures present in females of the closely related genera *Cirrochroa* and *Algia*, all 3 genera composing the *Cirrochroa* group discussed above. The name *clavatum* is presently restricted to this group, because of uncertainty as to the homologies of the various female androconial organs reported in Nymphalinae. However, it is expected that the similar structures present in Neotropical heliconiines and the above-mentioned Indo-Australian genera will, with detailed morphological and histological study of freshly caught specimens, prove to be homologous with clavata. In this case the term will become available for use in broader discussion of female androconial organs in these nymphaline groups (and possibly still others).

DISCUSSION

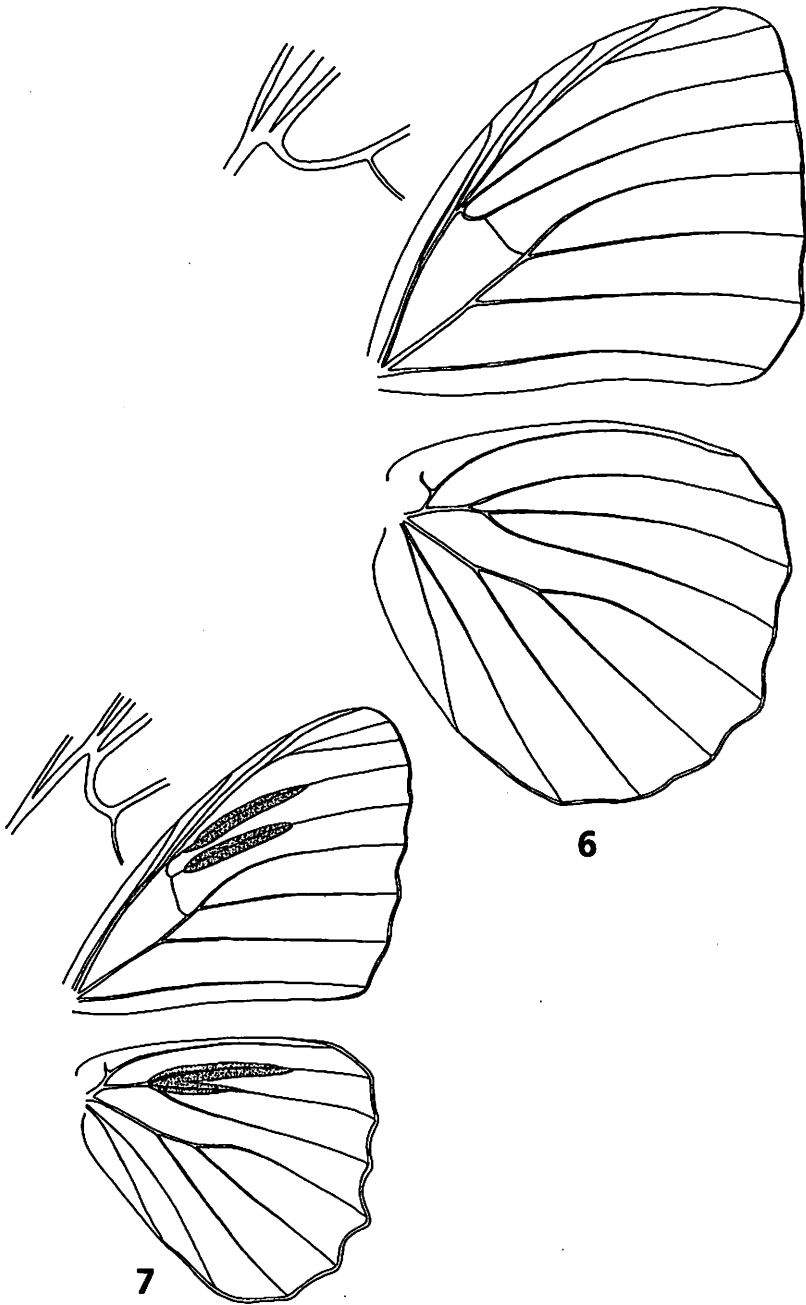
Müller (1878) was apparently the first author to observe, fully describe, and illustrate the lateral, club-like heliconiine female androconial organs, which he termed “stink-clubs,” and which he noted were associated with a bright yellow dorsal gland. He pointed out that the latter has a dorsal median furrow and is quickly exposed if a female *Heliconius* is captured. He found that the presence of the stink-clubs indicated the close relationships between heliconiine genera, and that they also exhibited clear morphological differences between species. Müller stated that he had not located stink-clubs in any other Lepidoptera he had studied. Müller (1877) had previously recorded that the odor produced from the female gland is rather nauseating and is exactly similar to a smell originating from yellowish glands in valvae of the males. The latter glands are invariably exposed by opening the valvae when males are captured. In his detailed study of the stink-clubs Müller noted, by cutting off their apices, that these knobbed, androconia-bearing portions are responsible for dispersing the strong smell. Eltringham (1925) also studied heliconiine stink-clubs in detail, including their histology, on the basis of field observations and fresh specimens provided by Dr. Withycombe from Trinidad. He concurred with Withycombe’s conclusions that the organs and glands were of “repugnatorial” function, producing an odor like the phenylcarbylamine-like smell of the male valval glands.

Emsley (1963) pointed out (with figures) that female Neotropical Heliconiini possess a pair of “ventro-lateral processes developed from the posterior margin of the eighth segment which project dorsally.” He stated that, as the abdomen tip is bent downwards, the heads of these clubs are withdrawn from the dorsal glands. The latter comprise a medianly divided structure developed from the dorsal membrane separating segments 8 and 9. They form a pair of highly infolded cuticular pouches whose lining is presumably secretory, and which are capable of eversion (inflation) by hydraulic pressure: if the abdomen is lightly squeezed, instead of being hidden “internal” pouches, the dorsal glands become exposed from beneath the 8th tergite and form 2 visible yellow dome-like structures (personal observation of live North American Gulf Fritillary, *Agraulis vanillae* [Linnaeus, 1758]). Emsley also noted that, during copulation, the lateral clubs fit into grooves on the inner lamina of the male valvae. Emsley (1963, 1965) found that there is specific variation in the *Heliconius* female “abdominal processes” and their androconia, and the sculpturing of the surface of the dorsal glands. In the latter work he maintained of the clubs that these “captitate processes” are one of a key group of features by which Heliconiinae could be defined.

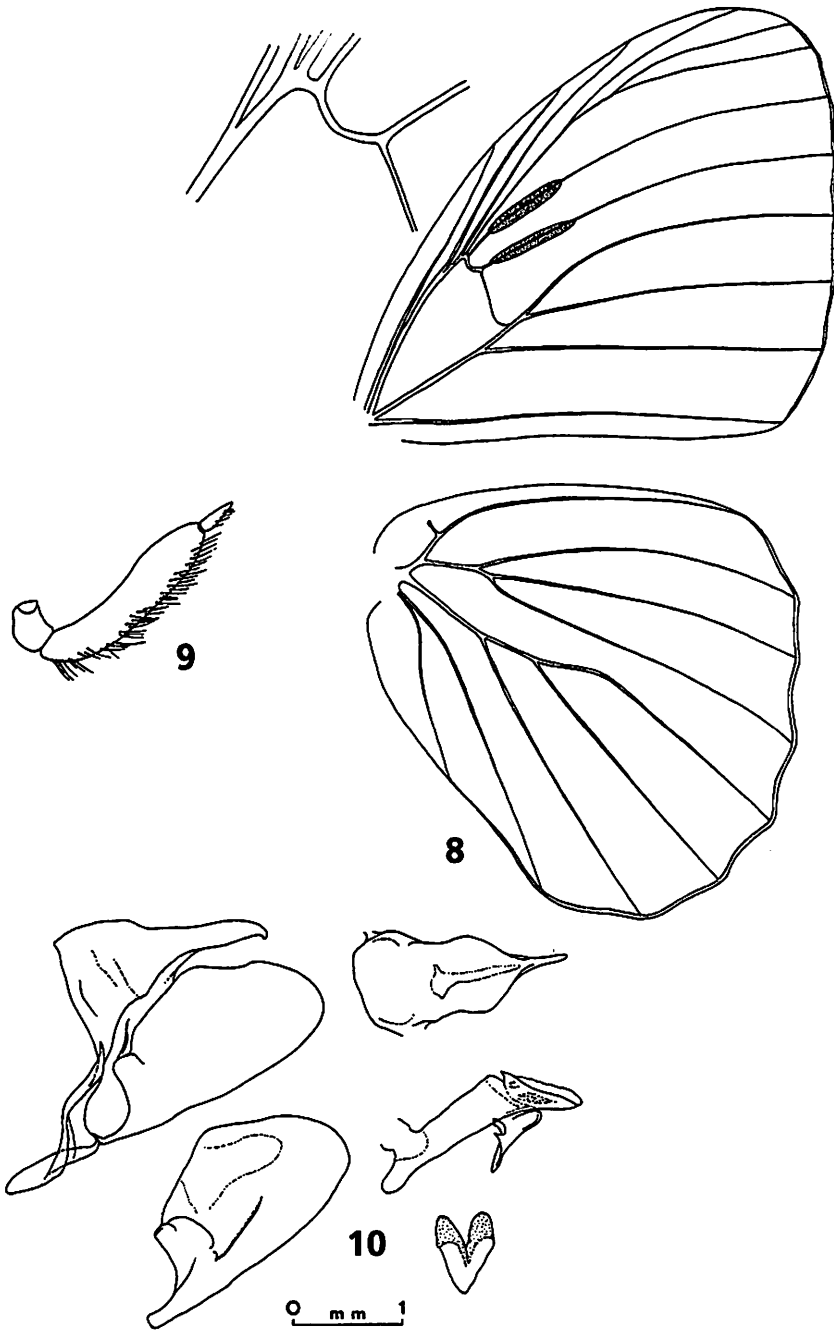
Gilbert (1976) found that the stink-clubs function to transfer a chemical from the male valval glands to the female dorsal glands. The resulting “antiaphrodisiac” pheromone (absent in virgin females) then serves to repel males after females have mated and, therefore, helps to enforce



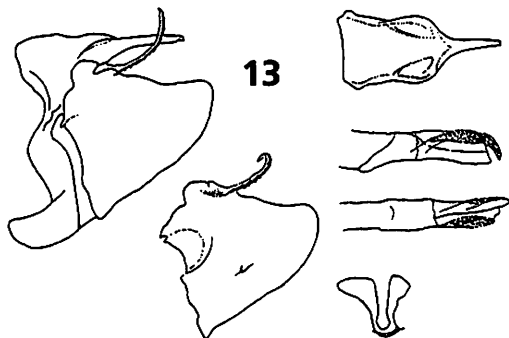
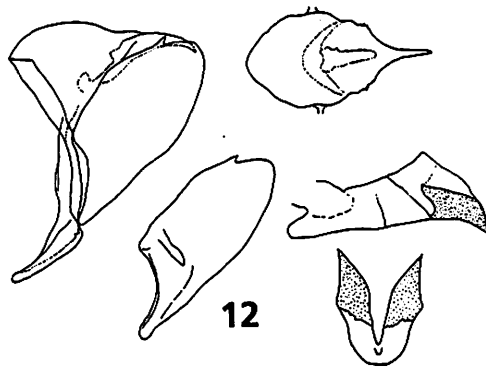
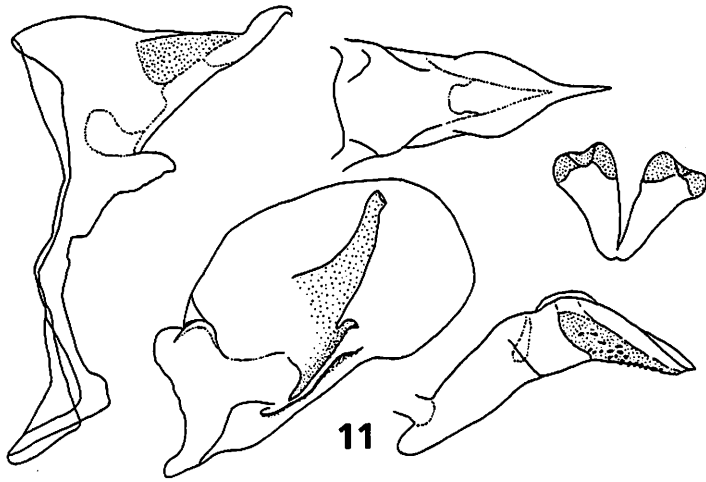
Figs. 1-5. Wing venation: 1, *Erycinidia hemileuca* hindwing; 2, *Erycinidia maudei* hindwing; 3, *Erycinidia virgo* hindwing; 4, *Erycinidia ducis* hindwing; 5, *Cirrochroa aoris* (Bhutan) (sex-brands between hatches) with forewing cell apex detail.



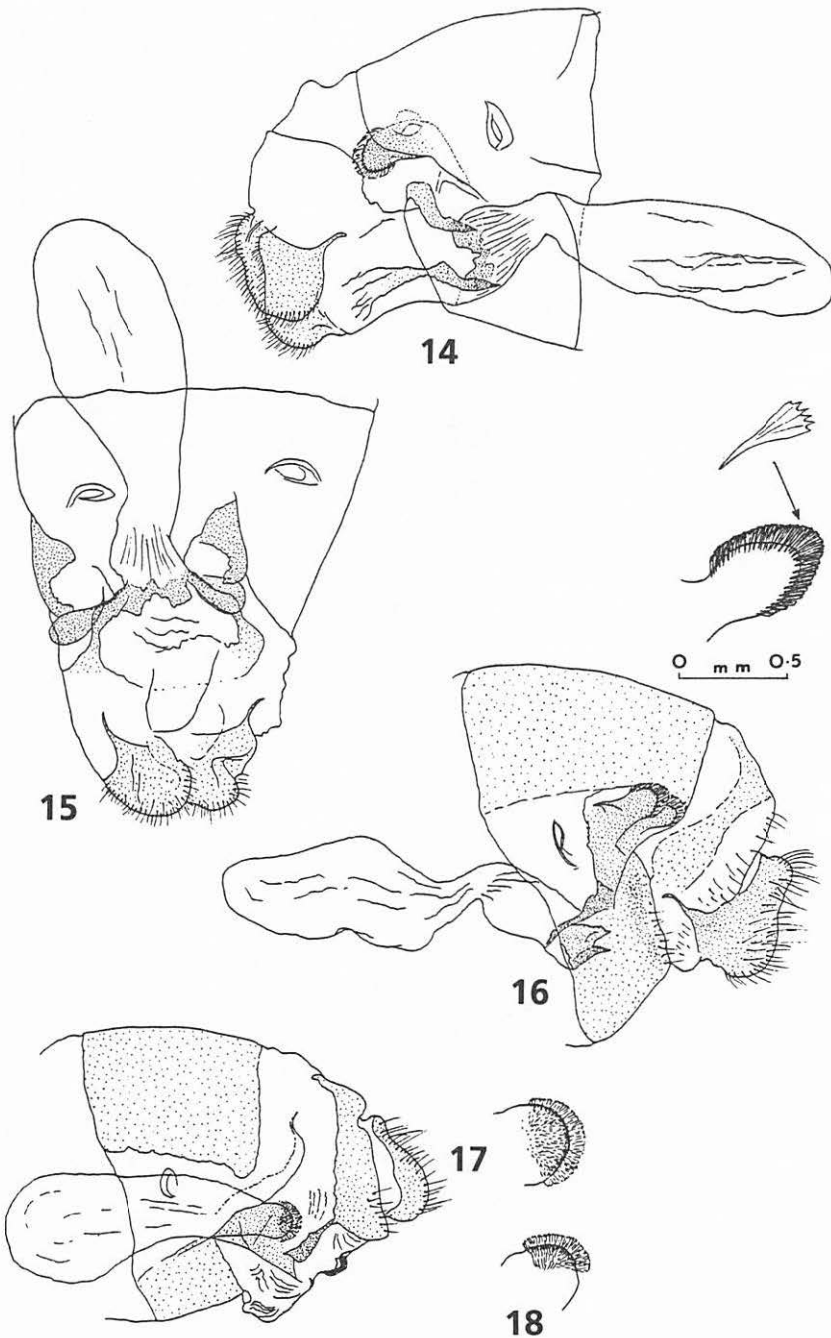
Figs. 6-7. Wing venation: 6, *Cupha prosope* (Papua New Guinea) with forewing cell apex detail; 7, *Algia fasciata* (Thailand) with sex-brands and forewing cell apex detail.



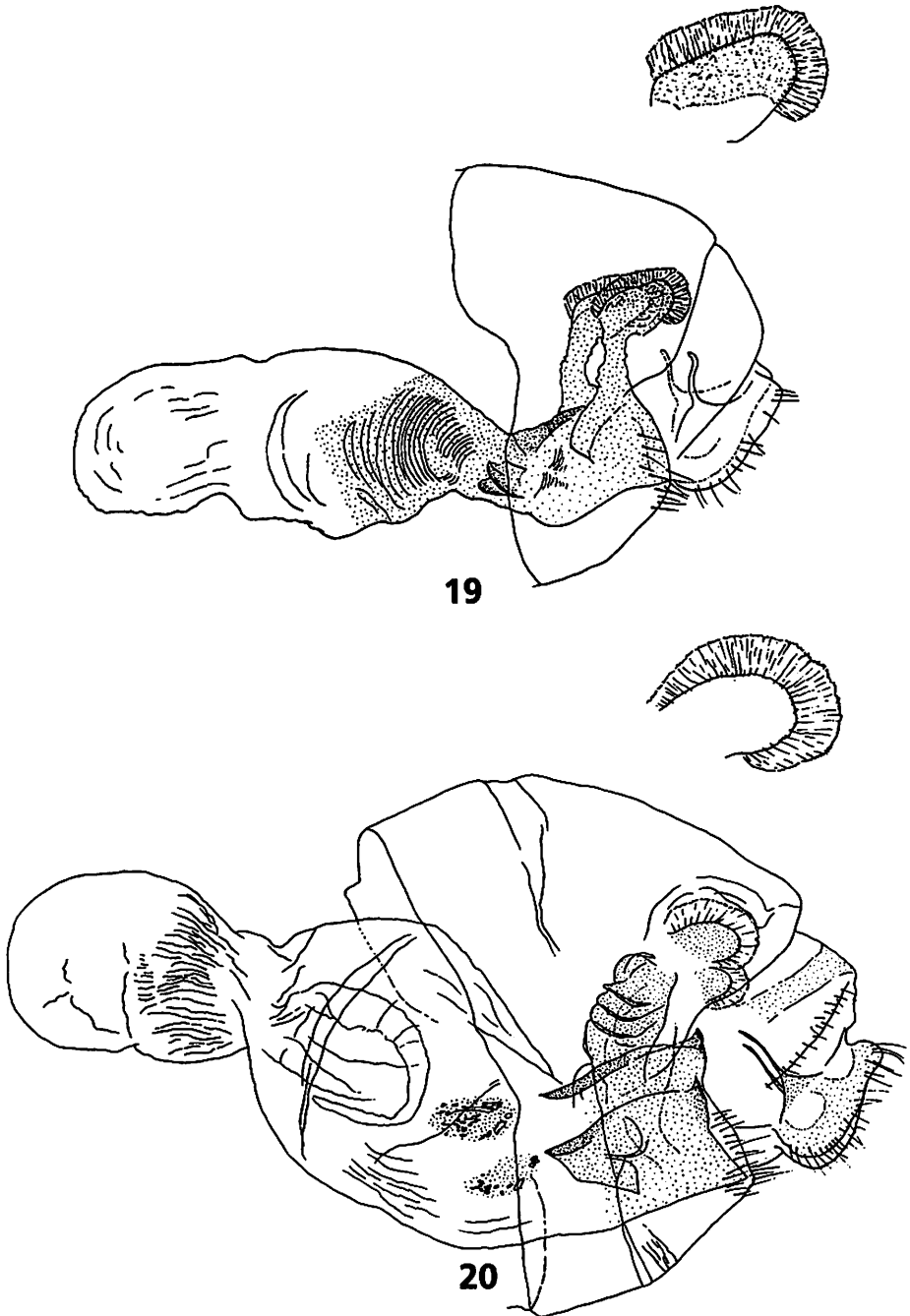
Figs. 8-10. *Algiachroa woodfordi*: 8, wing venation, sex-brands and forewing cell apex detail; 9, labial palpus (to same scale as forewing cell apex detail in Fig. 5); 10, male genitalia.



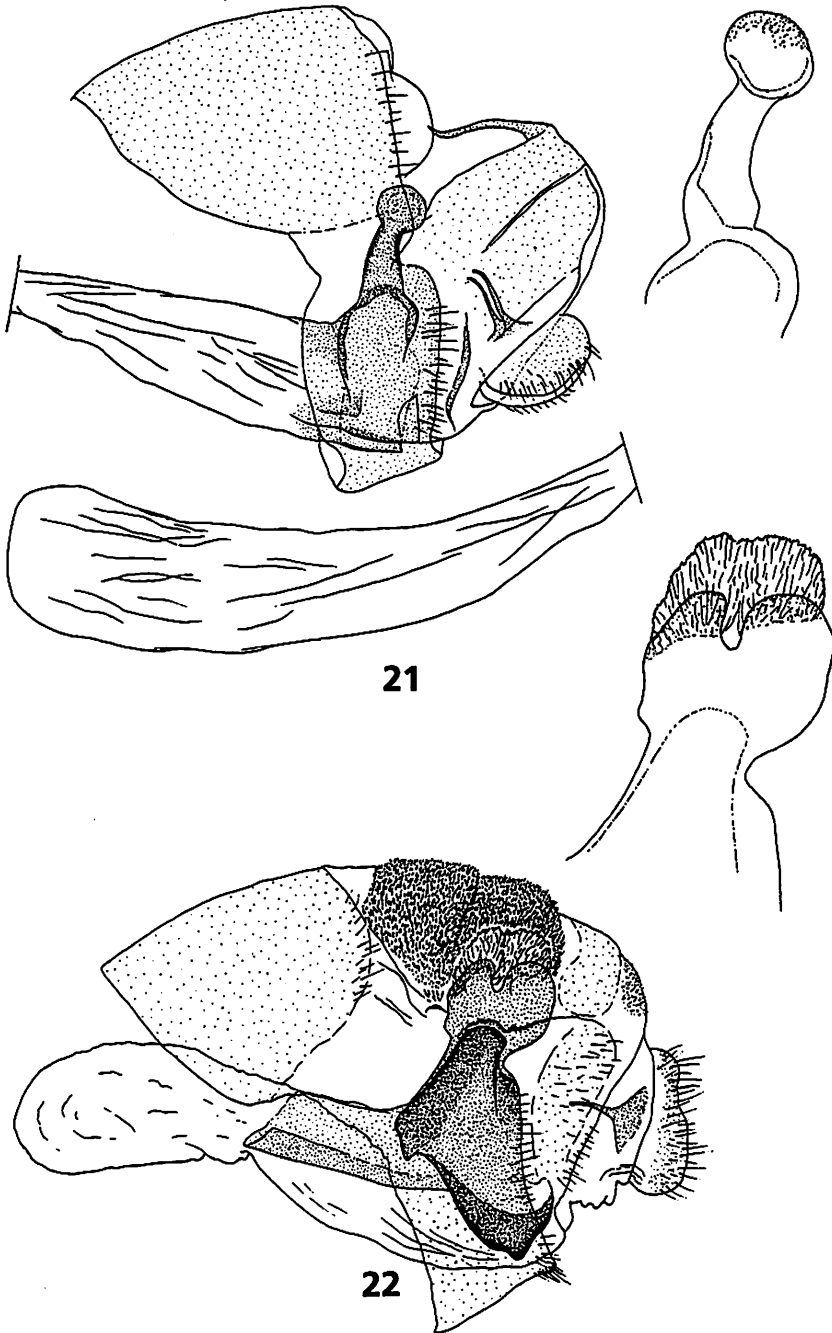
Figs. 11-13. Male genitalia: 11, *Cirrochroa regina* (Papua New Guinea); 12, *Algia felderi* (Papua New Guinea); 13, *Cupha melichrysos* (New Ireland).



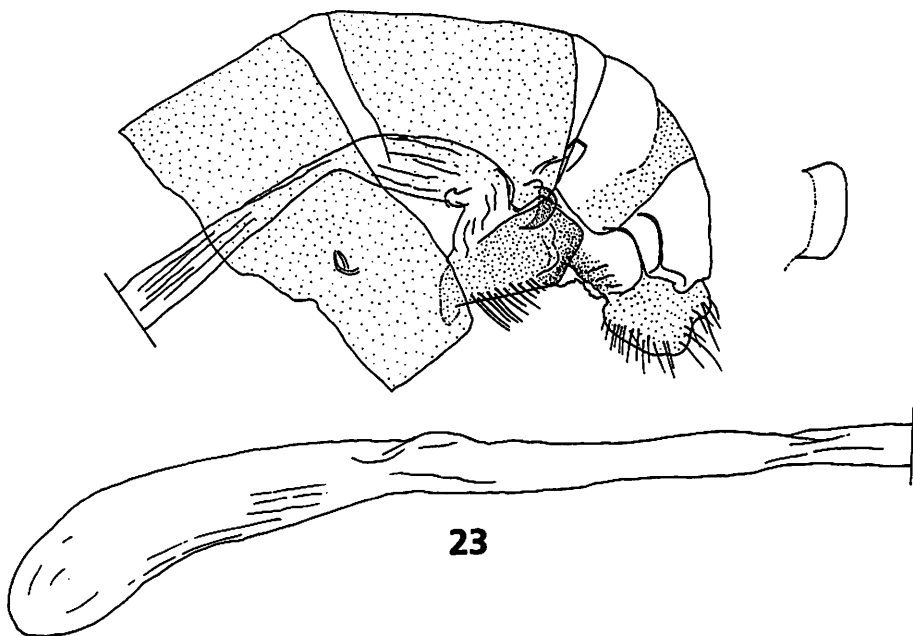
Figs. 14–18. Female genitalia and details of clavata: 14, *Algiachroa woodfordi* lateral aspect (from right-hand side); 15, *A. woodfordi* same specimen ventral aspect; 16, *A. woodfordi* another specimen lateral aspect (from lefthand side) with detail of one androconial scale; 17, *Algia felderi*; 18, *Algia fasciata* (clavatum only).



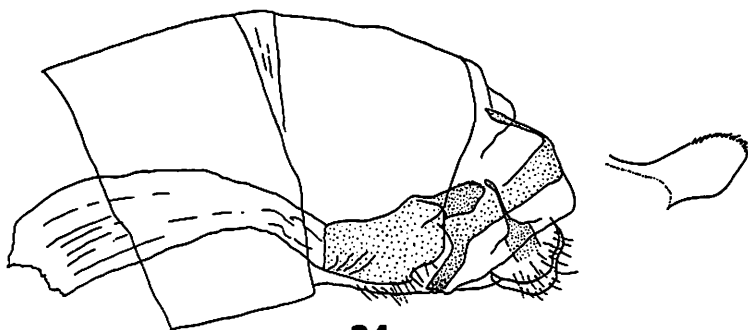
Figs. 19–20. Female genitalia and details of androconial organs: 19, *Cirrochroa aoris*; 20, *Cirrochroa regina*.



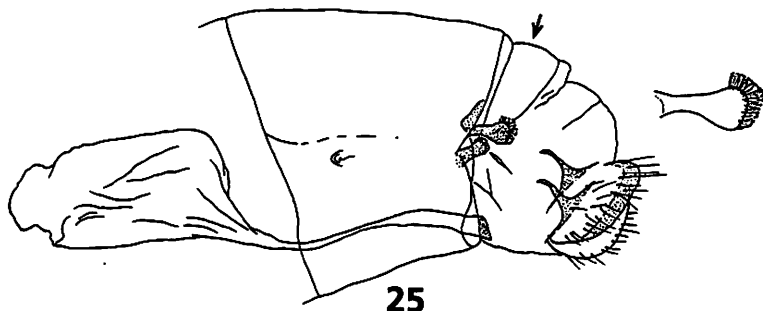
Figs. 21-22. Female genitalia and details of androconial organs: 21, *Terinos alurgis* (Papua New Guinea); 22, *Lachnoptera iole* (Uganda).



23



24



25

Figs. 23–25. Female genitalia and details of androconial organs: 23, *Cupha melichrysos*; 24, *Phalanta alcippe* (Papua New Guinea) (corpus bursae incomplete, but otherwise as long as in *C. melichrysos* above); 25, *Heliconius charitonius* (Jamaica), arrow indicates position of dorsal gland.

monogamy among females. It is still not clear, however, whether the antiaphrodisiac is wholly produced by the male, with some transferred to the female via the stink-clubs for storage in the sponge-like dorsal gland and subsequent use, or whether it is a similar but chemically different compound produced continuously by the female dorsal glands after mating, once an activating (or "trigger") chemical has been received from the male via the stink-clubs. Possibly it is the latter, as Gilbert found that males can tolerate the presence of each other, but that they will disperse in seconds if groups resting on female pupae are presented with the abdomen of a mated female of their species. He noted that the postmating female odor is strong and is said to resemble phenylcarbylamine, or witch hazel. Scott (1973) stated that the female's mate-repelling odor is developed about 1 hour after mating.

In a review of the literature on chemical interactions between butterflies Boppré (1984) reported that Urbahn (1913) and Götz (1951) had both described 2 small glandular sacs present in the female of the European Silver-washed Fritillary, *Argynnis paphia* (Linnaeus, 1758). These are situated in a similar position to the above-mentioned heliconiine dorsal glands, but there are no associated androconial clubs present (personal observation of dissected material). Boppré reported that Treusch (1967) observed that the glands were visibly exposed to an approaching male by bending the abdomen, the tip of which was always kept directed towards the male. Therefore, in this case, the glands are assumed to be a signal of the female's receptivity before copulation (i.e., a converse effect to that reported for the dorsal glands of *Heliconius*). Urbahn also located dorsal glands in members of several other argynnine genera.

Scott (1986) stated that females of the argynnine genus *Speyeria* Scudder, 1872, and of the genus *Nymphalis* Kluk, 1802 (Nymphalini), also have similar dorsal glands. C. Häuser (pers. comm. 1988) pointed out that von Siebold (1838) had termed female abdominal glands "glandulae odoriferae," and that Petersen (1900) and Weidner (1935) located dorsal abdominal glands in 5 European species of *Vanessa* Fabricius, 1807. C. Häuser (in prep.) discovered that dissected fresh females of the European argynnine nymphalid genera *Melitaea* Fabricius, 1807, and *Euphydryas* Scudder, 1872, and some European satyrine nymphalid genera, such as *Erebia* Dalman, 1816, also bear dorsal glands. Newly discovered paired sub-anal papillary glands in Acraeinae by Pierre (1986) are apparently not homologous with Nymphalinae glands under consideration here. However, they may be similar in function and were stated by Pierre to provide important morphological characters. In a review of mating in butterflies Scott (1973) pointed out that *Gonepteryx rhamni* (Linnaeus, 1758) (Pieridae) females produce repellent pheromones from abdominal glands that are extruded during rejection posture, but not during successful courtship.

It is likely that the female nymphaline clavatum will present an important morphological character for use in nymphalid classification and systematics. The clavatum, and other associated structures, such as the dorsal gland, should be employed in the character sets of future cladistic studies of the Nymphalidae.

The apparent relationship between the New World Neotropical Heliconiini and Old World Indo-Australian *Cethosia* has been suggested in the literature for a long time (e.g., Clark 1927). Shirōzu & Saigusa (1973) regarded the Argynninae as a subfamily that includes not only many Holarctic genera but also several Oriental and Afrotropical genera, such as *Phalanta* and *Cirrochroa*. Scott (1985) found that he could draw no conclusions as to the tribal evolution within the Nymphalinae, except for the close relationship between the Heliconiini and the Argynnini. He noted that groups such as the Biblidini, Eurytelini, Limenitidini, Marpesiini, etc., may not even be valid phenetically. Scott also commented that, on the basis of various characters (humeral vein, larval head horns, and passifloraceous [or other] foodplants), *Vindula*, *Cethosia*, *Terinos*, and other Oriental "Argynnini" should probably be combined into 1 tribe: Heliconiini (by priority). This is because, on a worldwide basis, the 2 tribes cannot be sustained because of the inconsistency of these features. Scott added that it remains to be seen whether this

combination is a monophyletic group or not. Eliot (in Corbet & Pendlebury 1978) regarded the genus *Cethosia* as being the sole representative of the "Cethosiini (Heliconiinae)" in the Oriental Region. He also included various genera (*Cupha*, *Phalanta*, *Vagrans*, *Vindula*, *Cirrochroa*, *Algia*, *Terinos*, and *Argyreus*) in the subfamily Argynniinae. Ackery (1984) employed only the subfamily Heliconiinae in his classification of the Nymphalidae. He pointed out that Brown (1981) had suggested that Old World passifloraceous-feeding *Cethosia* and *Vindula* should be more correctly placed in the Heliconiinae, and that the heliconiines will probably prove to represent a highly specialized subgroup of the Argynnini. However, Ackery (1988) used, as subfamilies, both Heliconiinae and Argynniinae, noting that records for passifloraceous foodplants are common to both groups.

Within the Nymphalidae clavata, or similar organs, are apparently absent in the following: Danainae (from figures and text in Ackery & Vane-Wright [1984]); Acraeinae (from figures and text in van Son [1963], and Pierre [1986]); genera of the Nymphalini, such as *Vanessa* (from figures and text in Field [1971]); *Doleschallia*, and Australian Region Satyrinae, such as *Platypthima* Rothschild & Jordan, 1905, and *Altiapa* Parsons, 1986 (all the latter from personal observation of dissected material; see also Parsons [1986b]). Probably all other Australian Region Satyrinae also lack such organs (from figures and text in Holloway [1974]). From these observations—together with the apparent synapomorphy with the androconial organs in *Heliconius*, and at least the above-mentioned Indo-Australian genera that possess them—it appears that the organ is a good indicator of a natural grouping within the Nymphalidae. It is unlikely that such a specialized organ, of sexual function, has evolved independently in Old and New World nymphalids, especially as only certain genera of the Nymphalidae (of all the butterflies) possess them. Nevertheless, the reduction and loss of these organs (if once present in an ancestor common to all of the modern-day androconial organ-bearing genera) is possible, as illustrated by their apparent reduction across the *Cupha* group genera (*Phalanta*, *Cupha*, and *Vagrans*), and their absence in supposedly heliconiine genera such as *Cethosia* and *Vindula*. However, whether or not the androconial organ-bearing genera should all be treated as belonging to the tribe Heliconiini is still open to question. Nevertheless, the present findings also suggest that genera such as *Algiachroa*, *Algia*, *Cirrochroa*, *Terinos*, and *Lachnoptera* might now be regarded as true heliconiines; also that other characters must be sought to resolve the tribal relationships of *Cethosia* and *Vindula*.

Regarding the problem of the tribal relationships of *Cethosia* and *Vindula*, it is unfortunate that the dorsal glands often present in androconial organ-bearing nymphalid females are not easily observable in vial (glycerol) or slide genitalic preparations. For example, their presence or absence in females of nearly all of the above-mentioned genera could not be easily confirmed from the vial preparations of abdomens used in this study (although the well-defined, androconia-bearing dorsal glands are obvious in *Lachnoptera*, Fig. 22). It is probably best, therefore, if their presence or absence is confirmed by squeezing the abdomens of live females, as dorsal glands, if present, will provide a further useful character for defining nymphalid relationships, even though they are apparently present in Nymphalinae (Nymphalini, Heliconiini, Argynnini), Satyrinae, and the unrelated family Pieridae.

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