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A GENERIC REVISION OF THE HELICONIINAE (LEPIDOPTERA, NYMPHALIDAE)

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The Heliconiinae is a New World subfamily of brilliantly colored butterflies which may be recognized by the large heads, elongate forewings, and particularly by the simple humeral vein of the posterior wing, curved anteriorly toward the wing base. All the genera are primarily Neotropical, and known larvae are spiny forms feeding on *Passiflora*.

The classification here proposed for this subfamily is based on a study of rather numerous morphological characters. In the past much emphasis has been placed on a few features such as the silver spotting, claw structure, etc. On the basis of the closed discal cell of the posterior wings, *Heliconius* (with *Eueides*) has frequently been regarded as constituting a subfamily distinct from the other genera here included. In view of the very few other characters correlated with this closed cell, however, it seems best to recognize the Heliconiinae in a broad sense, including such genera as *Dryas* and *Dione*.

The male genitalia have provided numerous characters correlated with other features and are of value in separating the genera and indicating their interrelationships. The harpés are figured, therefore, for each genus. The term costa is used for the dorsal area of each harpé, usually separated from the remainder by a groove on the outer surface. The lower margin of each harpé is curled to form the sacculus (not visible in figures) while the area intervening between the costa and the sacculus is termed the cucullus.

KEY TO THE GENERA OF HELICONIINAE

1.—Discal cell of posterior wing closed (Fig. 1);

¹ I wish to thank Mr. Wm. P. Comstock and Dr. A. B. Klots for their helpful suggestions concerning this paper.

- scales of wing fringes interspersed with simple setae. *Heliconius*.
Discal cell of posterior wing open (Figs. 2 and 3); fringes of wings consisting entirely of elongate scales. 2.
- 2.—Anal vein of anterior wing terminating basad of tornus, vein Cu₂ terminating at tornus (Fig. 2); base of M₂ of posterior wing transverse (Fig. 2) *Podotricha*.
Anal vein of anterior wing terminating at tornus, Cu₂ anterior to tornus (Fig. 3); base of M₂ of posterior wing oblique. 3.
- 3.—Sc of forewing ending little if any beyond apex of discal cell (Fig. 8); wings with pale areas green. *Philaethria*.
Sc of forewing ending considerably beyond apex of discal cell (Figs. 3 to 7); wings with pale markings orange. 4.
- 4.—Forewing with margin markedly angulate at apex of M₂; middle and posterior femora conspicuously hairy; M₃ of anterior wing at a distinct angle to m-cu. *Dione*.
Forewing with outer margin evenly curved or sinuate; middle and posterior femora merely scaled; M₃ of anterior wing continued almost without an angle as m-cu. 5.
- 5.—Claws without large basal seta; arolium reduced; M₂ of forewings arising behind angle in distal end of cell (Figs. 6 and 7) *Agraulis*.
Claws each with large basal seta beneath; arolium large; M₂ of forewings arising at or in front of angle in distal end of cell (Figs. 3 and 5) 6.
- 6.—Costal cell of posterior wing much narrower than cell R₁; M₃ of anterior wing scarcely bent beyond discal cell (Fig. 5); androconia not evident on wings. *Dryadula*.
Costal cell of posterior wing about as wide as cell R₁; M₃ of anterior wing strongly bent beyond discal cell (Fig. 3); forewing with black androconia along veins in male *Dryas*.

HELICONIUS KLUK

Figures 1, 4, 13, 14 and 15

Heliconius KLUK, 1802, *Zwierz. Hist. nat. pocz. gospod.*, IV, p. 82. Type: *Papilio charithonia* Linnaeus, 1767, designated by Hemming, 1933, *Entom.*, LXVI, p. 223.

Ajantis HÜBNER, 1816, *Verz. bekannt.*

Schmett., p. 13. Type: *Papilio sapho* Drury, 1782, designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 106.

Apostrophia HÜBNER, 1816, Verz. bekannt. Schmett., p. 13. Type: *Papilio charithonia* Linnaeus, 1767, designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 116.

Eueides HÜBNER, 1816, Verz. bekannt. Schmett., p. 11. Type: *Nereis dianasa* Hübner, [1806], designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 169.

Migonitis HÜBNER (not Rafinesque), 1816, Verz. bekannt. Schmett., p. 12. Type: *Papilio erato* Linnaeus, 1764, designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 218.

Sicyonia HÜBNER, 1816, Verz. bekannt. Schmett., p. 13. Type: (*Sicyonia thamar* Hübner, 1816) = *Papilio rhea* Cramer, designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 268.

Sunias HÜBNER, 1816, Verz. bekannt. Schmett., p. 12. Type: *Papilio melpomene* Linnaeus, 1758, designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 271.

Heliconia LATREILLE, 1820, in Latreille and Godart, Ency. Méth., IX, p. 203. Type: *Papilio charithonia* Linnaeus, 1767, designated by Hemming, 1933, Entom., LXVI, p. 223.

Laparus BILLBERG, 1820, Enum. Ins. in Mus. Blg., p. 77. Type: *Papilio doris* Linnaeus, 1771, designated by Hemming, 1934, Entom., LXVII, p. 37.

Phlogris HÜBNER, [1825], Sammlung Exot. Schmett., II, Pl. cckviii. Type: *Papilio melpomene* Linnaeus, 1758 (monobasic).

Semelia DOUBLEDAY, 1844, List Spec. Lepid. Ins. Brit. Mus., I, p. 64. Type: *Cethosia vibilia* Latreille, [1820], designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 267.

Blanchardia BUCHECKER, 1876, Syst. Ent., Pl. LI. Type: (*Blanchardia dismorphia* Buchecker, 1876) = *Heliconius hecuba choarina* Hewitson (monobasic).

Antennae variable in length and in breadth of club; tarsal claws with seta arising at base of each; arolium large; middle and posterior femora not hairy. Forewing with outer margin convex, not angulate; Sc ending far beyond apex of discal cell; R₁ usually arising basad of apex of discal cell but sometimes (*Semelia*) distad of it; M₂ arising near angle in apex of discal cell; M₃ scarcely bent beyond discal cell and at an angle to m-cu; first abscissa of Cu₁ usually at least twice as long as m-cu; posterior apical angle of discal cell about as far from wing base as anterior apical angle; vein Cu with basal spur; vein A ending at tornus. Posterior wing considerably longer than broad; discal cell closed; costal cell variable in width; vein Sc + R₁ gently

arcuate to subsinuate, free from R, almost to wing base. Fringe of wings rather short, its scales intermixed with setae; androconia absent along wing veins. Male genitalia with costal area of harpé large, often larger in lateral view than remainder of harpé; apex of cucullus usually extending but little beyond costa.

The butterflies here included in the genus *Heliconius* have commonly been separated on the basis of the length of the antennae into two genera, *Heliconius* and *Eueides*. It is usually stated that in *Heliconius* the antennae are more than half as long as the costal margin of the forewing, while in *Eueides* they are less than half as long. However, a complete series of intergrading lengths can be found from the species usually placed in *Eueides* through species such as *Heliconius aoede*, *sara*, *antroches* and *sapho* to the forms with very long antennae. Indeed, *H. charithonia*, the type species of *Heliconius*, has antennae only about half as long as the costal margin of the forewing. However, it appears to be possible to divide *Heliconius* into three subgenera as indicated below:

- 1.—Forewing with vein R₁ arising considerably basad of apex of discal cell (Fig. 1) 2.
Forewing with vein R₁ arising close to or even beyond apex of discal cell (Fig. 4);
cucullus of male genital harpé attenuated
and acutely pointed at apex (Fig. 14)
..... *Semelia*.
- 2.—Cucullus short and broadly rounded at apex
(Fig. 13) *Heliconius*.
Cucullus bidentate, lower point attenuated
and acute (Fig. 15) *Eueides*.

The subgenus *Heliconius* includes all the forms formerly placed in the genus *Heliconius*, and, in addition, *Eueides ricini* (Linnaeus) which has longer antennae than the other species usually included in *Eueides*. The subgenus *Semelia* includes the species usually placed in *Eueides* except *ricini* (Linnaeus), *isabella* (Cramer), *dianasa* (Hübner) and *cleobaea* (Geyer), the last three of which fall in *Eueides*. Thus, the species falling in *Heliconius* subgenus *Semelia* are *lampeto* (Bates), *edias* (Hewitson), *procula* (Doubleday), *vibilia* (Latreille), *aliphera* (Godart), *lybia* (Fabricius), *olympia* (Fabricius), *tales* (Cramer), *eanes* (Hewitson), etc.; those falling in *Heliconius*

conius subgenus *Eueides* are *dianasa* (Hübner), *isabella* (Cramer) and *cleobaea* (Geyer); while those in *Heliconius* subgenus *Heliconius* are the many species previously included in *Heliconius* and, in addition, *ricini* (Linnaeus).

Eueides and *Semelia* are forms with short antennae and similar male genitalia, although the middle tooth of the harpé (upper tooth of the cucullus) is large in *Eueides*, small to absent in *Semelia* (and always absent in *Heliconius*). Furthermore, the upper tooth of the harpé (the apex of the costa) is heavy in *Eueides*, slender in *Semelia*, and slender in the few *Heliconius* in which it is elongated. The wing venation of *Eueides* agrees with that of *Heliconius* rather than with that of *Semelia*. The discal cell of the forewing in *Semelia* is about half as long as the wing; in *Eueides* and most *Heliconius* it is more than half as long as the wing.

The genus *Heliconius* contains about eighty-five species, many of which are divided into numerous subspecies. It ranges from southern Florida southward throughout the Neotropical region.

Useful revisional papers on the genus are by Stichel and Riffarth (1905), Stichel (1906) and Eltringham (1916).

PHILAETHRIA BILLBERG

Figures 8 and 9

Philaethria BILLBERG, 1820, Enum. Ins. in Mus. Blg., p. 77. Type: *Papilio dido* Clerck, 1764, designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 248.

Metamandana STICHEL, 1907, Gener. Ins., LXIII, p. 6. Type: *Papilio dido* Clerck, 1764, by original designation.

Metamorphia auct., not Hübner [1818].

Antennae rather short, club at least three times as long as broad; tarsal claws each with thick seta arising at base beneath; arolium large; posterior tarsi as long as tibiae; middle and posterior femora not hairy. Forewing with outer margin not angulate, slightly concave medially; Sc ending near apex of discal cell; R₁ arising basad of apex of discal cell; M₂ arising in front of angle in distal end of discal cell; M₃ strongly bent beyond discal cell and at base almost in line with m-cu; first abscissa of Cu much longer than m-cu; posterior

apical angle of discal cell nearer base of wing than anterior apical angle; Cu with basal spur; vein A reaching tornus. Posterior wings nearly as broad as long; discal cell open; costal cell midway its length nearly as broad as cell R₁; vein Sc + R₁ gently curved. Fringe of wings rather short, consisting entirely of scales; androconia absent along wing veins. Male genital harpé with costa large, terminating in finely spiculate, broadly rounded enlargement; cucullus slender, concave basally, terminating in long, slender, upturned process.

This genus contains a single, large, green and black species, *P. dido* (Clerck). It has often gone under the name *Metamorphia*, but that name must be applied to another genus not included in the Heliconiinae (see Hemming, 1934).

PODOTRICHA, NEW GENUS

Figures 2 and 11

GENOTYPE.—*Colaenis euchroia* Doubleday, 1848.

Antennae of moderate length, club more than three times as long as broad, tarsal claws with heavy seta arising at base of each; arolium large; middle and posterior femora exceedingly hairy. Forewing slender; outer margin angulate at apex of cell M₂, broadly concave behind that point as in *Dione juno*; Sc ending well beyond apex of discal cell; R₁ arising at apex of discal cell; M₂ arising anterior to angle in distal end of discal cell; M₃ gently arcuate beyond discal cell, base at distinct angle to m-cu; first abscissa of Cu longer than m-cu; posterior apical angle of discal cell at least nearly as far from wing base as anterior apical angle; vein Cu with small basal spur; vein A ending much basad of tornus. Posterior wings considerably longer than broad; discal cell open; costal cell in middle about one-fourth as wide as cell R₁; vein Sc + R₁ almost straight, not sinuate. Fringes of wings short, consisting entirely of elongate scales; androconia absent or inconspicuous along wing veins. Male genital harpé broad and short with costa small, not well separated from cucullus, the apex of which is rounded, sometimes slightly serrate, extending somewhat beyond apex of costa.

Colaenis telesiphe Hewitson is also a member of this genus. *Podotricha euchroia* and *P. telesiphe* have usually been placed in *Colaenis*, or more recently in *Dryas*, together with *Dryas iulia* (Fabricius) and *Dryadula phaetusa* (Linnaeus). *Podotricha*, however, is one of the most distinctive genera of the Heliconiinae. Unlike other

genera of this subfamily, vein A of the forewing ends far before the posterior apical angle or tornus, which is supported by Cu_2 and the base of vein M_2 of the posterior wing is transverse. The hairy femora and the shape of the forewings suggest *Dione*, a genus lacking the large seta beneath the base of each claw.

DRYAS HÜBNER

Figures 3 and 12

Dryas HÜBNER, [1807], Sammlung Exot. Schmett., I, Pl. XLIII. Type: *Papilio iulia* Fabricius, 1775, designated by Hemming, 1934, Entom., LXVII, p. 156.

Colaenis HÜBNER, [1819], Verz. bekannt. Schmett., p. 32. Type: *Papilio iulia* Fabricius, 1775, designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 146.

Antennae of moderate length, club more than three times as long as broad; tarsal claws each with slender seta arising at base; arolium large; middle and posterior femora not hairy. Forewing with outer margin concave, not angulate; Sc ending far beyond apex of discal cell; R_1 arising basad of apex of discal cell; M_2 arising at or in front of angle in apex of discal cell; M_3 strongly bent beyond apex of discal cell, at a distinct angle to m-cu; first abscissa of Cu_1 longer than m-cu; anterior and posterior distal angles of discal cell about equidistant from wing base; Cu with basal spur. Posterior wings little if any longer than broad; discal cell open; costal cell at middle about equal in width to cell R_1 ; Sc + R_1 subsinuate. Fringes of wings rather short, consisting of elongate scales; androconia present along veins of forewing in male. Male genital harpé with costa large, almost reaching apex of cucullus, apices of both parts simple.

This genus contains a single species, *iulia* (Fabricius), which is widely distributed in the Neotropical region. Until recently this species has ordinarily been placed in *Colaenis* with the forms here regarded as *Podotricha* and *Dryadula*.

DRYADULA, NEW GENUS

Figures 5 and 10

GENOTYPE.—*Papilio phaetusa* Linnaeus, 1758.

Antennae of moderate length, club more than three times as long as broad; tarsal claws with slender basal seta; arolium large; middle and

posterior femora not hairy. Forewing with outer margin slightly crenulate, not or scarcely concave, not angulate; Sc ending beyond apex of discal cell; R_1 arising beyond apex of discal cell; M_2 arising at or anterior to angle in distal end of discal cell; M_3 scarcely bent beyond the discal cell and base at slight angle to m-cu; first abscissa of Cu_1 longer than m-cu; posterior apical angle of discal cell little if any farther from wing base than anterior distal angle; Cu with basal spur. Posterior wings scarcely longer than broad; discal cell open; costal cell at middle about one-third as wide as cell R_1 ; vein Sc + R_1 arcuate. Fringes of wing margins unusually long, consisting of elongate scales; androconia absent on wing veins. Costa of harpé much reduced, cucullus large, apex trifid, upper process long and slender, middle broader but acute, both spiculate, lower process broadly rounded.

The single species belonging to this genus is probably more closely related to *Dryas* than to any other genus but differs in the shorter, broader wings (shorter and broader than in any other Heliconiinae), the absence of conspicuous androconia along the wing veins, the gentle curvature of M_3 beyond the discal cell, the origin of R_1 beyond the discal cell in the forewing, the narrow costal cell of the posterior wing and especially the peculiar structure of the male genitalia.

While I am strongly opposed to the recognition of numerous small genera, it seems that in this subfamily the species other than those of *Heliconius* are divisible into small units morphologically extremely distinct and deserving of generic rank, especially when viewed in connection with the huge and relatively homogeneous genus *Heliconius*. As early as 1881 Godman and Salvin suggested that *phaetusa* might well be placed in a genus different from that of *iulia*.

DIONE HÜBNER

Figure 16

Dione HÜBNER, [1819], Verz. bekannt. Schmett., p. 31. Type: *Papilio juno* Cramer, 1779, designated by Scudder, 1875, Proc. Am. Acad. Arts Sci., X, p. 157.

Antennae of moderate length, the club over three times as long as broad; tarsal claws without large basal setae, but each with a basal lobe; arolium reduced; middle and posterior femora somewhat hairy, especially basally. Forewing with

outer margin partially concave and angulate at the apex of vein M_2 ; Sc ending well beyond apex of discal cell; R_1 arising at apex of discal cell; M_2 arising behind angle in apex of discal cell; M_3 scarcely bent beyond discal cell, its base at an angle to m-cu; first abscissa of Cu_1 about equal to m-cu; posterior distal angle of discal cell farther from wing base than anterior distal angle; Cu with basal spur small; vein A reaching tornus. Posterior wings about as broad as long; discal cell open; costal cell at least two-thirds as broad in middle as cell R_1 ; vein Sc + R_1 sinuate. Fringe of wings rather short, consisting of elongated scales; androconia present on veins of both fore and hind wings in the male. Male harpé with costa nearly reaching apex of cucullus which bears slender upturned apical process.

This genus, which includes three species, *juno* (Cramer), *moneta* Hübner and *glycera* (C. and R. Felder), is found from the extreme southern United States southward through much of the Neotropical region. Stichel (1907) divided *Dione* (including *Agraulis*) into two sections, the Goniosimi for *juno* and the Strongylytopici for *moneta*, *glycera* and *Agraulis vanillae*. From the numerous morphological characters here described it is evident that this is an unnatural division based on the peculiar wing shape of *juno*. The differences between *Dione* and *Agraulis* are emphasized in the discussion of the latter genus.

AGRAULIS BOISDUVAL AND LE CONTE

Figures 6, 7 and 17

Agraulis BOISDUVAL AND LE CONTE, [1836?], Hist. Gen. lépid. Chen. Amér. Sept., p. 142. Type: *Papilio vanillae* Linnaeus, 1758 (monobasic).

Antennae of moderate length, club about two and one-half times as broad as long;

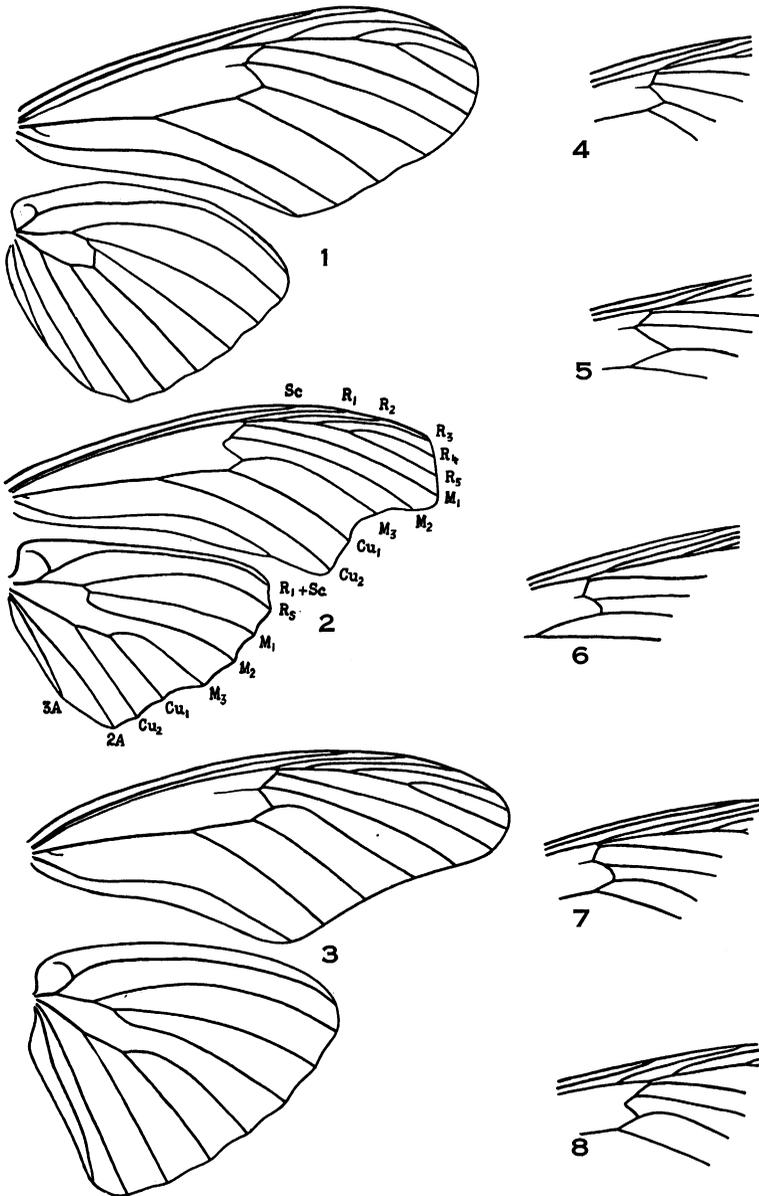
tarsal claws without basal setae but with inconspicuous basal angle or lobe; arolium reduced; femora of middle and posterior legs not hairy. Forewing with outer margin concave, not angulate; Sc ending far beyond apex of discal cell; M_2 arising behind angle in distal end of discal cell; R_1 arising at (female) or beyond (male) apex of discal cell; M_3 scarcely bent beyond discal cell, at base in line with m-cu, especially in male; first abscissa of Cu_1 equal to or shorter than m-cu in males, longer in females; posterior apical angle of discal cell farther from wing-base than anterior apical angle; vein Cu with basal spur small. Posterior wing about as broad as long; discal cell open; costal cell less than half as wide as cell R_1 , measured in middle of wing; vein Sc + R_1 arcuate. Fringes of wings rather short, composed of elongate scales; androconia present along veins of forewing in male. Male harpé with costa small, terminating far before apex of cucullus which is provided with serrate upturned apex.

This genus contains a single widespread species, *A. vanillae* (Linnaeus). While usually placed as a synonym of *Dione*, it appears to me that *Agraulis* is much more distinct from *Dione* than is *Eueides* or *Semelia* from *Heliconius*. Some of the characters separating *Agraulis* from *Dione*, in addition to those given in the key, are the shape of the antennal club and of the male genitalia; the length of the posterior tarsi, which in *Dione* are as long as the tibiae, in *Agraulis* longer; the sexual dimorphism in wing venation in *Agraulis*; the presence of an angle between the base of M_3 and m-cu in the forewing of *Dione*; and the absence of androconia on the posterior wings, the narrow costal cell of the posterior wing, and the arcuate rather than sinuate condition of Sc + R_1 of the posterior wing in *Agraulis*.

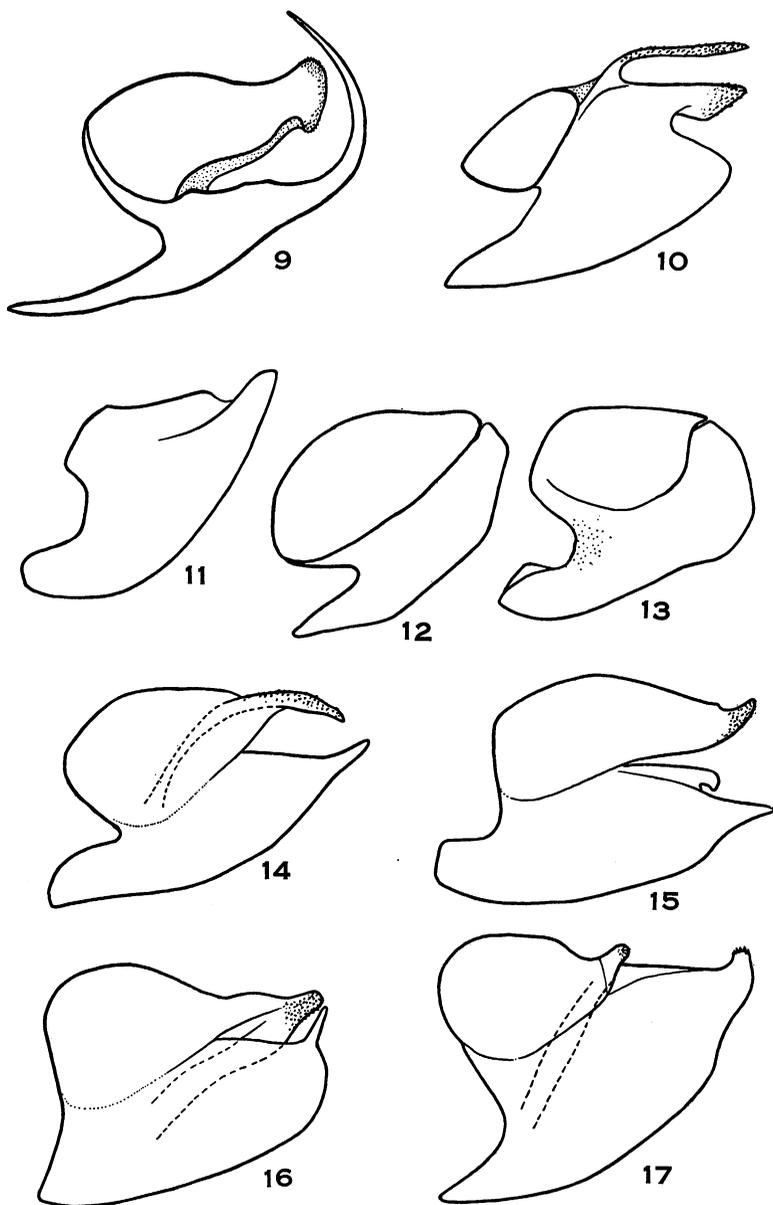
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- Fig. 1. *Heliconius (Heliconius) charithonia* (Linnaeus), fore and hind wings.
 Fig. 2. *Podotricha euchroia* (Doubleday), fore and hind wings.
 Fig. 3. *Dryas iulia* (Fabricius), fore and hind wings.
 Fig. 4. *Heliconius (Semelia) olympia* (Fabricius), region of apex of discal cell of forewing.
 Fig. 5. *Dryadula phaeusa* (Linnaeus), region of apex of discal cell of forewing.
 Fig. 6. *Agraulis vanillae* (Linnaeus), region of apex of discal cell of forewing of male.
 Fig. 7. *Agraulis vanillae* (Linnaeus), region of apex of discal cell of forewing of female.
 Fig. 8. *Philaethria dido* (Clerck), region of apex of discal cell of forewing.



- Fig. 9. *Phylaethria dido* (Clerck), lateral view of harpé.
 Fig. 10. *Dryadula phaetusa* (Linnaeus), lateral view of harpé.
 Fig. 11. *Podotricha euchroia* (Doubleday), lateral view of harpé.
 Fig. 12. *Dryas iulia* (Fabricius), lateral view of harpé.
 Fig. 13. *Heliconius* (*Heliconius*) *charithonia* (Linnaeus), lateral view of harpé.
 Fig. 14. *Heliconius* (*Semelia*) *olympia* (Fabricius), lateral view of harpé.
 Fig. 15. *Heliconius* (*Eueides*) *isabella* (Cramer), lateral view of harpé.
 Fig. 16. *Dione juno* (Cramer), lateral view of harpé.
 Fig. 17. *Agraulis vanillae* (Linnaeus), lateral view of harpé.