Clicking Butterflies, *Hamadryas*, of Panama: Their biology and identification

(*Lepidoptera: Nymphalidae*)

JULIÁN MONGE-NÁJERA

INTRODUCTION

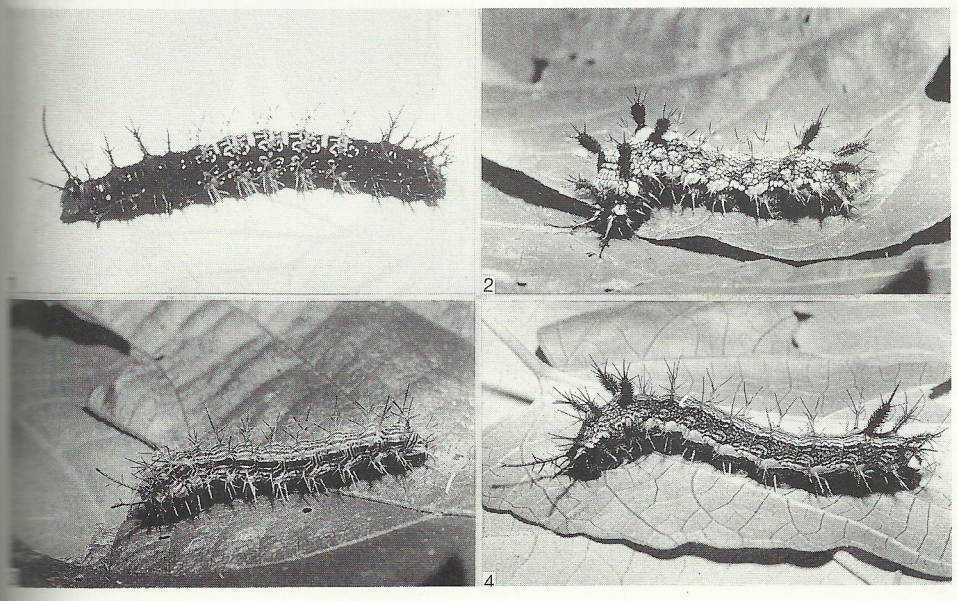
Butterflies of the genus *Hamadryas* (Hübner 1806) are well known to Neotropical field naturalists for their production of audible sound (Jenkins 1983). The phenomenon of sound emission in this genus apparently was reported for the first time by Langsdorff, who heard them in Brazil during the first decade of the 19th century (Darwin 1889). The emission of audible sound is uncommon in Lepidoptera (Monge-Nájera and Morera 1986), and *Hamadryas* is a classic example, partly because of its conspicuousness but also due to the many failed attempts to identify the acoustic mechanism (Dumortier 1963; Swihart 1967; Jenkins 1983). The study of *Hamadryas* is handicapped by the complex calico coloration of several species, which makes identification difficult (Jenkins 1983). This paper briefly reviews the natural history of *Hamadryas*, updating it with previously unpublished observations from Costa Rica, Panama, and Venezuela, and presents descriptions of and an illustrated key to the species occurring in Panama.

NATURAL HISTORY

There are basically two habitat groups of *Hamadryas* species: those of forest clearings, and those of forest canopy (Jenkins 1983). Recently, on the advice of Gilberto Barrantes, I collected *H. februa* and *H. feronia* in a mangrove in Chomes, Costa Rica, which adds a new habitat type to the list.

Eggs are laid singly or in suspended strings on species of Euphorbiaceae, particularly the vines *Dalechampia* spp. and *Tragia* spp. (Muyshondt and Muyshondt 1975*a–c*). *Hamadryas feronia* and *H. februa* show different patterns of vertical distribution of eggs (Otero 1988). The eggs are fed upon by ants and *Hamadryas* larvae (DeVries 1983).

The larvae (Figs. 36.1–36.4) that hatch from solitary eggs are solitary; those from egg clutches are gregarious (Muyshondt and Muyshondt 1975*a–c*), and may severely defoliate the host plant (Armbruster 1983). One suspects that the very spiny larvae may be distasteful, because they switch from camouflaged to aposematic coloration after the second instar (Young



Figs 36.1–36.4 Larvae of *Hamadryas* from Panama. **1**, *H. amphinome mexicana*; **2**, *H. feronia*; **3**, *H. februa*; **4**, *H. iphthime*. (Photographs by A. Aiello.)

1974; Muyshondt and Muyshondt 1975*c*). The larva of at least one species (*H. iphthime*) is an apparent mimic of an urticating lepidopteran larva (*Dirphiopsis* sp., Saturniidae) (Aiello, personal commun.). Gregarious larvae (e.g. *H. amphinome*) respond to being annoyed by emitting a disagreeable odour, jerking the fore portion of the body from side to side, and finally, dropping from the leaf (Muyshondt and Muyshondt 1975*a–c*). This behaviour may deter invertebrate predators and parasitoids such as tachinid flies (Muyshondt and Muyshondt 1975*a–c*). Annoyed *H. amphinome* larvae also can regurgitate a greenish fluid as early as the second instar. Unidentified ichneumonid wasps cause reduced activity, swelling, and finally the death of the larva; subsequently, the wasp larva pupates within its silk cocoon inside the butterfly larva's skin.

While the larvae of most species of *Hamadryas* are easily distinguishable, those of *H. amphichloe* and *februa* have proved difficult, but it has recently been brought to my attention that fifth instar larvae of *H. amphichloe* have the external surface of the mandibles entirely black, while larvae of *H. februa* do not (Otero personal commun.).

The pupae are cryptic, resembling a twisted leaf. They are polymorphic for colour (ranging from brown to green), and have a pair of long, flattened head projections the shape and orientation of which are characteristic for each species.

Adults feed on fermented fluids from rotting tissues, particularly fruits (*Psidium guajava, Mangifera indica, Spondias purpurea, Castilla gummifera, Manilkara* sp., and *Inga* sp.). They also sip from animal corpses, excrement, mouldy leaves, and mud (Young 1974; DeVries 1983; Jenkins 1983; A.M. Young 1983, personal commun.). I have seen *H. amphinome* visiting flowers of *Bougainvillea* sp.

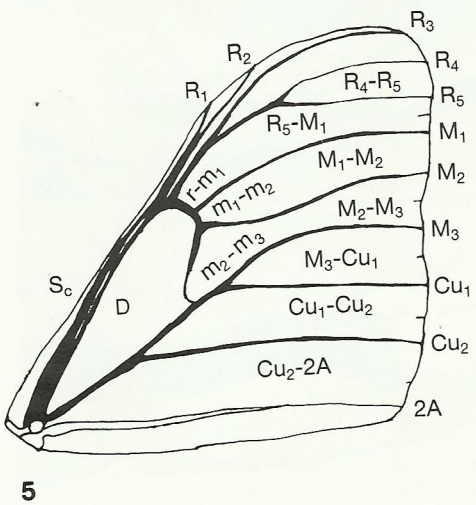
Hamadryas adults spend much of the day resting with their wings spread and appressed to the bark of tree trunks and branches (Young 1974). The calico pattern of species that rest in sunny areas of forest clearings is cryptic, as is the dark and less complex colour pattern of forest canopy species (Monge-Nájera 1988). The pattern on the underside of the wings is species specific (Figs 36.10, 36.12–36.14, 36.16) and can be aposematic in some species. Chai (1988) has shown that aposematic *Hamadryas* are distasteful to jays.

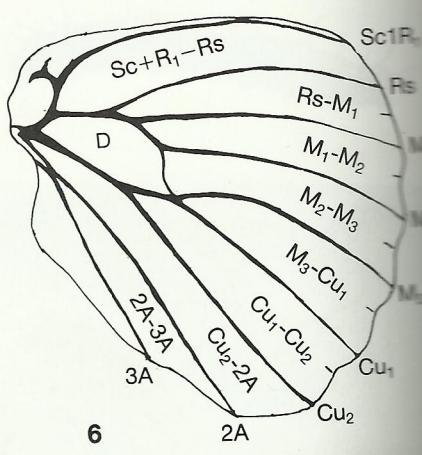
Birds and lizards have been seen to attack *Hamadryas* unsuccessfully (Jenkins 1983; J.M.N., personal observation), but Sharp (1899) reported one successful case of bird predation.

Perched males fly towards other insects, falling leaves, etc., and participate in spiral chases with other *Hamadryas* that are flying by (Jenkins 1983). The spiral flights are usually accompanied by sound emission, if both participants are males, even if they are different species (Monge-Nájera 1988). Agonistic sound emission by females, or attractive emission by one or both sexes during courtship, have been hypothesized to explain the clicking sounds (Darwin 1871, 1889; Swinton 1877; Hampson 1892; Jenkins 1983). It has also been suggested (Aiello, personal commun.) that the clicking is the equivalent of the male-release signals produced by some frogs and toads. Current thought is that the function of the clicking sound is territorial signalling among males and, in *H. feronia*, also courtship. Courtship is silent in *H. februa* (Monge-Nájera 1988).

Seven possible sound production mechanisms have proposed:
(1) collision of individuals;
(2) distortion of a basal membrane of the fore wings;
(3) friction between veins (Swinton 1877);
(4) a system consisting of a vesicle and hooks (Hampson 1892);
(5) collision of forewings (Seitz 1914);
(6) friction of rami against genitalic plates (Reverdin 1915);
(7) a tymbal (Swihart 1967).

The hypothesis of collision between individuals can be rejected because individual *Hamadryas* can 'click,' even when resting on bark (Hampson 1892; J.M.N. personal observation). The hearing function of the basal membrane has been demonstrated by Swihart (1967), and sound is still produced when fore- and hindwings have been decoupled (Otero 1988). The vesicle and hooks imagined by Hampson (1892) simply do not





Figs 36.5–36.6 Venation of *Hamadryas*.

exist (Calvert and Calvert 1917; Monge-Nájera 1988). The emission of sound in resting individuals coincides with wing beating, and more satisfactory functions have been proposed for rami (Monge-Nájera 1988). A detailed morphological study failed to locate any tymbal (Monge-Nájera 1988, 1990). Otero (1988) presented some experimental evidence supporting Seitz's (1914) idea of forewing collision. In conclusion, the origin of the clicking sound made by adult *Hamadryas* butterflies is still not understood but perhaps is produced when the forewings hit each other, and possibly involves percussion of modified veins (Otero 1988; Monge-Nájera 1988).

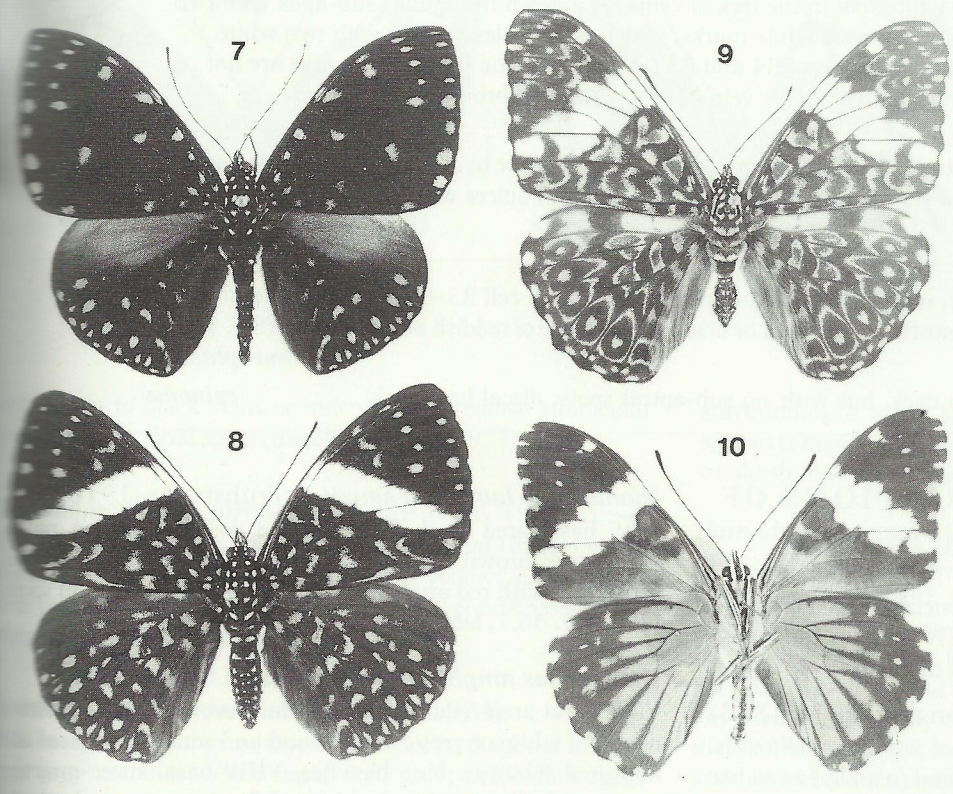
Key to Panamanian *Hamadryas* species

The key follows the vein nomenclature of Figs 36.5 and 36.6 (DFW = dorsal forewing; DHW = dorsal hindwing; VFW = ventral forewing; VHW = ventral hindwing).

1 VHW: basal area dark brown or black 2
– VHW: basal area gray, ochre, yellow, orange, or red 3

2 DHW: with elongated, marginal blue ocelli ***arinome arienis***
– DHW: without well-defined marginal ocelli (Figs 35.7, 35.8) ***laodamia (= arethusa) saurites***

3 VHW: basal area red or orange. VFW: may have several small sub-apical dots, but is without well-formed circular or oval spots (Figs 36.9, 36.10) ***amphinome mexicana***
– VHW: basal area grey, ochre, or yellow. VFW: with at least two circular or slightly oval white submarginal spots, one in cell M1–M2, and the other in cell M2–M3 (e.g. Fig. 36.14). 4



Figs 36.7–36.10 Adults of representative Panamanian *Hamadryas* species: **7**, *laodamia saurites* male, dorsal (Pipeline Rd., Canal Area, Aiello 83–72); **8**, *laodamia saurites* female, dorsal (BCI, Canal Area, Aiello 83–109); **9**, *amphinome mexicana* dorsal (Old Gamboa Rd., Canal Area, Aiello 84–30. no. 5); **10**, *amphinome mexicana* ventral (Old Gamboa Rd., Canal Area, Aiello 84–30, no. 4).

4 VHW: basal area dark mustard yellow, margin black and white (Fig. 36.12) ***fornax fornacalia***

— VHW: basal area grey to tan or ochre **5**

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5 VHW: ocelli with centres made up of a reddish brown crescent partially surrounding a white spot (e.g. Fig. 36.13) **6**

— VHW: ocelli with plain white or whitish centres **8**

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6 DFW: with a large chalky white patch in the distal third; VFW: with submarginal ocellus in cell Cu1–Cu2; VHW: with a small submarginal ocellus in cell Sc+R1–Rs ***glauconome glauconome***

— Wings lacking large white patch and both of these submarginal ocelli or with a faint one in Cu1–Cu2. **7**

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7 VFW: with two small sub-apical ocelli, one in cell R3–R4 and the other in cell R4–R5 (present also in *glauconome*) ***amphichloe ferox***

— VFW: with two small sub-apical crescents (sometimes not well defined), one in cell R3–R4 and the other in cell R4–R5 (Fig. 36.13) ***februa ferentina***

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8 VFW: with two additional white submarginal spots, one in cell M3–Cu1 and the other in cell Cu1–Cu2; discal bar mostly reddish brown bordered with dark brown or black **9**

– VFW: with no obvious additional submarginal spots; discal bar black, or mostly black with trace of reddish brown within **10**

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9 VFW: elongated white spot in the fork of veins R4 and R5 triangular; sub-apex with two irregular or crescent-shaped white marks, which may coalesce; apex with two white marks on or alongside apices of R4 and R5 (in *H. feronia* the sub-apical marks are not present or are very faint); VHW: vein apices with dark brown marks ***guatemalena guatemalena***

— VFW: white spot in the fork of veins R4 and R5 circular or oval (Fig. 36.16); apex mostly dark, with only a very faint whitish blotch. VHW: vein apices with dark brown marks (Fig. 36.16) ***feronia farinulenta***

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10 VFW: apex dark, with two pale sub-apical spots (one in cell R3–R4, and the other in R4–R5); discal bar mostly dark brown or black with a trace of reddish brown within (Fig. 36.14) ***iphthime iphthime***

— VFW: apex also dark, but with no sub-apical spots; discal bar black ***epinome***

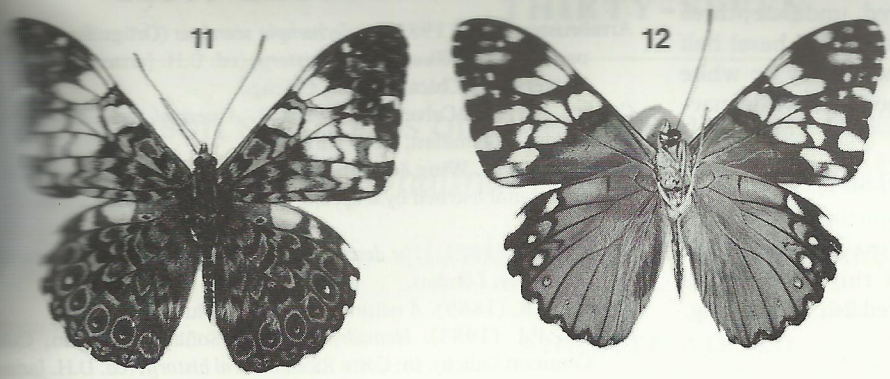
CHECKLIST AND DESCRIPTIONS OF PANAMANIAN *HAMADRYAS*

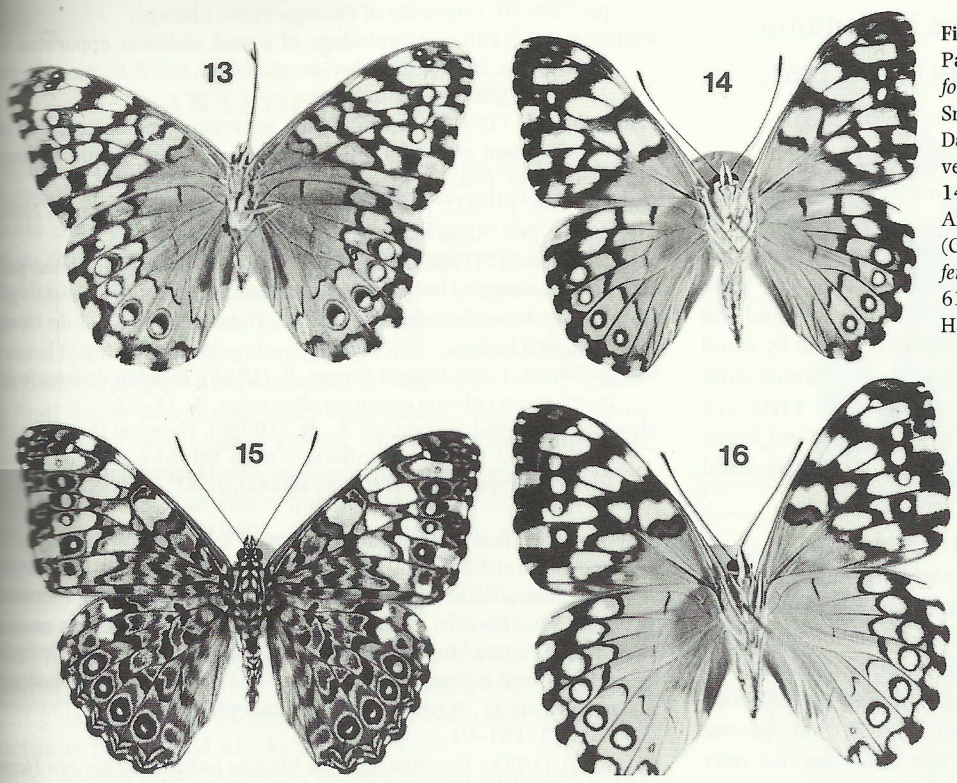
The descriptions follow the vein nomenclature of Figs 36.5 and 36.6 (DFW = dorsal forewing; DHW = dorsal hindwing; VFW = ventral forewing; VHW = ventral hindwing).

Hamadryas arinome arienis (Godman and Salvin, 1883)
VFW basal area black; diagonal band of white or yellowish. VHW black with submarginal red spots and (usually) a red bar in the anal angle.

Hamadryas laodamia saurites (Fruhstorfer, 1916)
VFW basal area black with a broad posterior brown patch. VHW dark brown or black, with red submarginal and anal spots, and with red anal bar (male only) and three basal spots. (Male Fig. 36.7, female Fig. 36.8)

Hamadryas amphinome mexicana (Lucas, 1853)
VFW basal area reddish, the rest dark brown or black with a diagonal white or grey median band and small sub-apical and marginal white or blue blotches. VHW basal three-quarters orange or brilliant red and with the following pattern elements:





Figs 36.11–36.16 Adults of representative Panamanian *Hamadryas* species: **11,** *H. fornax fornacalia* dorsal (Cana, Darien Prov., G.B. Small); **12,** *H. fornax fornacalia* ventral (Cana, Darien Prov., G.B. Small); **13,** *februa ferentina* ventral (Pedregal, Panama City, S. Buitrago); **14,** *iphthime iphthime* ventral (Pipeline Rd., Canal Area, Aiello 85–33); **15,** *feronia farinulenta* dorsal (Cerro Galera, Canal Area, Aiello 83-69); **16,** *feronia farinulenta* ventral (Arraiján, Aiello 85–63). (Photographs in Figs. 36.7–36.16 by Carl Hansen.)

dark brown to black veins or indentations, reddish submedial spots, blue marginal spots (usually). (Figs 36.9, 36.10)

Hamadryas fornax fornacalia (Fruhstorfer, 1907)
VFW basal area blackish brown; three diagonal rows of white maculae. VHW basal area dark mustard yellow; submarginal ocelli two large, (in cells Rs–M1 and M1–M2) plus three smaller; margin black and white. (Figs 36.11, 36.12)

Hamadryas februa ferentina (Godart, 1824)
VFW basal area light grey; discal bar reddish; diagonal rows of large grey maculae. VHW basal area grey; ocelli dark rings with centres consisting of a reddish-brown crescent partially surrounding a white spot; median line undulate, dark. This species is highly variable even locally, ranging from light brown to bluish in general appearance. (Fig. 36.13)

Hamadryas guatemalena guatemalena (Bates, 1864)
VFW dark buff to ochre; discal bar mainly reddish brown with blackish borders; with two sub-apical crescents or irregular white marks which may coalesce; elongated white triangular spot in fork of R4 and R5; submarginal spots present in cells M1–M2, M2–M3, M3–Cu1 (faint), and Cu1–Cu2. This species has been collected (by Philip J. DeVries) in Panama, only on the Azuero Peninsula, an area that is poorly known biologically and has yielded a number of Costa Rican insect species otherwise unknown in Panama.

Hamadryas feronia farinulenta (Fruhstorfer, 1916)
VFW basal area grey to ochre; discal bar red, undulate; three diagonal rows of greyish maculae, irregular. VHW basal half greyish to ochre; ocelli large dark rings with grey or white centres; margin dark brown to black splashed with white markings. (Figs 36.15, 36.16)

Hamadryas iphthime iphthine (Bates, 1864)
VFW median discal bar red or dark, sometimes teardrop-shaped; three diagonal rows of whitish grey maculations. VHW basal area dark tan to ochre, ocelli dark rings with white centres. Submarginal band irregular and reddish brown (Fig. 36.14)

Species of doubtful occurrence in Panama

Hamadryas glauconome glauconome (Bates, 1864)
See discussion under *H. amphichloe ferox*.

Hamadryas amphichloe ferox (Staudinger, 1886)
Hamadryas februa ferentina, glauconome glauconome, and *amphichloe ferox* all have VHW ocelli in which the centre consists of a dark crescent partially surrounding a white spot. *Hamadryas amphichloe ferox* and *glauconome glauconome* each have VFW with two small sub-apical ocelli (one in cell R3–R4, and the other in R4–R5), which in *februa ferentina* are replaced by small crescents. *Hamadryas glauconome glauconome* has a submarginal ocellus in VFW cell Cu1–Cu2, and a small one in VHW cell Sc + R1–Rs, which are lacking in *H. amphichloe ferox* and *februa ferentina*. Its DFW has a large chalky white patch in the distal third.

Hamadryas epinome (Felder and Felder, 1867)
Hamadryas feronia farinulenta, iphthime iphthime, and *epinome* all have VHW ocelli with white centres and no crescents. *Hamadryas feronia farinulenta* has a white submarginal spot in VFW cell Cu1–Cu2, which *epinome* and *iphthime iphthime* lack. *Hamadryas iphthime iphthime* VFW has two small, sub-apical spots, one in cell R3–R4 and the other in cell R4–R5, that *epinome* and *feronia farinulenta* lack, although the latter species may show a single very faint subapical blotch.

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