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# Immature stages of *Hamadryas fornax fornax* (Hübner) (Lepidoptera: Nymphalidae: Biblidinae)

Lucy Mila Garcia Salik[a,*], Luis Anderson Ribeiro Leite[b], Fernando Maia Silva Dias[a], Mirna Martins Casagrande[a], Olaf Hermann Hendrik Mielke[a]

[a] *Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brazil*
[b] *Laboratório de Entomologia, Departamento de Biologia, Universidade Federal de Sergipe, São Cristóvão, SE, Brazil*

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ABSTRACT

The external morphology and biology of the immature stages of *Hamadryas fornax fornax* (Hübner, [1823]) (Lepidoptera, Nymphalidae, Biblidinae) recorded on *Dalechampia triphylla* (Euphorbiaceae) in Curitiba, Paraná, Brazil are described. Morphological characters are illustrated and described, as a result of observations in scanning electron, stereoscope and optical microscopes, the last two attached to a camera lucida. Results are compared and discussed with immature stages of other species of Biblidinae.



## Introduction

*Hamadryas* Hübner, [1806] (Lepidoptera: Nymphalidae: Biblidinae) encompasses 20 species and 33 subspecies (Lamas, 2004); these butterflies are popularly known as crackers, due to the characteristic noise some species produce while flying (Jenkins, 1983; Otero, 1991; Monge-Nájera, 1992, 1995; Monge-Nájera and Hernández, 1993; Monge-Nájera et al., 1998; Yack et al., 2000; Marini-Filho and Benson, 2010; Murillo-Hiller, 2011). They are restricted to the Americas and occur in tropical and subtropical forests, savannas, arid and semi-arid lands (Jenkins, 1983). *Hamadryas fornax* (Hübner, [1823]) has two recognized subspecies (Lamas, 2004): *H. fornax fornax* (Hübner, [1823]) with South American distribution from Venezuela to Argentina and *H. fornax fornacalia* (Fruhstorfer, 1907) distributed from the South of United States to the Northern part of Colombia and Venezuela (DeVries, 1987; Jenkins, 1983; Neild, 1996; Lamas, 2004).

*Hamadryas fornax fornax* (Hübner, [1823]) usually perches upside down on tree trunks on valleys of rivers and clearings in forest habitats and despite its similarity with the other species of the genus, it is distinguished by its forewing on the ventral surface with the proximal area of the discal cell presenting white or grayish-white coloration, rarely pale-yellow and the mustard coloration on the ventral side of the hind wing (Jenkins, 1983). Immatures are associated to plants of the genus *Dalechampia* (Euphorbiaceae) (D'Almeida, 1922; Costa Lima, 1936; Armbruster, 1982, 1983; Jenkins, 1983; Neild, 1996; Canals, 2003; Pastrana, 2004). Females are similar to males, but frequently with larger size and forewings with a more rounded shape (Figs. 1–4) (Jenkins, 1983).

Despite the large amount of data on the geographic distribution and host plants found in the literature (Jenkins, 1983; DeVries, 1987; Neild, 1996; Pastrana, 2004; Contreras Chialchia and Contreras Roqué, 2010), currently there is information on the morphology and biology of immature stages of only eight species: *H. feronia feronia* (Linnaeus, 1758), (D'Almeida, 1922); *H. amphinome amphinome* (Linnaeus, 1767) (D'Almeida, 1922; Müller, 1886; Muyshondt and Muyshondt, 1975a); *H. fornax fornax* (Hübner, [1823]) (Müller, 1886); *H. februa februa* (Hübner, [1823]) (Comstock and Vasquez Garcia, 1961; D'Almeida, 1922; Muyshondt and Muyshondt, 1975b; Young, 1974); *H. arete* (Doubleday, 1847) (Müller, 1886); *H. guatemalena guatemalena* (H. W. Bates, 1864) (Muyshondt and Muyshondt, 1975c) and *H. epinome* (C. Felder & R. Felder, 1867) (Müller, 1886; D'Almeida, 1922; Leite et al., 2012b).

It is widely known that data on the immature stages are important for taxonomic and phylogenetic studies of Lepidoptera (Freitas et al., 1997; Freitas and Brown, 2004); therefore this study aims to provide information and extend the knowledge on the subfamily

* Corresponding author.
*E-mail:* lucymilas@gmail.com (L.M.G. Salik).

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**Figs. 1–4.** *Hamadryas fornax fornax* (Hübner, [1823]). 1, 2. Male: 1, dorsal view; 2, ventral view; 3, 4. Female: 3, dorsal view; 4, ventral view. Scale bar: 1 cm.

Biblidinae by describing the external morphology and the biology of the immature stages of *H. fornax fornax.*

## Material and methods

Eggs were collected in the Parque Municipal Barigui (25°25′ S, 49°18′ W, 910 m), Curitiba, Paraná, Brazil, along with branches of the host plant *Dalechampia triphylla* Lam. (Euphorbiaceae) and reared in laboratory (Laboratório de Estudos de Lepidoptera Neotropical at the Universidade Federal do Paraná). Laboratory procedures, such as the maintenance of the samples and the host plant, preparation and observation of the structures using stereoscopic microscope, drawings, photographs, scanning electron microscopy and terminology follows Leite et al. (2012b) and other recent studies on immatures of Biblidinae (Leite et al., 2012a, 2014). Voucher specimens are deposited at the Coleção Entomológica Pe. Jesus Santiago Moure; Universidade Federal do Paraná, Curitiba, Paraná, Brazil.

## Results

*Hamadryas fornax fornax (Hübner, [1823]) (Figs. 1–29)*

*Egg (Figs. 5–9)*

Elliptical, with several irregular carinae and flattened on the bottom pole. Uniformly pearly white in color. Micropilar region on the upper pole in the center of a round and slightly concave area.

Oviposition is normally gregarious; the eggs are laid on the upper side of the host plant *Dalechampia triphylla*, one on top of each other, the first instar hatch laterally.

Diameter: 1.01 mm. Average duration: 8 days ($n = 15$).

*First instar (Figs. 10, 19–22)*

Head rounded, black, and without scoli. Frons ventrally delimited by the clypeus, which appears as a sclerotized transverse band. Labrum bilobed. Mandibles strongly sclerotized with a serrated cutting edge. Six stemmata latero-ventrally, 1–4 and 6 arranged in semi-circle and 5 ventrally, and closer to the base of the antenna.

Pronotal plate black and divided, forming two sub-rectangular plates, with four pairs of setae on chalazae. Thoracic legs with the same color of the pronotal plate. Body translucent yellowish ochre, with rounded white spots regularly distributed on the dorsal and lateral areas. Numerous spiniform or clavate black setae distributed along the body, most of them on chalazae. Bases of all black setae forming circular blackened areas interspersed with white rounded areas. Spiracles of T1 and A8 elliptical and similar; other spiracles smaller and rounded. After the eclosion, the larvae are not gregarious, and feed independently. Chaetotaxy is given by Figs. 19–21.

Head capsule: width: 0.65 mm; height: 0.68 mm. Average length of the larva before molting: 5 mm. Average duration: 3 days ($n = 9$).

*Second instar (Figs. 11, 23)*

Head capsule black. Epicranium with a pair of short truncated dorsal scoli. Setae on lateral and lateroventral regions of the epicranium on cream-colored chalazae. Prothorax yellow ochre, with black and distally creamy white scoli. Remaining segments olive brown with a narrow yellow ochre lateral band in A1–A10, at the level of the supraventral setae. Thorax and abdomen with subdorsal black and distally creamy white scoli on T2, T3, A7 and A8, remaining scoli translucent yellow.

Head capsule: width: 1.04 mm, height: 0.95 mm. Length of the dorsal protuberance: 0.44 mm. Average length of the larva before molting: 6 mm. Average duration: 3 days ($n = 8$).

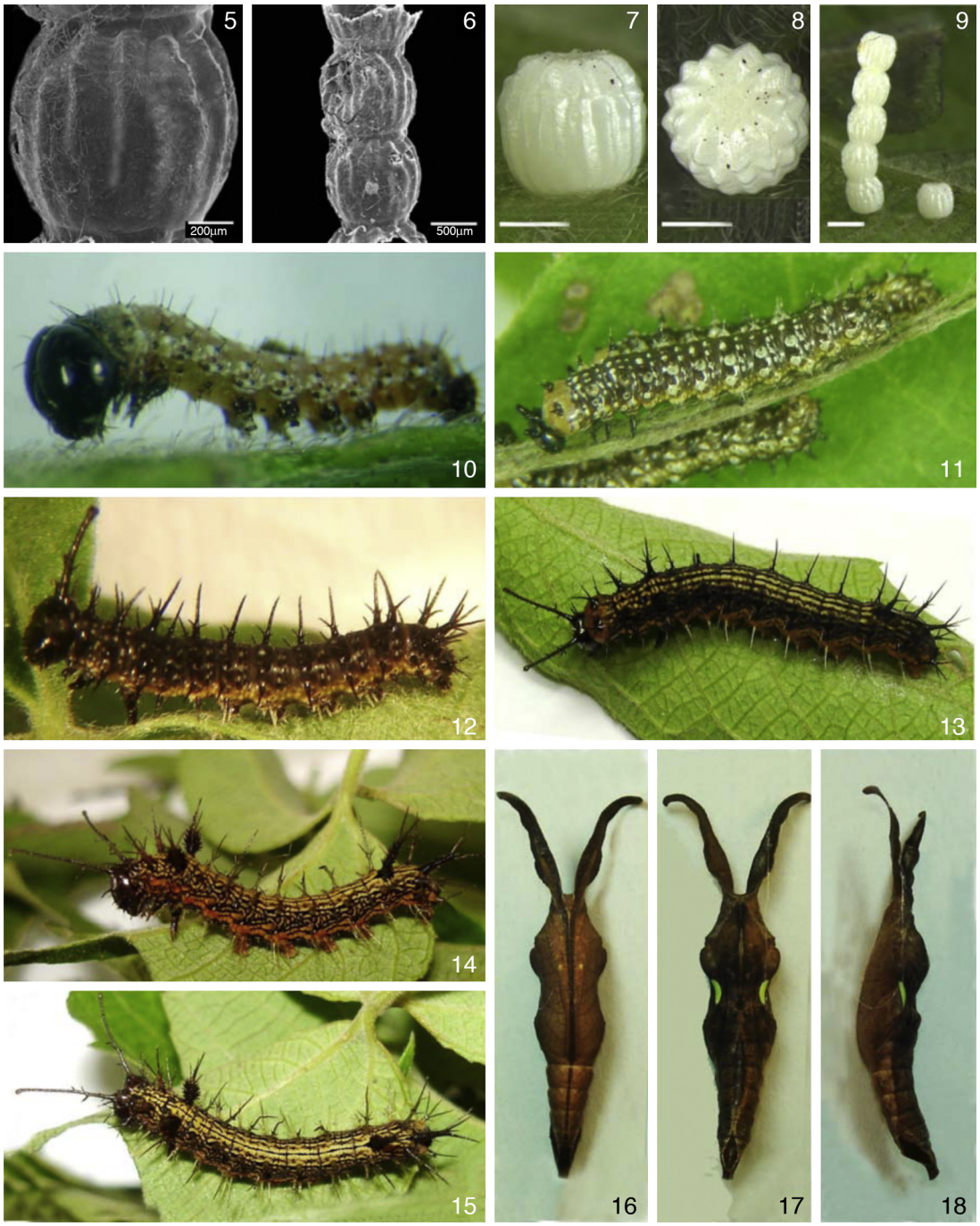
*Third instar (Figs. 12, 24)*

Head capsule black; dorsal scoli longer than the previous instar, blackened and with spiniform setae. Thorax and abdomen with the same coloration of the head, except for the yellow ochre supraventral and ventral areas. Most of the thoracic and abdominal scoli black, except for some lateral translucent yellow scoli from A3 to A6.

Head capsule: width: 1.63 mm; height: 1.66 mm. Length of the dorsal protuberance: 2.7 mm. Average length of the larva before molting: 13.5 mm. Average duration: 4 days ($n = 7$).

*Fourth instar (Figs. 13, 25)*

Head capsule similar to the previous instar. Prothorax anteriorly reddish-brown, with black pronotal plate. Dorsally, two pairs of yellow longitudinal bands from T2 to A9. Reddish-brown band




**Figs. 5–18.** *Hamadryas fornax fornax* (Hübner, [1823]). 5–9. Egg: 5, SEM lateral view; 6, SEM lateral view of the egg-laying; 7, lateral view; 8, dorsal view; 9, lateral view of the egg-laying. 10–15. Larvae: 10, 1st instar; 11, 2nd instar; 12, 3rd instar; 13, 4th instar; 14, 5th instar lateral view; 15, 5th instar dorsal view. 16–18. Pupae: 16, ventral view; 17, dorsal view; 18, lateral view. SEM – Scanning Electronic Microscopy. Scale bars Figs. 7–8: 0.5 mm, Fig. 9: 1 mm.

laterally disposed on T2 and T3 and on the abdominal segments at the level of the supraventral setae.

Head capsule: width: 1.8 mm, height: 1.7 mm. Length of the dorsal protuberance: 3.2 mm. Average length of the larva before molting: 23 mm. Average duration: 4 days ($n = 7$).

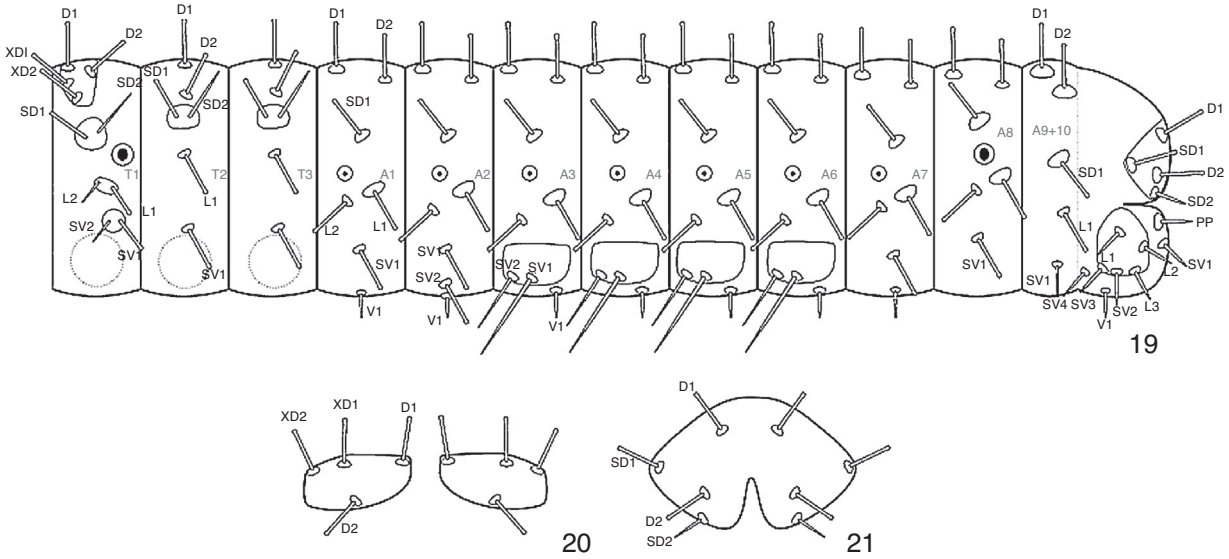
*Fifth instar larva (Figs. 14, 15 and 26)*

Head capsule dark brown. Pronotal plate black. Spiniform setae distributed along the body, sometimes grouped in scoli, sometimes individualized, light brown setae, except those from the supraventral and ventral regions from T1 to A8, which have yellow coloration. Thorax and abdomen yellow, with several black longitudinal bands and an orange lateral band from the spiracular to the ventral area. Abdominal legs orange.

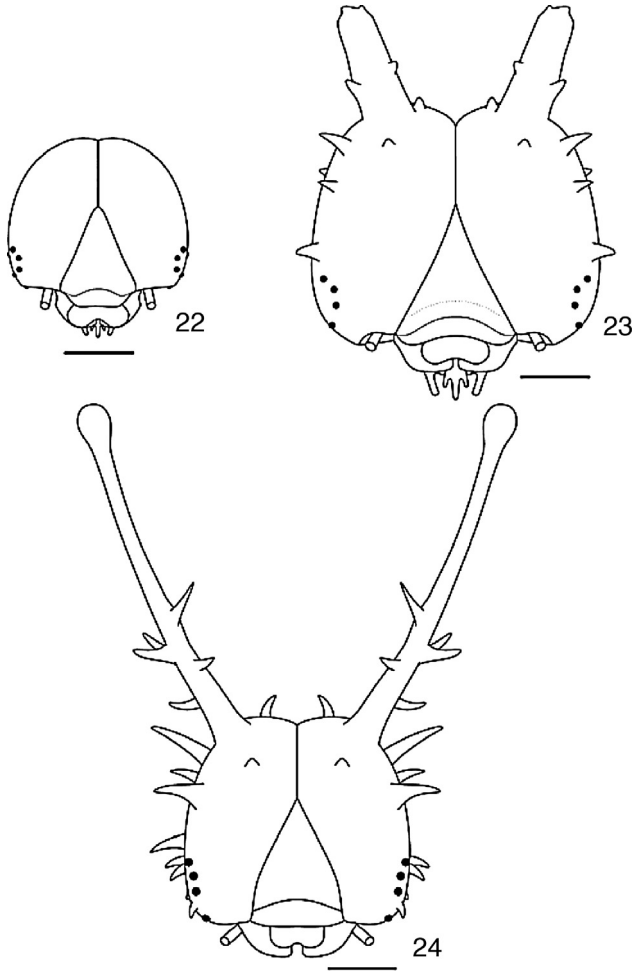
Head capsule: width: 3.4 mm, height: 3.2 mm. Length of the dorsal protuberance: 6.38 mm. Average length of the larva before molting: 33 mm. Average duration: 7 days, 1 more day on prepupa ($n = 7$).

*Pupa (Figs. 27–29)*

Adecticous and obtect, suspended by the cremaster. Elongated, median-dorsally projected on T2 and A2, forming crests. Freshly formed pupae light green, darkening to brownish dark green in about one day. Light green semicircular spot dorsolaterally on T2.

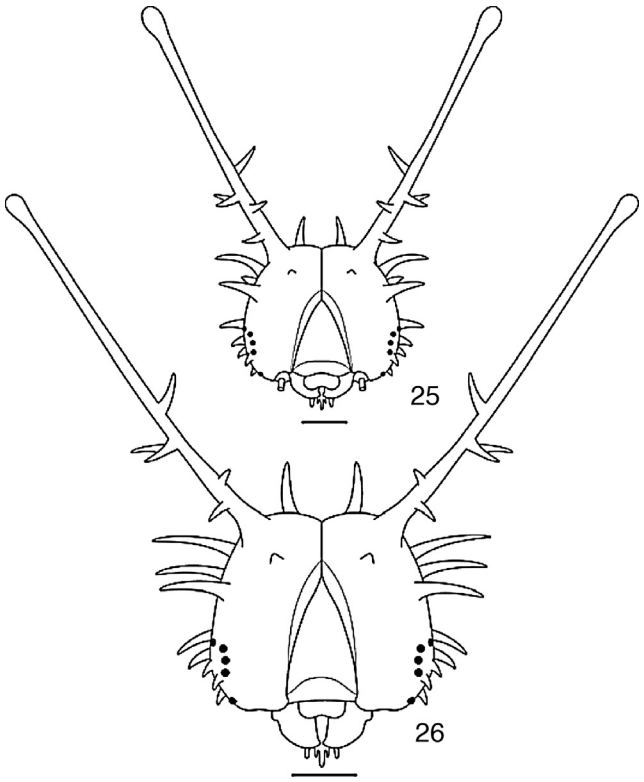



**Figs. 19–21.** *Hamadryas fornax fornax* (Hübner, [1823]). 1st instar chaetotaxy: 19, map of setae of the thorax and abdomen; 20, pronotal plate; 21, anal plate.




**Figs. 22–24.** *Hamadryas fornax fornax* (Hübner, [1823]). Head capsule frontal view: 22, 1st instar; 23, 2nd instar; 24, 3rd instar. Scale bar Figs. 22, 23: 0.25 mm; Fig. 24: 0.5 mm.

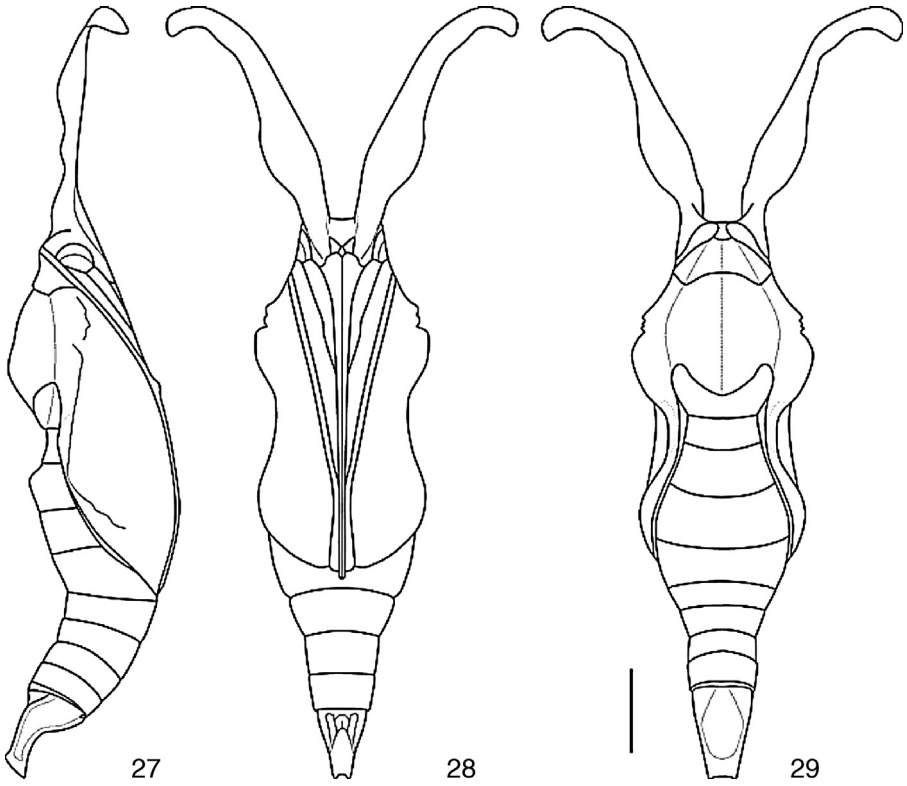
A pair of foliaceous dorsolateral appendices on the head vertex. Frons smooth, subtriangular clypeus; mandibles lateroventrally to the clypeus; labrum as a small lozenge shaped structure inferiorly to the clypeus and between the mandibles; dark brown galeae




**Figs. 25–26.** *Hamadryas fornax fornax* (Hübner, [1823]). Head capsule frontal view: 25, 4th instar; 26, 5th instar; 24. Scale bar Fig. 25: 0.5 mm; Fig. 26: 1 mm.

arising inferiorly to the mandibles and lateroinferiorly to the labrum and ending next to the distal portion of the antennae; eyes laterally to the mandibular region; striated antennae extendly, lateral to the eyes, proximal portion at the base of the foliaceous appendices and distal portion on the forewing margins.

Pronotum subrectangular and small, with a median suture. Mesonotum large and convex. Metanotum narrow, with a convex margin on its anteromedian region. Base of the prothoracic legs at the inferior portion of the eye, laterally to the galeae and ending on the anterior half of these last ones; base of the mesothoracic legs on the anterior third of the antennae and ending at its posterior third.




**Figs. 27–29.** *Hamadryas fornax fornax* (Hübner, [1823]). Pupa: 27, lateral view; 28, ventral view; 29, dorsal view. Scale bar: 0.5 cm.

Abdomen with ten segments, lateral elliptical spiracles from A2 to A8. Narrow median dark brown band ventrally from A4 to A8. Cremaster dark brown, with distal simple hooks on the apex of A10.

Average length of the pupa, from the vertex to the cremaster: 30 mm. Average length of the foliaceous appendices: 15 mm. Average duration: 7 days ($n = 6$).

## Discussion

Species of *Hamadryas* feed on species of *Dalechampia*, and *D. tryphilla* is recorded as host plant of *H. fornax* and further eight species of the genus (Beccaloni et al., 2008). Records of species of *Hamadryas* feeding on other genera of host plants provided by Beccaloni et al. (2008) are unlikely and need confirmation.

Biblidinae usually present eggs with well defined crests, as in species of *Temenis laothoe liberia* (Fabricius, 1793) (Muyshondt, 1974), *Dynamine* Hübner, [1819] (Leite et al., 2012a, 2014) and some species of Ageroniini, *Panacea* Godman and Salvin, 1883 and *Batesia* C. Felder and R. Felder, 1862 (DeVries et al., 2000; Daniels et al., 2008). In contrast, species of *Hamadryas*, such as *H. fornax fornax* and *H. epinome* (Leite et al., 2012b) present eggs with irregular ornamentation of the chorion, indicating that this character might be characteristic of the genus. In the first instar, the shape of the base of SD1 and SD2 on T1, T2 and T3, and the localization of D2 on the pronotal plate differ from those found in *H. epinome* (Leite et al., 2012b). In the fifth instar, similar to *H. guatemalena*, *H. februa*, and *H. amphinome* (Muyshondt and Muyshondt, 1975a,b,c), *H. fornax fornax* presents dorsal scoli only on A7 and A8, with three and five branches respectively. In *H. epinome* (Müller, 1886; Jenkins, 1983; Leite et al., 2012b) additional dorsal scoli are present in all abdominal segments, although simple and smaller than the those in A7 and A8 and the subdorsal scoli. *Hamadryas* (Muyshondt and Muyshondt, 1975a,b,c) and *Ectima* Doubleday, [1848] (Janzen, 2010) present long foliaceous projections on the vertex of the pupa. Pupae of other Ageroniini, *Batesia* C. Felder and R. Felder, 1862 and *Panacea* Godman and Salvin, 1883 do not have these projections (DeVries et al., 2000; Daniels et al., 2008). In Epiphilini, species of *Temenis* Hübner, [1819] (Muyshondt, 1974) also have these extensions, although not as long as in *Hamadryas*; other species of Biblidinae often have a slightly pronounced vertex (*i.e.* DeVries, 1987), but never greatly extended as the above-cited taxa. The dorsolateral color of T2 of the pupae differentiates *H. fornax fornax* from *H. epinome* (Leite, 2012b), which are lime green in the former and brown in the latter.

The current understanding of the phylogenetic relationships of *Hamadryas* (Garzón-Orduña, 2012; Garzón-Orduña et al., 2013) lack morphological and biological evidence from immature stages of potential evolutionary importance, such as the above-mentioned differences in egg gregariousness, chaetotaxy, and scoli distribution, for example. Unfortunately, most descriptions of immature stages of *Hamadryas* are brief, which limits comparisons. Studies like this are essential to provide a new array of characters for phylogeny and a better understanding the systematic of the genus.

## Conflicts of interest

The authors declare no conflicts of interest.

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## References


Armbruster, W.S., 1982. Seed production and dispersal in *Dalechampia* (Euphorbiaceae): divergent patterns and ecological consequences. Am. J. Bot. 69, 1429–1440.

Armbruster, W.S., 1983. *Dalechampia scandens* (*Ortiguilla, Bejuco de Pan*). In: Janzen, D.H. (Ed.), Costa Rican Natural History. The University of Chicago Press, Chicago, pp. 230–233.

Beccaloni, G.W., Hall, S.K., Viloria, A.L., Robinson, G.S., 2008. Catalogue of the hostplants of the Neotropical butterflies (Catálogo de las plantas huésped de las mariposas neotropicales). Mongr. Terc. Milênio 8, 1–536.

Canals, G.R., 2003. Mariposas de Misiones. Literature of Latin America, Buenos Aires.

Comstock, J.A., Vasquez Garcia, L., 1961. Estudios de los Ciclos Biologicos en Lepidopteros Mexicanos. An. I. Biol. 31, 349–448.

Contreras Chialchia, A.O., Contreras Roqué, J.R., 2010. Presencia del género *Hamadryas* Hübner, 1825 (Lepidoptera: Nymphalidae: Biblidinae), en la Ecorregión del Ñeembucú y en el resto del Paraguay Oriental. Azariana 1, 225–242.

Costa Lima, A.C., 1936. Terceiro Catálogo de insectos que vivem nas plantas do Brasil. Escola Nacional de Agronomia, Rio de Janeiro.

D'Almeida, R.F., 1922. Mélanges Lépidoptérologiques. Études sur les Lépidoptères du Brésil. Friedländer and Sohn, Berlin.

Daniels, J.C., Rodriguez, E., Whelan, J.C., 2008. The biology and immature stages of *Panacea procilla lysimache* (Lepidoptera: Nymphalidae) from Costa Rica, with report of a new locality record. Trop. Lepid. 18, 70–73.

DeVries, P.J., 1987. The Butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, and Nymphalidae. Princeton University Press, Princeton.

DeVries, P.J., Penz, C.M., Walla, T.R., 2000. The biology of *Batesia hypochlora* in an Ecuadorian rainforest. Trop. Lepid. 10, 43–46.

Freitas, A.V.L., Brown Jr., K.S., Otero, L.D., 1997. Juvenile stages of *Cybdelis*, a key genus uniting the diverse branches of the Eurytelinae. Trop. Lepid. 8, 29–34.

Freitas, A.V.L., Brown Jr., K.S., 2004. Phylogeny of the Nymphalidae (Lepidoptera). Syst. Biol. 53, 363–383.

Garzón-Orduña, I.J., 2012. Phylogenetic evidence for loss of sound production and a shift in sexual recognition signals in *Hamadryas* butterflies (Nymphalidae: Biblidinae). Syst. Entomol. 37, 84–101.

Garzón-Orduña, I.J., Marini-Filho, O., Johnson, S.G., Penz, A.M., 2013. Phylogenetic relationships of *Hamadryas* (Nymphalidae: Biblidinae) based on the combined analysis of morphological and molecular data. Cladistics 29, 629–642.

Janzen, D.H., Hallwachs, W., 2010. Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservacion Guanacaste (ACG), northwestern Costa Rica, Available at: http://janzen.sas.upenn.edu (accessed 05.08.15).

Jenkins, D.W., 1983. Neotropical Nymphalidae. I. Revision of *Hamadryas*. Bull. Allyn. Mus. 81, 1–146.

Lamas, G., 2004. Checklist: part 4A. Hesperioidea – Papilionoidea. In: Heppner, J.B. (Ed.), Atlas of Neotropical Lepidoptera, vol. 5A. Association for Tropical Lepidoptera, Scientific Publishers, Gainesville, pp. 238–239.

Leite, L.A.R., Casagrande, M.M., Mielke, O.H.H., Freitas, A.V.L., 2012a. Immature stages of the Neotropical butterfly *Dynamine agacles agacles*. J. Insect Sci. 12, 1–12.

Leite, L.A.R., Dias, F.M.S., Carneiro, E., Casagrande, M.M., Mielke, O.H.H., 2012b. Immature stages of the Neotropical cracker butterfly *Hamadryas epinome*. J. Insect Sci. 12, 1–12.

Leite, L.A.R., Freitas, A.V.L., Barbosa, E.P., Casagrande, M.M., Mielke, O.H.H., 2014. Immature stages of nine species of genus *Dynamine* Hübner, [1819]: morphology and natural history (Lepidoptera: Nymphalidae: Biblidinae). SHILAP – Rev. Lepidoptera 42, 27–55.

Marini-Filho, O.J., Benson, W.W., 2010. Use of sound and aerial chases in sexual recognition in Neotropical *Hamadryas* butterflies (Nymphalidae). J. Res. Lepidoptera 42, 5–12.

Monge-Nájera, J., 1992. Clicking butterflies, *Hamadryas*, of Panama: their biology and identification (Lepidoptera: Nymphalidae). In: Quintero, D., Aiello, A. (Eds.), Insects of Panama and Mesoamerica. Selected Studies. Oxford University Press, Oxford, pp. 567–572.

Monge-Nájera, J., 1995. Mariposas que producen sonido: cuál es la situación de *Hamadryas* (Nymphalidae) en Cuba? Cocuyo 4, 11.

Monge-Nájera, J., Hernández, F., 1993. A morphological search for the sound mechanism of *Hamadryas* butterflies (Lepidoptera: Nymphalidae). J. Res. Lepidoptera 30, 196–208.

Monge-Nájera, J., Hernández, F., González, M.I., Soley, J., Araya, J., Zolla, S., 1998. Spatial distribution, territoriality and sound production by tropical cryptic butterflies (*Hamadryas*, Lepidoptera: Nymphalidae): implications for the "industrial melanism" debate. Rev. Biol. Trop. 46, 297–329.

Müller, W., 1886. Südamerikanische Nymphalidenraupen. Versuch eines natürlichen Systems der Nymphaliden. Zool. Jahrb. (Syst.) 1, 453–461.

Murillo-Hiller, L.R., 2011. The spiral organ responsible for producing sound signals, an essential taxonomic character in the phylogenetic analysis of the genus *Hamadryas* (Nymphalidae: Biblidinae): the case of *Hamadryas chloe chloe* (Stoll) [1787] from South America. Int. Sch. Res. Net Zool., 1–3.

Muyshondt, A., 1974. Notes on the life cycle and natural history of butterflies of El Salvador. III.A. *Temenis laothoe liberia* Fabricius (Nymphalidae – Catonephelinae). J. N. Y. Entomol. Soc. 81, 224–233.

Muyshondt, A., Muyshondt Jr., A., 1975a. Notes on the life cycle and natural history of butterflies of El Salvador. III.B. *Hamadryas amphinome* L. (Nymphalidae – Hamadryadinae). J. N. Y. Entomol. Soc. 83, 181–191.

Muyshondt, A., Muyshondt Jr., A., 1975b. Notes on the life cycle and natural history of butterflies of El Salvador. I.B. – *Hamadryas februa* (Nymphalidae – Hamadryadinae). J. N. Y. Entomol. Soc. 83, 157–169.

Muyshondt, A., Muyshondt Jr., A., 1975c. Notes on the life cycle and natural history of butterflies of El Salvador. II B. – *Hamadryas guatemalena* Bates (Nymphalidae – Hamadryadinae). J. N. Y. Entomol. Soc. 83, 170–180.

Neild, A.F.E., 1996. The Butterflies of Venezuela. Part I: Nymphalidae (Limenitidinae, Apaturinae, Charaxinae). Meridian Publications, London.

Otero, L.D., 1991. The stridulatory organ in *Hamadryas* (Nymphalidae): preliminary observations. J. Lepid. Soc. 44, 285–288.

Pastrana, J.A., 2004. Los lepidópteros argentinos: sus plantas hospedadoras y otros sustratos alimenticios. Sociedad Entomológica Argentina, Buenos Aires.

Yack, J.E., Otero, L.D., Danson, J.W., Surlykke, A., Fullard, J., 2000. Sound production and hearing in the blue cracker butterfly *Hamadryas feronia* (Lepidoptera, Nymphalidae) from Venezuela. J. Exp. Biol. 203, 3689–3702.

Young, A.M., 1974. On the biology of *Hamadryas februa* (Lepidoptera: Nymphalidae) in Guanacaste, Costa Rica. Z. Angew. Entomol. 76, 380–393.