

THE ECOLOGY AND LIFE CYCLE OF THE AMAZONIAN *MORPHO CISSEIS PHANODEMUS* HEWITSON, 1869, WITH A COMPARATIVE REVIEW OF EARLY STAGES IN THE GENUS *MORPHO* (LEPIDOPTERA: NYMPHALIDAE: MORPHINAE)

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Abstract – We studied the ecology and life-cycle of *Morpho cisseis phanodemus* Hewitson, 1869, in north-eastern Peru. Data on adult flight activity are provided and the egg, larval instars and pupa are described for the first time. The hostplant belongs to the genus *Abuta* (Menispermaceae). The life cycle length is compared with available information for other *Morpho* species and the diversity of early stages in the genus *Morpho* is discussed from a phylogenetic perspective.

Key words: Morphinae, *Morpho*, *M. cisseis*, eggs, larvae, hostplant, life cycle, diversity, phylogeny, north-eastern Peru

INTRODUCTION

Morpho cisseis C. Felder & R. Felder, 1860 is one of the largest South-American butterflies, with its wingspan attaining more than 15 cm. It is a polytypic species, widely distributed in Amazonia, all along the Andes from Bolivia to southern Colombia, in the western Amazonian lowlands, and south of the Amazon River as far as the limit between the Brazilian states of Pará and Maranhão (Blandin, 2007a). North of the Amazon River, it reaches south-eastern Venezuela (Bolívar; Neild, 2008), but it is absent eastward, from Guyana to French Guiana and the Brazilian state of Amapá (Blandin, 2007a).

With *Morpho hecuba* (Linnaeus, 1771), *M. cisseis* forms the subgenus *Laurschwartzia* Blandin, 2007 (= *Schwartzia* Blandin, 1988, preoccupied, cf. Blandin, 2007b). The systematics of *M. cisseis* were misinterpreted by Le Moulton & Réal (1962), who divided it into two species, *M. cisseis* and *M. phanodemus* Hewitson, 1869. Blandin's (1988) taxonomic arrangement, with *phanodemus* as a subspecies, was followed by Lamas (2004). *M. cisseis phanodemus* is widespread in western Amazonia, where it is known in San Martín and Loreto Departments (Peru), Napo and Orellana (K. Willmott, pers. comm.) Provinces (Ecuador), and from Putumayo Department (Colombia).

Despite the wide geographical distribution of *M. cisseis*, and despite being relatively common, at least locally, its early stages have remained unknown. According to a personal communication from Luis Otero to Luis Constantino, the hostplant pertains to the genus *Abuta* (Menispermaceae) (Constantino, 1997; Beccaloni *et al.*, 2008). In the area of Tarapoto (San Martín Department, Peru), we have performed field research on the ecology of *Morpho* species for many years. In this paper, we present observations on the ecology and life cycle of *M. cisseis phanodemus* from the egg to the adult, and we compare its life cycle and early stages with other *Morpho* species.

METHODS

Study area

We performed observations and sampling in the middle basin of the Río Huallaga (San Martín Department, Peru), between the area of Juanjuí, to the south, and the area of Tarapoto, to the north. Juanjuí and Tarapoto are historical butterfly localities, where the famous collector Otto Michael (1859-1934) worked and collected specimens of *M. cisseis* (Michael, 1911, 1931). We conducted ecological and biological studies in various localities along the slopes of the Cordillera Escalera (Fig. 1), a NW-SE trending range which is the final north-eastern Peruvian cordillera before the Amazonian lowlands and which reaches 1633 m near Tarapoto. Tarapoto is located around 350 m at the limit between dry forests ("bosques secos"), which are widely destroyed, and lowland tropical rainforest ("selva baja"), with the latter reaching at least 700-800 m on the Cordillera Escalera slopes. There is probably a complex transition to montane rainforest depending on the orientation of slopes. For example, we observed *M. theseus juturna* Butler, 1870 as low as 800-850 m, while this montane taxon is known to live generally between 1100 and 1500 m in the Alto Mayo "Bosque de protección," some 200 km NW from Tarapoto (Blandin, 2008).

Field survey

We observed adult behaviour from an observation tower near Tarapoto, along the Río Shilcayo (06°27'07"S, 76°20'47"W; ca. 450 m) (Fig. 2). Other observations were made along the Río Cumbasa, near the village of San Antonio de Cumbasa, to the NW of Tarapoto (06°24'24"S, 76°24'25"W; ca. 470 m), and at higher altitude along the road from Tarapoto to Yurimaguas (ca. 06°27'S, 76°18'W). Generally, we began observations ca. 9 a.m., except when we had the opportunity to bivouac near the Shilcayo tower, where we began observations at ca. 7 a.m. Observations were completed by ca. 2 p.m., as no more *Morpho* were observed in flight in the final half hour,



Fig. 1. The Cordillera Escalera, beyond the town of Tarapoto, Departamento San Martín, Peru (PB).

except, sometimes, a few *M. helenor theodorus* Fruhstorfer, 1907, *M. achilles phokylides* Fruhstorfer, 1912, or *M. deidamia diomedes* Weber, 1944. Observations were interrupted earlier when the weather became overcast and subsequently no *Morpho* was observed.

Near Tarapoto, on the SW slopes of the Cordillera Escalera, in an area named Urahuasha, a committee of farmers protects the forest over a large area, close to the Area de Conservación Regional Cordillera Escalera. One of us (Cesar Ramírez) owns 20 ha, a property named Centro de Interpretación Wayrasacha, where a few hectares are devoted to organic agriculture, the forest being strictly protected all around. The property is located at 06°27'40''S, 76°20'02''W, ca. 750 m. In this area, a few years ago, we discovered the hostplant of *M. telemachus martini* Niepelt, 1933 (Gallusser *et al.*, 2010) to be *Abuta grandifolia* (Mart.) Sandwith (Fig. 3), a small tree belonging to the family Menispermaceae. This plant species is common, but occurs in low density (ca. 2 trees/ha) from 400 m to at least 800-900 m. On the 10th of October 2008, while looking for *M. telemachus* caterpillars, which are gregarious and exhibit red and whitish colours, we found solitary larvae with a different pattern (Fig. 4). We successfully reared one of them, and obtained a *M. cisseis phanodemus* male in February 2009. Subsequently we therefore looked for other caterpillars, but it was not until August and November 2009 that we found additional larvae, and also a few isolated eggs.

Rearing

We performed the rearing experiments at Wayrasacha under ambient conditions. Eggs and larvae were placed in individual plastic boxes. Fresh *Abuta* leaves were provided daily and events were noted (hatching of eggs, molts, pupa formation, hatching of adult, death). We obtained three adults, of which two were released in the field.

Pictures

Most pictures were taken by Cesar Ramírez (CR), Stéphanie Gallusser (SG) or Patrick Blandin (PB) with ordinary digital cameras (for example: Nikon Coolpix). Moreover, several colleagues have provided pictures of larvae of various *Morpho* species; their names are indicated in the legends.

Nomenclature

We follow Blandin's (2007a) species and subspecies classification and Blandin & Purser's (2013) subgeneric classification, with the latter based on recent phylogenetic studies (Cassildé *et al.*, 2012; Penz *et al.*, 2012).

RESULTS

Taxonomic status of populations in the middle basin of the Río Huallaga

In the area of Tarapoto, populations can be referred to *Morpho cisseis phanodemus* Hewitson, 1869, while in the area of Juanjuí they can be referred to *M. cisseis gahua* Blandin, 1988, described from the area of Tingo María, some 300 km southward on the Huallaga. The latter is characterized by the coloured areas on the forewings being much reduced in comparison with the former, although some specimens from Juanjuí are intermediate.

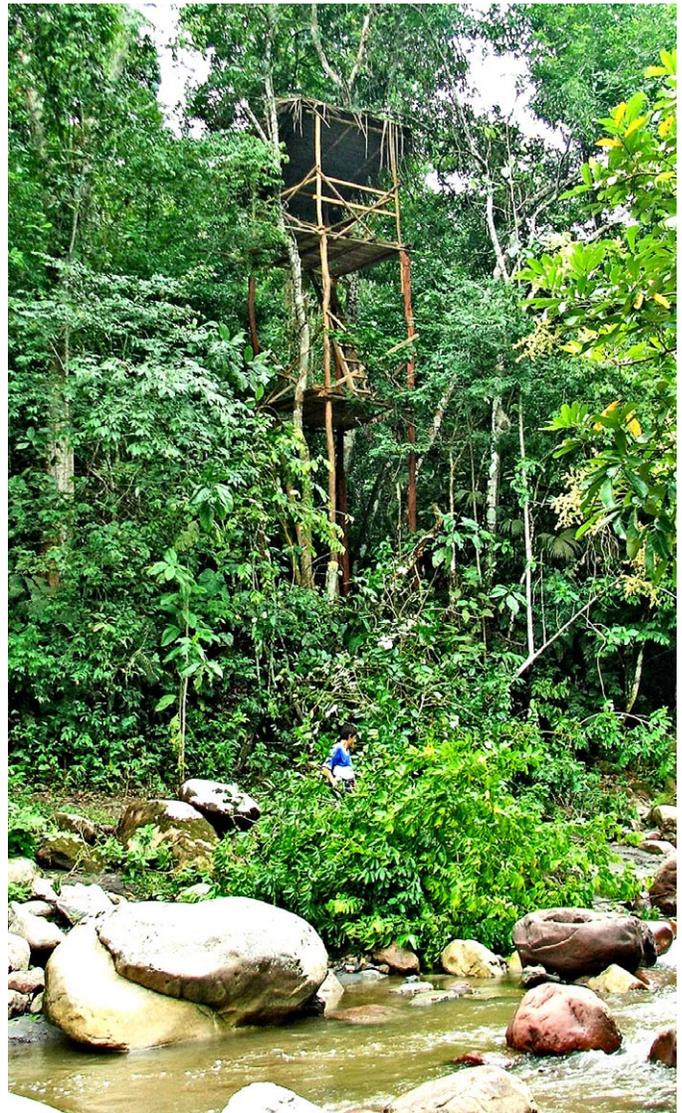


Fig. 2. The observation tower constructed on the right bank of the Río Shilcayo, near Tarapoto (SG).



Fig. 3. Leaves of *Abuta grandifolia* (Mart.) Sandwith (Menispermaceae), the hostplant of *Morpho telemachus martini* and *M. cisseis phanodemus* in the Tarapoto area (PB).



Fig. 4. A 5th instar larva of *Morpho cisseis phanodemus* resting under an *Abuta grandifolia* leaf, illustrating the difficulty to find larvae, particularly in the 1st or 2nd instar (CR).

Habitat and adult behaviour

We observed *Morpho cisseis phanodemus* adults along the rivers Shilcayo and Cumbasa as well as at Wayrasacha. Along the road which crosses the Cordillera Escalera, joining Tarapoto to the Amazonian town of Yurimaguas, *M. cisseis phanodemus* was commonly seen around 800-900 m; surprisingly, we also observed it on slopes above the road, around 1200 m. Males are more commonly observed than females and they fly above the canopy, and also along streams or paths, between 5 and 10 m, sometimes lower, gliding in a majestic manner (Fig. 5A). Their flight is slow and nonchalant, although they often turn suddenly to interact with other males, not only of the same species, but also including *M. telemachus martini* and *M. menelaus occidentalis*, as we observed several times. When males fly through open areas, for example crossing a large road or shrubby area, they usually fly lower to the ground (1-2 m), and occasionally individuals can be encountered at rest on low vegetation (Fig. 5B). Females may be seen flying similarly to males, but more often we observed them flying around trees. During favorable periods, several males, and sometimes females,

can be observed within a few hours, their activity beginning around 9 a.m. on sunny days (Table 1). The earliest observation was made at 8.35 a.m. on a sunny and hot morning, along the Shilcayo river. When the sky is overcast, and moreover if there is weak, continuous rain, *M. cisseis* and other *Morpho* species do not fly, except *M. menelaus occidentalis*, as we observed in March 2006. Our observations are consistent with those reported by Neild (2008). Neild (pers. comm.) observed *M. cisseis* from 10 a.m. (sometimes earlier) until ca. 2 p.m., with 3 p.m. corresponding to the very latest sighting. Obviously, *M. cisseis* usually needs sunshine to fly, even if Neild (2008) once observed a male flying during a period of fine, light rain on an overcast morning.

Life cycle

Despite regular searching after our first discovery in October 2008, we were unable to discover more larvae until the end of August 2009, when we encountered nine small solitary larvae and eight isolated hemispheric eggs on four *Abuta* trees. At the end of November, four older larvae were found on the tree where eggs were collected at the end of August, and two others on a new tree. Eggs were deposited on the upper side of leaves, but we found larvae on the lower surface, where they had woven a small carpet of silk (Fig. 6). Several years later, on the 22nd of March 2013, a short survey allowed us to discover two eggs, isolated and on different leaves of a tree previously noted in 2009 (Fig. 7).



Fig. 5. A: *Morpho cisseis phanodemus* male gliding down along the left bank of the Río Shilcayo (picture taken by Catherine Cassildé from the observation tower).- B: *M. cisseis phanodemus* male at rest in low vegetation (CR).



Fig. 6. A larva of *Morpho cisseis phanodemus* on its silk carpet (CR).



Fig. 7. Two views of a *Morpho cisseis phanodemus* egg (PB).



Fig. 8. Parasites emerging from a larva of *Morpho cisseis phanodemus* (CR).

Attempts to rear the immature stages resulted in a significant mortality rate (Table 2). We obtained only three adults (~ 13% of the individuals), of which only one came from a L1 larva, while the others were obtained from 5th instar larvae collected in the field. Three out of 7 eggs did not hatch. The end of the development, from the 4th instar, was critical, with 10 out of 12 larvae which reached 4th instar dying either during this instar or during the 5th instar. During the L1, L2 and L3 instars, mortality was lower, and all L3 larvae moulted into L4. We could not identify mortality factors, except for two cases of parasitism in larvae collected in the field on the 24th November 2009. The emergence of parasitoids began one day later from the first larva (collected as 5th instar), and ended on the 30th. The second larva was collected as the 3rd instar, and successfully completed its L3 to L4 moulting, but parasitoids emerged and the larva died on the 24th December 2009 (Fig. 8).

The dates of egg laying being unknown, the numbers of days from the discovery of eggs to the hatching of L1 larvae are minimum estimates of the length of the embryonic development, which may last *ca.* 13 days on average (Table 3). The L1 stage lasts *ca.* 16 days and the following stages *ca.* 20-23 days, but individual variations seem substantial. The duration of the pupal stage is approximately 19 days. On average, the development lasts approximately 134 days, but obviously varies from one individual to another.

Our field observations of adults were made in March, September and November. Moreover, in several localities in the basin of the middle Huallaga, specimens were collected for our research from 2008 to 2011, in January, February, May, June to August, October and December. Therefore, *M. cisseis phanodemus* appears to fly all year.

Morphological characteristics of immature stages

Egg

The diameter of the hemispheric egg is approximately 3 mm. There is an irregular rounded, pale reddish-brown patch at the top, and a circle of reddish-brown figures in the form of more-or-less irregular hemispherical patches with a variable number of projections, from one to five (Figs. 7, 9A).

Larvae

From the 1st to the 5th instars, there are several changes in the pattern and colour, and in the size, colour and distribution of setae.

The 1st instar larva (Fig. 9B) has a reddish-brown head, covered by long dark brown to black setae. Dorsally, the body presents two oval, yellow patches on a brownish-red background. Laterally there are yellow patches incompletely separated by oblique, brownish-red lines. There are dorso-lateral isolated black setae and latero-ventral groups of white setae. At the anal extremity, the caudal tails are reddish-brown, with a few black setae.

The 2nd instar larva (Fig. 9C) closely resembles the 1st instar, but some off-white markings appear on the brownish-red colour. On the second (T2) and third (T3) thoracic segments, there are pairs of long, curved setae directed towards the head. There are pairs of dense tufts of setae on the first (A1) and



Fig. 9. The development of *Morpho cisseis phanodemus* (CR).-A: egg.- B: 1st instar larva.- C: 2nd instar larva.- D: 3rd instar larva.- E: 4th instar larva, exhibiting drops of the fluid produced by the grooming gland (cf. DeVries & Ramirez, 1994).- F: 4th instar larva.- G: 5th instar larva.- H: Prepupa.- I: Pupa.- J: A hatched male. T2, T3: 2nd and 3rd thoracic segments. A1- A9: abdominal segments. CT: caudal tails.

fifth (A5) abdominal segments. The A5 tufts are formed by an anterior group of long whitish and pink setae, and a posterior group of short reddish-brown setae. Latero-ventral white setae are denser than on 1st instar larva. The caudal tails are a pale ochre-yellow, with white setae.

Off-white markings are much more developed in the 3rd instar larva, while the brownish-red is darker (Fig. 9D). Very dark reddish-brown lines underline the two dorsal yellow patches, which exhibit a light greenish tint; a small dorsal yellow patch is present on the 9th abdominal segment (A9). The 3rd instar is characterized by the addition of supplementary pairs of tufts on segments A2, A4 and A8 segments. The A8 tufts are formed by groups of whitish and reddish-brown setae, as are the A5 tufts, the latter being much longer. On segment A7 a few setae hint at a future pair of tufts which are fully formed at the 4th instar. The caudal tails are a pale ochre-yellow, with white setae.

The 4th instar larva is similar to the 3rd instar, but the greenish tint of dorsal and lateral yellow patches is more developed (Fig. 9E). The dorsal patch on A9 is larger, extending onto A8, and there is another small dorsal patch on the 1st abdominal segment (A1). Laterally, there are 7 yellow-green patches well separated by transverse dark brownish-red bordered by off-white lines. The caudal tails are darker than in previous instars, with whitish and reddish-brown setae. As in *M. cypris* Westwood, 1851 (DeVries & Martinez, 1994), *M. amathonte* Deyrolle, 1860 (Constantino, 1997), and *M. sulkowskyi sulkowskyi* Kollar, 1850 (Heredia & Alvarez-López, 2007), there is a “grooming gland” producing drops of a liquid on the A1 tufts that we observed on a 4th instar larva (Fig. 9G).

In the 5th instar larva, the green tint of the dorsal and lateral patches is more intense (Fig. 9F). The tufts and the caudal tails are similar to those of the 4th instar. The pattern does not change until the transformation of the larva into the prepupa, which is totally green (Fig. 9H).

The pupa (Fig. 9I) is ovoid, with short cephalic horns. The colour is green with white markings, which do not prefigure the pattern of the wings. The figures 9J and 10 illustrate the three adults that were obtained. A male (Fig. 10A) corresponds to the typical blue phenotype of *M. cisseis phanodemus*, while the female (Fig. 10B) shows an orange tint within the blue (that can be much more developed in both sexes).

Fig. 11. A: Egg of *Morpho menelaus occidentalis* with a complete brownish ring (CR).- B: Eggs of *M. rhodopteron nevadensis*, showing an interrupted ring (picture by Fredy Montero Abril).- C: Egg of *M. marcus intermedia*, showing a ring of separated marks (CR; this egg was collected in October 2013, at several meters high in a Fabaceae tree, after an ovipositing female was observed).

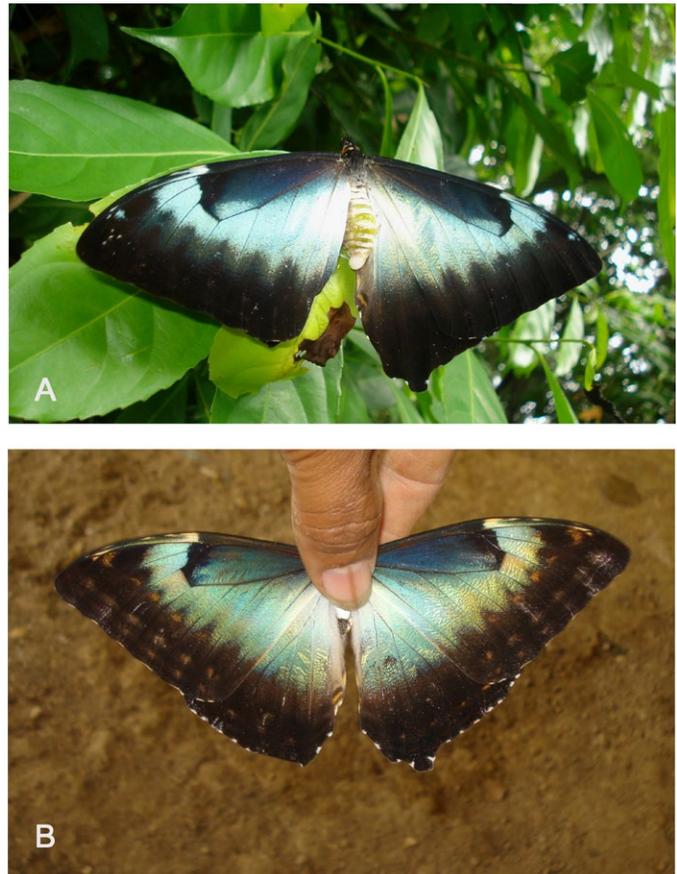


Fig. 10. A male (A) and a female (B) of *Morpho cisseis phanodemus* which were released in the field (CR).

DISCUSSION

Comparison of *Morpho cisseis phanodemus* life cycle with other *Morpho* species

As in the rearing of several other *Morpho* species (Young & Muyschondt, 1972; DeVries & Ramirez, 1994; Constantino & Corredor, 2004; Heredia & Alvarez-López, 2007), we observed a high rate of mortality. Beyond the impact of parasitoids, viruses may play an important role (DeVries & Martinez, 1994; Constantino & Corredor, 2004). Despite the fact that we performed the rearing of *M. cisseis phanodemus* in the environmental context of its natural habitat, we cannot exclude the possible effects of artificial conditions in closed boxes (that, however, do protect the larvae from parasitoids and potential predators).



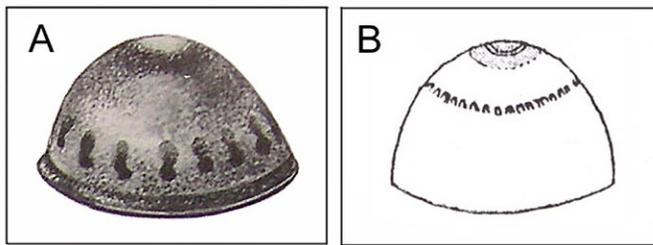


Fig. 12. A: George E. Martinez's drawing of an egg of *Morpho cypris* (from Fig. 2 in DeVries & Martinez, 1994).- B: Eugen Krüger's drawing of an egg of *M. hecuba* (from Krüger, 1929, p. 27).

Table 4 allows us to compare our estimate of the length of the life cycle of *M. cisseis phanodemus* with available information for sixteen other *Morpho* species. It should be emphasized that in several studies larvae were not reared under natural or precisely controlled conditions, and data may therefore be imprecise, but nevertheless, some points may be noted.

A majority of species, including *M. cisseis phanodemus*, have life cycle lengths ranging from ca. 3 to ca. 6 months. The shortest life cycles of less than 3 months have been observed only in *M. helenor* (Cramer, 1776), in all its subspecies except *M. helenor carillensis* Le Moutt & Réal, 1962, of which the cycle lasts 3-4 months. Longer life cycles of 7-8 months have been observed in univoltine species from south-eastern Brazil, including: *M. menelaus coeruleus* (Perry, 1810), *M. epistrophus epistrophus* (Fabricius, 1796) *M. hercules* (Dalman, 1823), *M. anaxibia* (Esper, 1801). These data were obtained by Otero (1966), who indicated that his experiments were performed with favourable temperatures that probably accelerated the development. This may also explain the life cycle length (ca. 6 months) that Otero obtained for another univoltine species, *M. iphitus iphitus* C. Felder & R. Felder, 1867. Interestingly, Otero & Marigo (1990) indicated that, in the field, larvae of *M. epistrophus catenaria* (Perry, 1811) do not eat during several winter weeks. Rather long cycles (6-7 months) have been obtained for two montane species, *M. rhodopteron nevadensis* E. Krüger, 1925 and *M. godartii lachaumei* Blandin, 2007. However, *M. sulkowskyi sulkowskyi*, which lives at high altitudes (1800-3000 m, at least), seems to have a shorter cycle (less than 6 months); as this species was reared at 1000 m (Heredia & Alvarez-López, 2007), the development may have been accelerated. Therefore, it is difficult to relate the length of life cycles to the climatic characteristics of natural habitats. Moreover, marked differences can be observed between subspecies, as illustrated by *M. polyphemus* Westwood, 1850. In El Salvador, according to Young & Muysshondt (1972), the subspecies *polyphemus*, a population of which was studied at ca. 800 m, has a ca. 4 months life cycle, while the subspecies *catalina* Corea & Chacón, 1984, observed in the cloud forest of the Area de Conservación Guanacaste (Costa Rica), has a very long cycle, lasting about 11 months, perhaps in relation with the relatively cold conditions of its habitat (Miller *et al.*, 2006).

As for several lowland species, the length of the *M. cisseis phanodemus* cycle is consistent with the existence of two or three generations a year. In western Amazonia, adults of *M. cisseis* were observed by Otto Michael throughout the

year (reported by Fruhstorfer, 1912), observations which we confirmed by our observations. However, it is interesting to identify whether there is marked variation in the abundance of adults in relation to seasonal variation in rainfall. In Venezuela, for example, where there are clearly defined rainy and dry seasons, adults of *Morpho* species are more abundant at the start of the two rainfall peaks (April/May/June and October/November), and some species are absent during the drier months of the year; this is notably the case for *M. cisseis* (Neild, pers. comm.). In French Guiana, *M. hecuba*, the sister-species of *M. cisseis*, was exclusively observed flying in April-May and October-November, a seasonal pattern shared with several other *Morpho* species (Lacomme, 2007). We hypothesize that marked seasonal climatic variations tend to synchronize individual developments, and, conversely, the presence of adults throughout the year, as it is the case for *M. cisseis phanodemus* in north-eastern Peru, results from generation overlap and individual variations of development length, in a less seasonal context.

Comparison of *Morpho cisseis phanodemus* early stages with other *Morpho* species

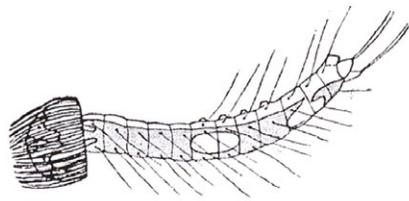
In the genus *Morpho*, the egg is hemispheric. As far as we know, the freshly oviposited egg is a translucent light green, off-white, or very pale yellow (Otero, 1966; Young & Muysshondt, 1972, 1973; Tákács & Tello, 1993; Constantino, 1997; DeVries & Martinez, 1994; Constantino & Corredor, 2004; Guerra-Serrudo & Ledezma-Arias, 2008; Montero Abril & Ortiz Perez, 2010). In several species, within a short time (1-4 days), a brownish-red or crimson circular band appears that can form a more or less continuous circle, as in *M. menelaus occidentalis* (Fig. 11A), and *M. helenor macrophthalmus* Fruhstorfer, 1913 (Constantino & Corredor, 2004). It can be interrupted, as in *M. rhodopteron nevadensis* (Fig. 11B), and *M. sulkowskyi sulkowskyi* (Heredia & Alvarez-López, 2007). The circle is broken in more or less regular dots in *M. marcus intermedia* Kaye, 1917 (Fig. 11C), *M. polyphemus polyphemus*, (Young & Muysshondt, 1972), *M. amathonte* (Constantino, 1997), two subspecies of *M. deidamia* (Hübner, [1819]) (Tákács & Tello, 1993; Furtado, 2000), and several subspecies of *M. helenor*; (Otero, 1966; Young & Muysshondt, 1972; Guilbot & Plantrou, 1980; Constantino & Corredor, 2004). In *M. rhetenor* (Cramer, 1775), there is a circle of reddish elliptic figures (Tákács & Tello, 1994), and the sister-species *M. cypris* presents irregular, vertically oriented peanut-shaped large dots all around the egg (Fig. 12A). Krüger (1929) provided a drawing of an egg of *M. hecuba* (presumably ssp. *werneri* Hopp, 1921); the circle is also made of separated dots, in form of "II", "M" or inverted "V" that recall the *phanodemus* figures, but are much smaller (Fig. 12B). Thus, the egg of *M. cisseis phanodemus*, although having a circle of separated markings as in several species, is unique with its large, strange markings (Fig. 7).

In species that have solitary larvae, the pattern of the 1st instar larva is generally characterized by a brownish-red colour, associated with two dorsal, whitish-yellow patches. In the two *Laurschwartzia* species, the 1st instar larvae are probably very similar, with rather wide, oval patches, as suggested by Krüger's (1929) drawing of the larva of *M. hecuba* (Fig. 13A), compared to the larva of *M. cisseis phanodemus* (Fig. 13B).

A similar pattern exists in representatives of several other subgenera: *Grasseia* Le Moult & Réal, 1962 (*M. menelaus occidentalis* (Fig. 14A) and *M. amathonte* in Constantino, 1997), *Iphixibia* Le Moult & Réal, 1962 (*M.anaxibia* in Otero, 1966), *Megamede*, Hübner, [1819] (*M. cypris* in DeVries & Martinez, 1994; *M. rhetenor* in Tákács & Tello, 1994), and *Morpho* (*M. polyphemus polyphemus* in Young & Muysshondt, 1972, *M. deidamia neoptolemus* in Furtado, 2000, and various subspecies of *M. helenor* in Otero, 1966 and Constantino & Corredor, 2004). The pattern is different in two species of the subgenus *Cytheritis* Le Moult & Réal, 1962 *sensu stricto* (cf. Cassildé *et al.*, 2010), *M. rhodopteron nevadensis* (Fig. 14B) and *M. sulkowskyi sulkowskyi* (Heredia & Alvarez-López, 2007), that have narrow, linear dorsal patches.

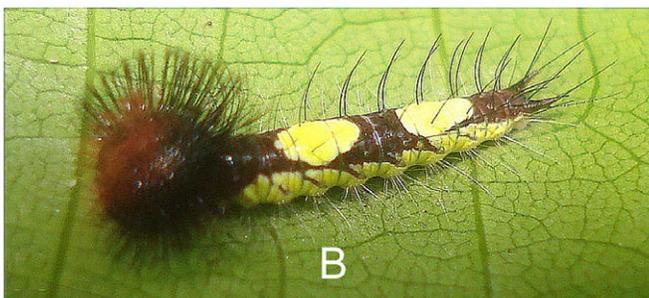
In species which have gregarious larvae, the 1st instar larvae also exhibit a reddish colour, with whitish or yellowish marks, the design of which may strongly differ from that of the previous species. For example, in *M. telemachus martini*, the anterior and posterior whitish marks are both divided in two parts by a reddish transversal line, a pattern not modified in the 2nd instar larvae (Fig. 15). In *M. iphitus* there are dorsal marks in form of “H” (Otero, 1966). However, in *M. godartii lachaumei*, there are more or less oval dorsal patches (Guerra-Serrudo & Ledezma-Arias, 2008), as in *M. menelaus*.

The comparison of 4th and 5th instars reveals common features among several species, as well as clear differences. *M. cisseis phanodemus* (Fig. 16A) and *M. hecuba hecuba* (Fig. 16B) larvae are very similar, with two medio-dorsal wide patches, that extend on abdominal segments A2-A3-A4 and A5-A6-A7. Such patches, with the same extent, also exist in *M. cypris* (Fig. 16C), *M. rhetenor* (Tákács & Tello, 1994), *M.anaxibia* (Fig. 16D), *M. theseus aquarius* Butler, 1872 (Fig. 16E, F). All these species belong to a clade named the “canopy clade”, in relation with flight behaviour of males (Penz & DeVries, 2002).



frisch geschlüpfte Raupe von *Morpho hecuba*
(vergrößert)

A



B

Fig. 13. A: Eugen Krüger's drawing of a 1st instar larva of *Morpho hecuba* (from Krüger, 1929, p. 27).- B: First instar larva of *M. cisseis phanodemus* (CR).



A



B

Fig. 14. A: 1st instar larva of *Morpho menelaus occidentalis*, reared at Wayrasacha (CR).- B 1st instar larva of *M. rhodopteron nevadensis* (Colombia – picture by Fredy Montero Abril).

A similar pattern exists in species belonging to a different clade: *M. menelaus occidentalis* (Fig. 16J), *M. menelaus coeruleus* (Otero & Marigo, 1990), *M. amathonte* (Constantino, 1997), and *M. godartii lachaumei* (Guerra-Serrudo & Ledezma-Arias, 2008). *Morpho godartii tingomariensis* Blandin, 2007 should be associated with this group, although the two dorsal patches are connected between A4 and A5 segments (Fig. 16K).

In a second group, the wide dorsal patches cover only the A2-A3 and A5-A6 segments. This group includes *M. granadensis polybaptus* C. Felder & R. Felder, 1867 (Fig. 16G;



Fig. 15. 1st and 2nd instars larvae of *Morpho telemachus martini*, reared at Wayrasacha (CR).

Young, 1982), several subspecies of *M. helenor* (Fig. 16H; Otero, 1966; Young & Muysshondt, 1973; Guilbot & Plantrou, 1980; Urich & Emmel, 1990; Constantino & Corredor, 2004), *M. achilles phokylides* (Blandin *et al.*, 2014), *M. deidamia grambergi* Weber, 1944 (Tákács & Tello, 1993) and *M. deidamia neoptolemus* Wood, 1863 (Furtado, 2000). These species belong to the *helenor* clade (Blandin & Purser, 2013), which also includes the Brazilian white *M. epistrophus* and *M. iphitus*, that have gregarious larvae.

Blandin & Purser (2013) tentatively included the Central-American white *M. polyphemus* in the *helenor* clade. In fact, the 5th instar larva of *M. polyphemus polyphemus* Westwood, 1850 has dorsal patches extending on A2-A3-A4 and A5-A6-A7 segments respectively (Young & Muysshondt, 1972, Fig. 2). However, in the 5th instar larva of *M. polyphemus catalina*, the extension of the anterior patch on A4 is reduced to a small spot, and there is practically no extension of the posterior patch on A7 (Fig. 16I). Thus, *M. polyphemus* cannot be associated on the basis of the immature stages with either of the two previous groups.

A third group is illustrated by *M. rhodopteron nevadensis* (Fig. 16L), the larva of which presents two narrow dorsal patches. Another species of the subgenus *Cytheritis sensu stricto*, *M. aega* (Hübner, 1822), also has elongated but less narrow dorsal patches (Otero & Marigo, 1990), while these patches are very narrow in *M. sulkowskyi sulkowskyi* (Heredia & Alvarez-López, 2007).

Species that have gregarious larvae belong to different clades: the *telemachus* clade (*M. telemachus*, *M. hercules*), the *menelaus* clade (*M. godartii*), and the *helenor* clade (*M. epistrophus*, *M. iphitus*). Despite clear differences in the structure and colour of dorsal patches, their larvae exhibit a predominantly red pattern, as illustrated by *M. godartii tingomariensis* (Fig. 16K), *M. telemachus martini* and *M. epistrophus catenaria* (Fig. 17). This pattern possibly has an aposematic function, as the larvae form conspicuous masses in the vegetation.

In various species belonging to different subgenera, the 5th instar presents important changes, as illustrated by *M. theseus aquarius* (Fig. 16E,F), and subspecies of *M. helenor*, such as *macrophthalmus* and *telamon* Röber, 1903 (Constantino & Corredor, 2004). A similar phenomenon has been described in *M. cypris* by DeVries & Ramirez (1994), who distinguished two phases in the evolution of colour within the 5th instar (see also Purser & Urbina, 2008). In *M. cisseis phanodemus*, there is no major change between the 4th and the 5th instars, except that the colour of the dorsal patches and lateral marks becomes a bright green. Similarly, we did not notice marked changes in *M. menelaus occidentalis* (unpublished data), an observation consistent with Otero's data (1966) on *M. menelaus coeruleus*. The 5th instar is also quite similar to the 4th instar in *M. anaxibia* (Otero, 1966) and *M. amathonte* (Constantino, 1997).

Beyond the coloration pattern, the organization of setae also provides interesting characters for interspecific comparison. In all species, the 1st instar larva presents dorsal and lateral setae on the body, which are in low numbers. More often, the dorsal setae are black and the lateral setae are white, as illustrated in species as different as *M. cisseis phanodemus* (Fig. 13B), *M.*

menelaus occidentalis and *M. rhodopteron nevadensis* (Fig. 14A,B).

The subsequent development is characterized by the progressive apparition, from the 2nd to the 4th instars, of dorso-lateral pairs of setae forming dense tufts, which differ between species in number, size and colour. *M. cisseis phanodemus* (Fig. 16A) and *M. hecuba hecuba* (Fig. 16B), present 6 pairs of tufts on abdominal segments A1, A2, A4, A5, A7 and A8. In 5th instar larvae of both species, the A4 and A5 tufts are of similar size, with not very long setae. This is also the case for *M. menelaus occidentalis* (Fig. 16J), *M. menelaus coeruleus* (Otero & Marigo, 1990), and *M. godartii lachaumei* (Guerra-Serrudo & Ledezma-Arias, 2008). Curiously, differing from *M. godartii lachaumei*, *M. godartii tingomariensis* (Fig. 16K) has also pairs of tufts on A3 and A6 segments. This intraspecific variation is interesting, as *M. godartii* belongs to the sister-clade of the *Cytheritis* clade (Blandin & Purser, 2013), in which species such as *M. rhodopteron nevadensis* (Fig. 16L), *M. sulkowskyi sulkowskyi* (Heredia & Alvarez-López, 2007), and *M. aega* (Otero & Marigo, 1990) also have pairs of tufts on the A3 and A6 segments.

Among species having 6 pairs of tufts, the A5 tufts are longer than the A4 tufts, notably thanks to long white or off-white setae, in *M. cypris cypris* (Fig. 16C), *M. anaxibia* (Fig. 16D), and *M. theseus aquarius* (Fig. 16E,F). On the contrary, the longest tufts are situated on A4 in *M. helenor theodorus* (Fig. 16H) and *M. deidamia* (Tákács & Tello, 1993). In *M. granadensis polybatus* (Fig. 16G), *M. polyphemus catalina* (Fig. 16I) and *M. polyphemus polyphemus* (Young & Muysshondt, 1972; Fig. 2) A4 and A5 tufts are more similar in size.

The gregarious larvae of *M. telemachus martini* and *M. hercules* strongly differ from the previous species, having 8 pairs of abdominal tufts from A1 to A8 made of red and blackish hairs in the former (Fig. 17A; Brévignon, 2007), white and black in the latter (Otero, 1966). In another gregarious species, *M. epistrophus catenaria* (Perry, 1811) (Fig. 17B), there are tufts also from A1 to A8, the relative importance of white and red setae changing between segments.

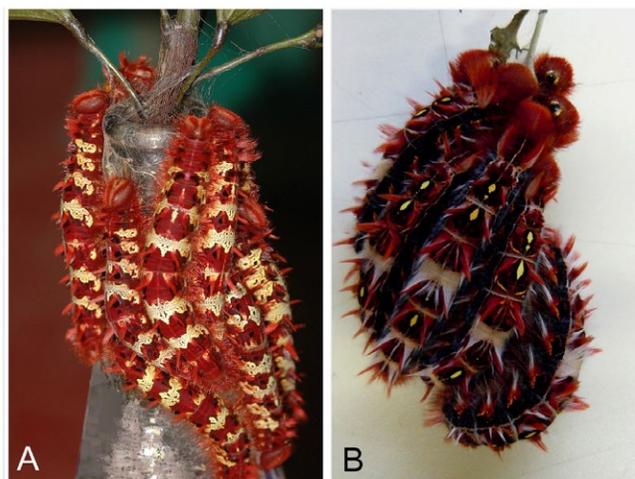


Fig. 17. Gregarious larvae. A: *Morpho telemachus martini*, 5th instar (CR). B: *M. epistrophus catenaria*, 4th instar (Brazil – PB).



Fig. 16. Larvae of various *Morpho* species (NB: pictures are at different scales). A1-A8: abdominal segments. A: 5th instar of *M. cisseis phanodemus* (CR). - B: 5th instar of *M. hecuba hecuba* (French Guyana – EVO-DHE004523A © Photoshot/age fotostock). - C: 4th instar of *M. cypris cypris* (Colombia – picture by Bruce Purser). - D: 4th instar of *M. anaxibia* (Brazil – PB). - E: 5th instar, first period, of *M. theseus aquarius* (Costa Rica – picture by Daniel Janzen). - F: 5th instar, second period, of *M. theseus aquarius* (Costa Rica – picture by Daniel Janzen). - G: 5th instar of *M. granadensis polybaptus* (Costa Rica – picture by Daniel Janzen). - H: 5th instar of *M. helenor theodorus* (reared at Wayrasacha – CR). - I: 5th instar of *M. polyphemus catalina* (Costa Rica – picture by Daniel Janzen). - J: 4th instar of *M. menelaus occidentalis* (reared at Wayrasacha – CR). - K: 4th (or 5th?) instar of *M. godartii tingomariensis* (Peru – picture by Michael Büche). - L: 5th instar of *M. rhodopteron nevadensis* (Colombia – picture by Fredy Montero).

Do hostplants support the monophyly of *Laurischwartzia*?

The phylogeny of the genus *Morpho* is not definitely established, but Blandin & Purser (2013) proposed a synthetic tree, based on recent phylogenetic studies using morphological characters of adults (Penz & DeVries, 2002; Cassildé *et al.*, 2010), sequences of mitochondrial genes (Cassildé *et al.*, 2012) and finally a combination of morphological characters and mitochondrial and nuclear genes sequences (Penz *et al.*, 2012). These studies demonstrated that *M. cisseis* and *M. hecuba* form a well supported clade, corresponding to the subgenus *Laurischwartzia*, the sister-clade to the subgenus *Iphimedeia*.

According to Luis Otero (pers. comm. in Constantino, 1997), *M. hecuba* larvae feed on an undetermined genus of Menispermaceae, and *M. cisseis* larvae also feed on Menispermaceae, specifically an *Abuta* species. Our work confirms Luis Otero's hostplant record for *M. cisseis*. Reliable information for the sister clade *Iphimedeia* indicates that *M. hercules*, *M. theseus* and *M. telemachus* also feed on Menispermaceae, notably *Abuta* species (Otero, 1966; Miller *et al.* 2007; Brévignon, 2007; Beccaloni *et al.*, 2008; Neild, 2008; Gallusser *et al.*, 2010). Moreover, we discovered that the larvae of *M. cisseis phanodemus* and *M. telemachus martini* feed on the same *Abuta* species in our study area. Interestingly, *Laurischwartzia* + *Iphimedeia* is a well supported clade within the "canopy clade", which includes two other branches, the subgenus *Iphixibia* (*M. anaxibia*), and the subgenus *Megamede* (*M. rhetenor* and *M. cypris*). These last three species feed on plants belonging to different families: *M. iphixibia* on Quinaceae, Erythroxylaceae, Lauraceae, Guttiferaceae, and Myrtaceae, *M. rhetenor* on Fabaceae and Mimosaceae, and *M. cypris* on Mimosaceae, but none of them has been reported feeding on Menispermaceae (Beccaloni *et al.*, 2008). Therefore, we hypothesize that the divergence of the (*Iphimedeia* + *Laurischwartzia*) branch from the (*Iphixibia* + *Megamede*) branch was associated with a shift to a single and different hostplant family. However, it is necessary to discover the hostplants of the two other *Iphimedeia* species, *M. amphitryon* and *M. niepelti*, to check this hypothesis and eventually confirm the *Iphimedeia* + *Laurischwartzia* branch as a "Menispermaceae clade".

Are early stages characters congruent with phylogenetic relationships within the genus *Morpho*?

An apparent lack of congruence between phylogenies as revealed by adult and early stage characters was recently suggested for the tribe Brassolini (Morphinae) (Penz *et al.*, 2013). In the genus *Morpho*, the similar characters of *M. cisseis* and *M. hecuba* larvae are consistent with the monophyly of the subgenus *Laurischwartzia*. Similarly, the close resemblance between larvae of *M. granadensis* and *M. helenor* is consistent with their phylogenetic relationships, while their differences in comparison with *M. deidamia* larvae support the position of the latter on a separate branch (Penz *et al.*, 2012; Blandin & Purser, 2013). Moreover, some unresolved taxonomic issues might be clarified with the help of larval characters. For example, the position of *M. polyphemus* remained uncertain in previous phylogenetic studies (Cassildé *et al.*, 2012; Penz *et al.*, 2012), and Blandin & Purser (2013) tentatively included this

species in the subgenus *Morpho*, with the other white species, *M. epistrophus* and *M. iphitus*. However, larval phenotypic characters do not support this suggestion, and indicate that *M. polyphemus* may belong to an isolated clade.

Larval characters, however, do not always provide clear phylogenetic signals. For example, while *Laurischwartzia* adults differ from *Iphimedeia* adults by obvious morphological characters, including wing shape and many details in the ventral pattern of the wings (Blandin, 1988), there are no obvious diagnostic larval characters, notably because the comparison between the two subgenera is blurred by the existence of gregarious larvae in two *Iphimedeia* species that have very distinctive patterns.

That the understanding of the evolution of a butterfly genus may be improved when both early stages and adult characters are considered was emphasized as early as 1984 in a pioneering study by Aiello (1984) on the genus *Adelpha* (Nymphalidae: Limenitidini). Aiello (1984) suggested that adult and early stages are subject to different selective pressures that drive different morphological evolution in adults and early stages, meaning that phylogenetic information in these two character systems is often complementary. Our comparative approach, despite its preliminary nature, suggests that the genus *Morpho* should provide an interesting model to further explore this issue, even though the early stages of several species are still unknown. The unexpected discovery of the early stages of a common and widely distributed species emphasizes the necessity of patient, meticulous observation in the field.

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Table 1. Numbers of observations of *Morpho cisseis phanodemus* flying in the Cordillera Escalera. * beginning of observation.- X: observation was ended when no *Morpho* individual had been seen in flight for half an hour.

Localities	road Tarapoto-Yurimaguas 800-900 m		Río Shilcayo, observation tower 450 m						Río Cumbasa 470 m		
	16-03-2006	20-03-2006	18-03-2006	19-03-2006	17-03-2007	18-03-2007	3-11-2009	7-11-2009	16-03-2008	18-03-2008	22-09-2011
7-8 H	-	-	*0	*0	*0	*0	-	-	-	-	-
8-9 H	-	*0	0	0	0	0	-	*1	*0	*0	-
9-10 H	*1	1	0	0	1	0	*1	2	0	0	*2
10-11 H	1	0	0	1	2	2	2	0	3	2	5
11-12 H	4	1	0	2	1	0	0	0	0	0	1
12-13 H	3	3	0	1	0	0	X	0	X	X	0
13-14 H	1	5	0	-	0	0	-	X	-	-	0
14-15 H	X	X	X	X	0	0	-	-	-	-	X
15-17H	-	-	-	-	0	X	-	-	-	-	-
17-18 H	-	-	-	-	X	-	-	-	-	-	-

Table 2. Data from the rearing of *Morpho cisseis phanodemus*. ω : egg.- L1-5: larva instars.- PP: prepupa.- P: pupa.- Ad: adult. ?: date not noted.- †: death during moulting.- !†: death between moulting

Day of collect	Collected instar	Dates of events								
		$\omega \rightarrow L1$	L1 \rightarrow L2	L2 \rightarrow L3	L3 \rightarrow L4	L4 \rightarrow L5	L5 \rightarrow PP	PP \rightarrow P	P \rightarrow Ad	
20/08/09	L1	-	08/09 †	-	-	-	-	-	-	-
20/08/09	L1	-	09/09	02/10	25/10	15/11	08/12 †	-	-	-
20/08/09	L1	-	08/09	28/09	23/10	15/11	04/12	05/12 †	-	-
20/08/09	L1	-	12/09	29/09	22/10	10/11	30/11	03/12	21/12 ♂	-
20/08/09	L1	-	08/09	29/09	26/10	15/11	04/12 †	-	-	-
28/08/09	ω	09/09	26/09	29/10	16/11	?	13/12 †	-	-	-
28/08/09	ω	09/09 †	-	-	-	-	-	-	-	-
28/08/09	ω	09/09 †	-	-	-	-	-	-	-	-
28/08/09	ω	10/09	27/09	17/10	07/11	30/11 †	-	-	-	-
28/08/09	ω	10/09	26/09	11/10	26/10	13/11 †	-	-	-	-
28/08/09	ω	10/09	26/09	11/10	05/11	02/12	20/12 †	-	-	-
28/08/09	ω	!†	-	-	-	-	-	-	-	-
30/08/09	L1	-	!†	-	-	-	-	-	-	-
30/08/09	L1	-	10/09	25/09	15/10	08/11	!†	-	-	-
30/08/09	L1	-	17/09 †	-	-	-	-	-	-	-
30/08/09	L1	-	08/09	29/09	22/10	11/11	29/11 †	-	-	-
30/08/09	ω	10/09	23/09	17/10	06/11	24/11 †	-	-	-	-
24/11/09	L2	-	-	25/11 †	-	-	-	-	-	-
24/11/09	L3	-	-	-	04/12	24/12 †	-	-	-	-
24/11/09	L3	-	-	!†	-	-	-	-	-	-
24/11/09	L5	-	-	-	-	-	!†	-	-	-
24/11/09	L5	-	-	-	-	-	04/12	06/12	26/12 ♀	-
24/11/09	L5	-	-	-	-	-	04/12	08/12	26/12 ♂	-

Table 3. Instar duration (days) * The dates of egg laying being unknown, the numbers of days from the discovery of eggs to the hatching of L1 larvae are minimum estimates of the length of the embryonic development.

Day of collect	Collected instar	Instar lengths (days)							
		egg*	L1	L2	L3	L4	L5	PP	P
20/08/09	L1	-	-	22	23	21	23	-	-
20/08/09	L1	-	-	20	25	23	19	-	-
20/08/09	L1	-	-	17	23	19	20	3	18
20/08/09	L1	-	-	21	27	20	19	-	-
28/08/09	ω	12	17	33	17	-	-	-	-
28/08/09	ω	12	-	-	-	-	-	-	-
28/08/09	ω	12	-	-	-	-	-	-	-
28/08/09	ω	13	17	20	21	-	-	-	-
28/08/09	ω	13	16	15	15	-	-	-	-
28/08/09	ω	13	16	15	25	18	-	-	-
28/08/09	ω	13	-	-	-	-	-	-	-
30/08/09	L1	-	-	15	20	24	-	-	-
30/08/09	L1	-	-	21	23	20	18	-	-
30/08/09	ω	13	13	24	19	-	-	-	-
24/11/09	L3	-	-	-	-	20	-	-	-
24/11/09	L5	-	-	-	-	-	-	2	20
24/11/09	L5	-	-	-	-	-	-	4	18
Rounded average values		13	16	20	22	21	20	3	19

Table 4. Life cycle length in different *Morpho* species, arranged from longer to shorter cycles. * Authors indicate 10 months as a caterpillar, and 6 weeks pupating.

Species and subspecies (names according to Blandin, 2007a)	Locality	Life cycle length in days	Authors and names they used
<i>M. polyphemus catalina</i>	Costa Rica, 800-1400 m	>340*	Miller, Janzen & Hallwachs, 2006 <i>M. polyphemus</i>
<i>M. menelaus coeruleus</i>	Brazil, Rio de Janeiro area	240	Otero, 1966 <i>M. menelaus tenuilimbata</i>
<i>M. epistrophus epistrophus</i>	Brazil, Rio de Janeiro area	233	Otero, 1966 <i>M. laertes</i>
<i>M. hercules</i> (probably ssp. <i>hercules</i>)	Brazil, Rio de Janeiro area	227	Otero, 1966 <i>M. hercules</i>
<i>M. anaxibia</i>	Brazil, Rio de Janeiro area	213	Otero, 1966 <i>M. anaxibia</i>
<i>M. rhodopteron nevadensis</i>	Colombia, Sierra Nevada de Santa Marta, 1500 m	199	Montero Abril & Ortiz Perez, 2010 <i>M. rhodopteron nevadensis</i>
<i>M. godartii lachaumei</i>	Bolivia, La Paz, 1300-1500 m	187-218	Guerra-Serrudo & Ledezma-Arias, 2008 <i>M. menelaus godartii</i>
<i>M. iphitus iphitus</i>	Brazil, Rio de Janeiro State	188	Otero, 1966 <i>M. athena</i>
<i>M. sulkowskyi sulkowskyi</i>	Colombia, 2400-2500 m (reared at ca. 1000 m)	161-178	Heredia & Alvarez-López, 2007 <i>M. sulkowskyi</i>
<i>M. rhetenor rhetenor</i>	Peru, Madre de Dios	170	Tákács & Tello, 1994 <i>M. rhetenor</i> f. <i>cacica</i>
<i>M. cypris bugaba</i>	Costa Rica, Pacific coast	157-160	DeVries & Martinez, 1994 <i>M. cypris</i>
<i>M. telemachus martini</i>	Peru, San Martín	132-175	Gallusser et al, 2010 <i>M. telemachus martini</i>
<i>M. telemachus telemachus</i>	French Guiana	106-152	Brévignon, 2007 <i>M. telemachus telemachus</i>
<i>M. cisseis phanodemus</i>	Peru, San Martín	134	Present work
<i>M. granadensis polybaptus</i>	Costa Rica	129-136	Young, 1982 <i>M. granadensis polybaptus</i>
<i>M. polyphemus polyphemus</i>	El Salvador	127	Young & Muysshondt, 1972 <i>M. polyphemus</i>
<i>M. cypris cypris</i>	Colombia	120-125	Purser & Urbina, 2008 <i>M. cypris</i>
<i>M. amathonte ecuadorensis</i>	Colombia, Chocó	120	Constantino, 1997 <i>M. amathonte</i>
<i>M. helenor carillensis</i>	Costa Rica	96-119	Young & Muysshondt, 1973 <i>M. peleides limpida</i>
<i>M. deidamia grambergi</i>	Peru, Madre de Dios	95-112	Tákács & Tello, 1993 <i>M. deidamia</i>
<i>M. deidamia neoptolemus</i>	Brazil, Mato Grosso	107	Furtado, 2000 <i>M. deidamia neoptolemus</i>
<i>M. helenor achillaena</i>	Brazil, Rio de Janeiro area	79	Otero, 1966 <i>M. achillaena</i>
<i>M. helenor montezuma</i>	El Salvador	74-82	Young & Muysshondt, 1973 <i>M. peleides hyacinthus</i>
<i>M. helenor macrophthalmus</i>	Colombia, Pacific slopes, 1500 m	75	Constantino & Corredor, 2004 <i>M. macrophthalmus</i>
<i>M. helenor violaceus</i>	Brazil, Paraná, Santa Catarina	73	Otero, 1966 <i>M. violacea</i>
<i>M. helenor insularis</i>	Trinidad	74	Urich & Emmel, 1991 <i>M. peleides insularis</i>
<i>M. helenor telamon</i>	Colombia, Río Cauca valley, 1450 m	69	Constantino & Corredor, 2004 <i>M. peleides telamon</i>

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