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Evolution of extreme proboscis lengths in Neotropical Hesperiidae (Lepidoptera)

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Abstract

Exaggerated morphologies have evolved in insects as adaptations to nectar feeding by natural selection. For example, the suctorial mouthparts of butterflies enable these insects to gain access to floral nectar concealed inside deep floral tubes. Proboscis length in Lepidoptera is known to scale with body size, but whether extreme absolute proboscis lengths of nectar feeding butterflies result from a proportional or disproportional increase with body size that differs between phylogenetic lineages remains unknown. We surveyed the range of variation that occurs in scaling relationships between proboscis length and body size against a phylogenetic background among Costa Rican Hesperiidae. We obtained a new record holder for the longest proboscis in butterflies and showed that extremely long proboscides evolved at least three times independently within Neotropical Hesperiidae. We conclude that the evolution of extremely long proboscides results from allometric scaling with body size, as demonstrated in hawk moths. We hypothesize that constraints on the evolution of increasingly long butterfly proboscides may come from (1) the underlying scaling relationships, i.e., relative proboscis length, combined with the butterfly's flight style and flower-visiting behaviour and/or (2) developmental constraints during the pupal phase. Lastly, we discuss why butterflies did not evolve similar scaling relationships as hawk moths.

Keywords

Skippers; hawk moths; scaling relationship; allometry; flower-visiting behaviour; metamorphosis

Introduction

Exaggerated morphologies in animals are mainly known from traits that evolved by sexual selection and competition for access to mates, such as the antlers of elk or the horns of beetles (Emlen, 2001). Typically, these extraordinary features vary intraspecifically, so that

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not all individuals of a species express the trait to the same extent, and trait size often, but not always, scales with body size (Emlen & Nijhout, 2000). The slopes of the scaling relationships between the dimensions of each trait and variation in body size can vary from no slope (size-invariant trait expression), very steep slopes (traits become disproportionately larger with increasing body size) to negative slopes (traits become proportionately smaller with increasing body size; Emlen & Nijhout, 2000). Scaling relationships for morphological traits in insects have evolved and can be measured by comparing related taxa. This is because scaling relationships result from developmental processes that regulate the growth of body parts and these processes are influenced by the manner in which genotypes respond to environmental conditions during growth (for a review see Emlen & Nijhout, 2000).

Exaggerated morphologies in insects do not evolve by sexual selection alone, but also by natural selection. For example, the extremely elongate mouthparts of hawk moths, butterflies, nemestrinid flies or euglossine bees evolved as adaptations for gaining access to food resources, i.e., floral nectar concealed in deep corolla tubes (Darwin, 1862; Johnson & Steiner, 1997; Alexandersson & Johnson, 2002; Johnson *et al*., 2002; Borrell, 2005; Pauw *et al*., 2009; Krenn, 2010). These studies present examples of how adaptive departures from the usual proportional scaling relationships can represent a selective advantage in foraging (Kunte, 2007). Interspecific comparative studies on hawk moths and butterflies showed that proboscis length is correlated positively with body size (Agosta & Janzen, 2005; Corbet, 2000; Kunte, 2007), and that nectar feeding butterflies have disproportionately longer proboscides than non-nectar feeding butterflies (Kunte, 2007). Until now, there are have been no studies on the differences between the scaling relationships of butterflies with extremely long and short proboscides in relation to their phylogenetic background.

Here, we surveyed the range of variation that occurs in scaling relationships between proboscis length and body size in Neotropical Hesperiidae butterflies. We tested whether extreme absolute proboscis lengths in skippers results from a proportional increase of proboscis length and body size or from a disproportional increase, i.e., greater relative proboscis lengths. To the end, the significance of scaling relationships on the evolution of ever longer mouthparts in butterflies is discussed.

Material and Methods

Study site and field work

Sampling of Hesperiidae was carried out in the garden and surroundings of the Tropical Station La Gamba (SW Costa Rica: Puntarenas Province, Piedras Blancas National Park, 8°45′N, 83°10′W; 81 m a.s.l.) in September-October 2010, September-October 2012 and January-February 2013. The Tropical Research Station is surrounded by a mosaic of habitats including primary forest, secondary forest and intensively used land (Weissenhofer *et al*., 2008; Krenn *et al*., 2010). Skippers were collected with a hand net and stored in 70 % ethanol. Classification of taxa follows the most recent phylogeny of Hesperiidae (Warren *et al*., 2009).

Morphometrics

Body length and proboscis length was measured in representatives of 75 species belonging to three subfamilies of Hesperiidae (Hesperiinae: 41; Eudaminae: 17; Pyrginae: 17). The numbers of measurements for each species depended on its commonness and ease of capture, and ranged from 1 to 39. Mean body size, proboscis length and relative proboscis length (absolute proboscis length divided by body length) for each species are given in Table 1.

In the year 2010, body length and proboscis length of live specimens was measured. Skippers were cooled to approximately 20° C. Subsequently, body length of immobilized butterflies was measured with a digital caliper. The proboscis was uncoiled manually with the aid of a dissection needle, fixed with insect pins and photographed with an Olympus μ-Tough 6000 digital camera (Olympus, Tokyo, Japan). These photographs were imported to ImageJ (U.S. National Institutes of Health, Bethesda, USA) and measured with the aid of the segmented line tool.

In the years 2012 and 2013, body length and proboscis length of ethanol-preserved specimens was measured. Body length was measured by pinning the body of each specimen in a lateral position to a foam mat. After taking a micrograph of the body, the proboscis of each specimen was separated from the head at its base, uncoiled and fixed on a foam mat using insect pins. Micrographs of the body and the proboscis were taken using a Nikon SMZ 1500 stereomicroscope (Nikon, Tokyo, Japan) equipped with an Optocam-I digital camera (Nikon, Tokyo, Japan). Micrographs were imported to ImageJ and body length as well as proboscis length was measured with the aid of the segmented line tool.

Statistical analyses

We used analyses of covariance for testing if the scaling relationships between body size and proboscis length, i.e., relative proboscis length of Hesperiidae species, differs among the three subfamilies Hesperiinae, Eudaminae and Pyrginae. ANCOVA was used to test the assumption of homogeneity of slopes among these three groups. Analyses were conducted with untransformed data in the statistical package IBM SPSS Statistics 21.0 (IBM Corporation, New York, USA). Graphical illustrations were prepared using SigmaPlot 12.5 (Systat Software Incorporated, San Jose, California, USA) and CorelDRAW X6 (Corel Corporation, Munich, Germany).

Results

Body size and proboscis length were measured for a total of 370 individuals of Hesperiidae belonging to 75 species and 50 genera. Mean proboscis length per species varied eightfold between 6.4 mm and 51.8 mm, whereas mean body length per species ranged from 9.0 mm to 30.4 mm, varying only threefold (Table 1). Mean relative proboscis length also varied considerably between 0.5 (i.e., proboscis is half as long as the body) and 2.4 (i.e., proboscis is more than twice as long as the body). The longest proboscis ever discovered in butterflies thus far was in a specimen of *Damas immaculata* Nicolay, 1973 (Hesperiinae: Calpodini) and measured 52.7 mm. Several individuals had proboscides measuring more than 50 mm, such as specimens of *Damas clavus* (Herrich-Schäffer, 1869) (Hesperiinae: Calpodini), *Perichares adela* (Hewitson, 1867) (Hesperiinae: Clade 113), *Saliana salius* (Cramer, 1775) (Hesperiinae: Calpodini) and *Saliana severus* (Mabille, 1895) (Hesperiinae: Calpodini). The shortest proboscis measuring only 5.3 mm was found in a representative of the species *Apaustus gracilis gracilis* (C. Felder & R. Felder, 1867) (Hesperiinae: Moncini).

Proboscis lengths of 75 species were categorized according to the quartiles of the data range as (1) short: ≤ 12.6 mm (first quartile), (2) medium: > 12.7 to ≤ 17.8 mm (second quartile), (3) long: > 17.9 to ≤ 29.9 mm (third quartile) and (4) extremely long: > 30.0 mm (fourth quartile; see Figure 1). 70 % of the species representing the subfamily of Hesperiinae were characterized by long (12 out of 41 species) and extremely long (17 out of 41 species) proboscides. By contrast, most Pyrginae had short proboscides (12 out of 17 species). Within Eudaminae, medium sized proboscides were most abundant (9 out of 17). Extremely long proboscides occurred within Hesperiinae, but also in a single species of Eudaminae.

Within all three subfamilies, proboscis length increased with increasing body length (Hesperiinae: $F_{(1, 39)} = 184.3$, $p < 0.0001$; Eudaminae: $F_{(1, 15)} = 83.0$, $p < 0.0001$; Pyrginae: $F_{(1, 15)} = 7.3$, $p < 0.05$). The regression slopes of the three subfamilies differed significantly (Figure 2). For every 1 mm body length gain, proboscis length increased by 2.4 mm within Hesperiinae, by 1.5 mm within Eudaminae and by 0.7 mm within Pyrginae.

Hesperiinae had the steepest slope, indicating that these butterflies had disproportionately long proboscides, i.e., higher relative proboscis lengths. Within Hesperiinae, two groups (Calpodini and clade 113) had the highest relative proboscis lengths (mean = 1.8) and departed from the isometric scaling relationships of other Hesperiinae such as Moncini (mean = 1.2), Anthoptini (mean = 1.0) and Hesperiini (mean = 1.1).

Discussion

Longest proboscis among butterflies found within Hesperiidae

Among insects, the world record holder concerning absolute proboscis length is *Amphimoea walkeri* (Boisduval [1875]) (Sphingidae). The proboscis of this Neotropical hawk moth measures up to 280 mm (Amsel, 1938). Among butterflies, the standing record regarding proboscis length has been held by the riodinid butterfly *Eurybia patrona* Staudinger, 1876. Its proboscis measures up to 49.9 mm (Kunte, 2007). In addition, exceptionally long proboscides were noted in at least four genera of Hesperiidae (Kunte, 2007). Here, we provide further evidence that Hesperiidae comprise many species with exceptionally long proboscides. Further, we now have a new record holder for absolute proboscis length in butterflies: *D. immaculata* with a proboscis length of up to 52.7 mm.

Evolution of extremely long proboscides

Mapped onto a cladogram (Warren *et al.*, 2009), we conclude that extremely long proboscides among Neotropical Hesperiidae presumably evolved at least three times independently (Figure 3), once within the subfamily Eudaminae and twice within groups of Hesperiinae: viz. Hesperiinae-Calpodini, and Hesperiinae-clade 113 (Table 1). Nearly all members of the tribe Calpodini analysed in this study were characterized by long or even extremely long proboscides, except *Panoquina ocola ocola* (W. H. Edwards, 1863), which had a medium-sized proboscis measuring only 13.7 mm on average. However, it is possible that other extremely long-proboscid species could also be found among Palaeotropical Hesperiidae. By contrast, extremely long proboscides in butterflies outside of the Hesperiidae are known to occur only within a single genus of Riodinidae, *Eurybia* (Kunte, 2007; Bauder *et al*., 2011; Bauder *et al*., 2013).

Our data showed that each of the three investigated skipper subfamilies Hesperiinae, Eudaminae and Pyrginae featured a characteristic scaling relationship between body size and proboscis length, i.e., relative proboscis length. Hesperiinae had the steepest slope, indicating that these butterflies had disproportionately long proboscides. Therefore, extreme absolute proboscis lengths in skipper butterflies are the result of allometry (slope of regression line: 2.4 for Hesperiinae) and do not scale isometrically with body size (slope of regression line would be 1.0).

What prevents butterflies from evolving even longer mouthparts?

The evolution of extreme absolute proboscis lengths in skipper butterflies is closely linked to extreme relative proboscis lengths, since body size and absolute proboscis length scaled allometrically. In hawk moths, the extreme proboscis length of *Amphimoea walkeri*, 280 mm, corresponds to the fourfold of body length (Amsel, 1938), whereas our present data and those of former studies (Kunte, 2007; Bauder *et al*., 2011; Bauder *et al*., 2013) showed that relative proboscis length in butterflies never exceeds 2.5. These results indicate that proboscis length in hawk moths can exceed that of butterflies not only because hawk moths are larger, but also because of a steeper scaling relationship between body size and proboscis length. Two not mutually exclusive explanations for what keeps butterflies from evolving equally long mouthparts in relation to body size as hawk moths could be found in differences regarding the flower-visiting behavior and/or metamorphosis.

A crucial difference between butterflies and hawk moths regards their flower-visiting behavior: hawk moths typically hover over or in front of flowers during nectar uptake (Farina *et al*., 1994), whereas nearly all butterflies need to sit on the flower to feed (Krenn, 2008), except for Troidini (Papilionidae). In butterflies, uncoiling a very long proboscis is limited by how far a butterfly can bend back its head and stretch its legs to allow for straightening of the proboscis spiral while sitting on the flower. None of these problems apply to hawk moths, which can modulate the space needed for uncoiling by hovering at an acceptable distance in front of or over the flower. Although absolute proboscis length determines access to nectar in flowers with deep tubes, relative proboscis length plays a crucial role during the uncoiling process and might constrain butterflies from evolving even longer mouthparts.

Further, developmental constraints could limit the evolution of proboscis length in butterflies since proboscis formation takes place in a developmental sheath on the ventral side of the pupa (Lowe *et al*., 2013), where the galeae are straight and arranged parallel to each other. Since the developmental sheath contains the full length of the unfolded proboscis, this organ grows accordingly to accommodate the extreme length of the adult proboscis and may extend a full body length beyond the last abdominal segment (Figure

40A, p. 137: DeVries, 1997). Further elongation of this fragile and thin pupal organ might constrain proboscis length evolution in butterflies. By contrast, the pupae of long-proboscid hawk moths during metamorphosis develop a heavily sclerotized, hook-shaped external outgrowth that contains a loop of the developing proboscis that allows for the formation of a proboscis of much greater length (Patočka, 1993).

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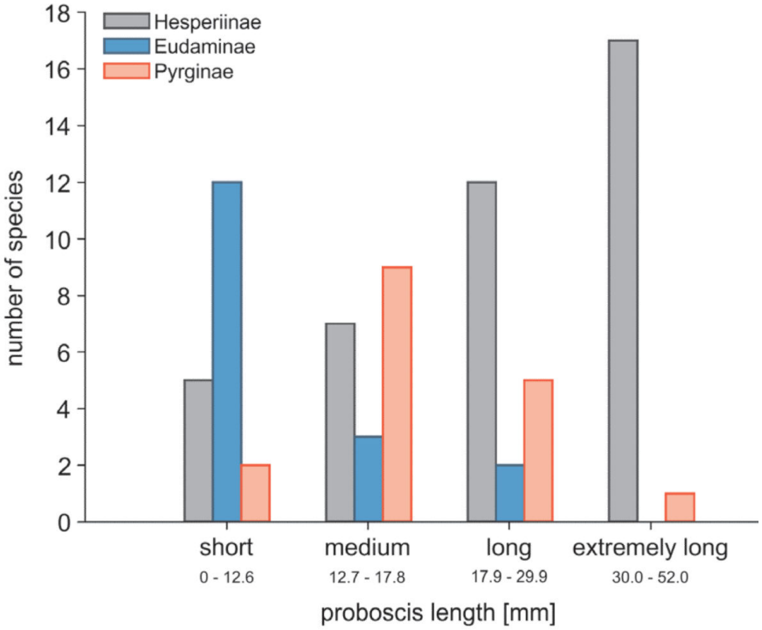

Figure 1.

Categorization of proboscis lengths measured in 75 species representing three subfamilies of Hesperiidae (Hesperiinae, Eudaminae, Pyrginae) according to quartiles of data range: short: ≤12.6 mm; medium: 12.7 to 17.8 mm; long: 17.9 to 29.9 mm; and extremely long: 30.0 to 52.0 mm.

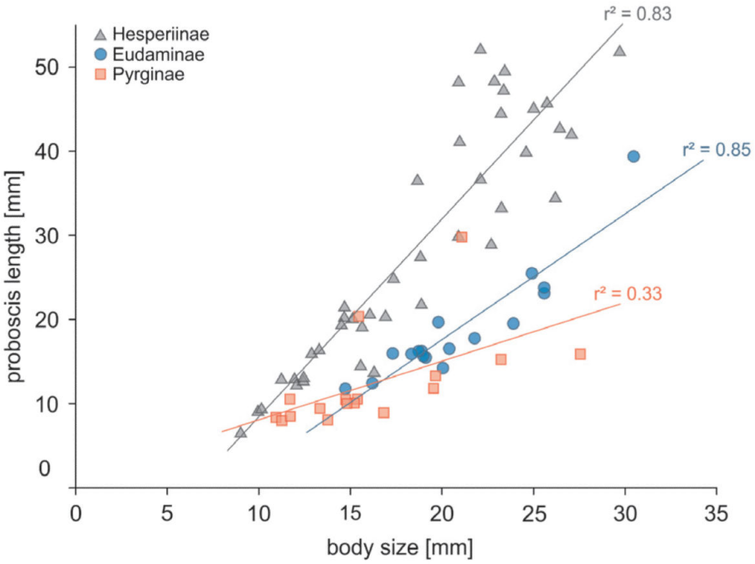

Figure 2.

The allometric relationship between body size and proboscis length in Costa Rican Hesperiidae butterflies. Hesperiinae (N = 41 species) had significantly longer proboscides for a given body size compared to Eudaminae (N = 17 species) or Pyrginae (N = 17 species). Regression lines were fitted as: Hesperiinae: $y = 2.4\times - 15.1$; Eudaminae: $y = 1.5\times - 12.3$; and Pyrginae: $y = 1 + 0.7\times$. Scaling relationships differed significantly among the three subfamilies (ANCOVA, homogeneity of regression slopes, Hesperiinae-Eudaminae: $p < 0.05$; Eudaminae-Pyrginae: $p < 0.05$; Hesperiinae-Pyrginae: $p < 0.0001$).

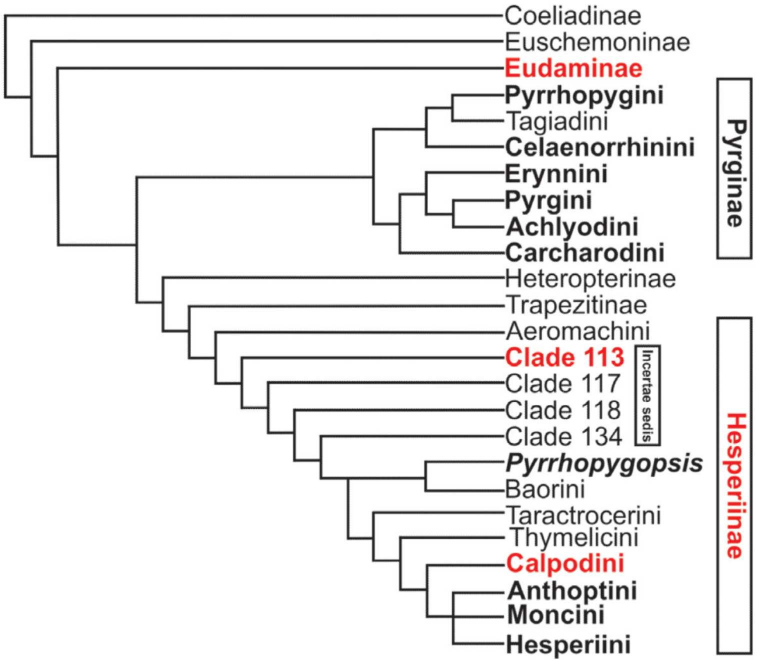

Figure 3.

Simplified cladogram of the family Hesperiidae (Warren *et al*., 2009). Extremely long proboscides evolved at least three times independently within Neotropical Hesperiidae in representatives of the subfamilies Eudaminae and two tribes of Hesperiinae. Note: Taxa printed in bold are represented in this study, taxa printed in red include species with extremely long proboscides that exceed 30 mm in length.

Table 1

Body length, absolute proboscis length and relative proboscis length, measured in 370 individual skippers representing 75 species and 50 genera. Note: Given are mean values (± standard deviation), whenever more than one individual per species was measured.

Species	**N**	**Body length [mm]**	**Proboscis length [mm]**	**Relative proboscis length**
Eudaminae				
Astraptes fulgerator azul (Reakirt, [1867])	1	25.5	23.1	0.9
Astraptes alardus latia Evans, 1952	2	25.5 (± 2.1)	23.8 (± 0.4)	0.9 (± 0.1)
Astraptes anaphus annetta Evans, 1952	1	23.9	19.5	0.8
Astraptes brevicauda (Plötz, 1886)	1	19.8	19.7	1.0
Astraptes talus (Cramer, 1777)	1	21.7	17.8	0.8
Autochton longipennis (plötz, 1882)	9	17.3 (± 1.3)	16.0 (± 1.3)	0.9 (± 0.05)
Autochton zarex (Hübner, 1818)	2	18.8 (± 0.3)	16.3 (± 1.5)	0.9 (± 0.1)
Bungalotis quadratum quadratum (Sepp, [1845])	1	30.4	39.4	1.3
Cogia calchas (Herrich-Schäffer, 1869)	7	14.7 (± 1.3)	11.8 (± 1.2)	0.8 (± 0.03)
Drephalys heraclides E. Bell, 1942	1	20.0	14.3	0.7
Dyscophellus porcius porcius (C. Felder & R. Felder, 1862)	1	24.9	25.5	1.0
Spathilepia clonius (Cramer, 1775)	9	19.1 (± 2.0)	15.5 (± 1.3)	0.8 (± 0.04)
Typhedanus undulatus (Hewitson, 1867)	1	16.2	12.4	0.8
Urbanus procne (Plötz, 1881)	5	18.9 (± 1.5)	15.6 (± 0.8)	0.8 (± 0.07)
Urbanus simplicius (Stoll, 1790)	16	18.7 (± 1.6)	16.3 (± 0.7)	0.9 (± 0.06)
Urbanus tanna Evans, 1952	9	20.4 (± 1.3)	16.6 (± 0.6)	0.8 (± 0.03)
Urbanus teleus (Hübner, 1821)	13	18.3 (± 1.5)	15.9 (± 0.9)	0.9 (± 0.04)
Pyrginae				
Pyrrhopygini				
Mysoria ambigua (Mabille & Boullet, 1908)	4	23.2 (± 1.0)	15.3 (± 0.6)	0.7 (± 0.03)
Pyrrhopyge phidias evansi E. Bell, 1947	1	27.5	15.9	0.6
Celaenorrhini				
Celaenorrhinus darius Evans, 1952	1	21.1	29.8	1.4
Celaenorrhinus monartus (Plötz, 1884)	1	15.4	20.4	1.3
Erynnini				
Chiomara mithrax (Möschler, 1879)	1	15.4	10.6	0.7
Ebrietas osyris (Staudinger, 1876)	1	19.5	11.8	0.6
Pyrgini				
Pyrgus orcus (Stoll, 1780)	3	13.7 (± 0.3)	8.1 (± 0.1)	0.6 (± 0.01)
Xenophanes tryxus (Stoll, 1780)	3	11.7 (± 0.2)	8.5 (± 1.7)	0.7 (± 0.1)
Achlyodini				
Achlyodes busirus heros Ehrmann, 1909	1	19.6	13.3	0.7
Milanion marciana Godman & Salvin 1895	1	13.3	9.4	0.7
Ouleus panna Evans, 1953	1	11.7	10.6	0.9
Carcharodini				

Species	N	Body length [mm]	Proboscis length [mm]	Relative proboscis length
Nisoniades ephora (Herrich-Schäffer, 1870)	1	15.2	10.1	0.7
Nisoniades godma Evans, 1953	3	14.7 (± 0.3)	10.5 (± 0.3)	0.7 (± 0.03)
Nisoniades rubescens (Möschler, 1877)	3	14.8 (± 0.4)	10.0 (± 0.7)	0.7 (± 0.1)
Noctuana stator (Godman, 1899)	1	16.8	8.9	0.5
Staphylus ascalaphus (Staudinger, 1876)	1	10.9	8.4	0.8
Staphylus carribea (Williams & E. Bell, 1940)	4	11.2 (± 0.9)	8.0 (± 0.2)	0.7 (± 0.05)
Hesperiinae				
Clade 113				
Lycas godart boisduvalii (Ehrmann, 1909)	1	25.7	45.7	1.8
Perichares adela (Hewitson, 1867)	8	23.2 (± 1.5)	44.5 (± 4.9)	1.9 (± 0.1)
Perichares lotus (A. Butler, 1870)	1	22.8	48.3	2.1
Pyrrhopygopsis socrates orasus (H. Druce, 1876)	1	26.1	34.4	1.3
Calpodini				
Aroma henricus henricus (Staudinger, 1876)	4	20.9 (± 1.6)	29.9 (± 1.8)	1.4 (± 0.04)
Calpodes ethlius (Stoll, 1782)	6	24.6 (± 2.5)	39.8 (± 3.9)	1.6 (± 0.04)
Carystoides escalantei H. Freeman, 1969	5	23.2 (± 1.1)	33.2 (± 1.5)	1.4 (± 0.09)
Carystoides hondura Evans, 1955	2	22.7 (± 1.4)	28.9 (± 0.3)	1.3 (± 0.1)
Damas clavus (Herrich-Schäffer, 1869)	20	23.4 (± 1.9)	49.5 (± 2.1)	2.1 (± 0.1)
Damas immaculata Nicolay, 1973	2	22.1 (± 2.0)	52.0 (± 1.0)	2.4 (± 0.2)
Panoquina ocola ocola (W. H. Edwards, 1863)	14	16.3 (± 0.9)	13.7 (± 0.5)	0.8 (± 0.05)
Saliana esperi esperi Evans, 1955	8	18.6 (± 1.0)	36.5 (± 2.5)	2.0 (± 0.2)
Saliana longirostris (Sepp, [1840])	1	26.4	42.7	1.6
Saliana salius (Cramer, 1775)	3	23.3 (± 0.6)	47.2 (± 5.7)	2.0 (± 0.2)
Saliana severus (Mabille, 1895)	1	29.7	51.8	1.8
Saliana triangularis (Kaye, 1914)	9	20.9 (± 1.5)	41.1 (± 2.1)	2.0 ± (0.1)
Talides hispa Evans, 1955	2	25.0 (± 1.5)	45.0 (± 0.7)	1.8 (± 0.1)
Talides sergestus (Cramer, 1775)	1	22.1	36.6	1.7
Thracides phidon (Cramer, 1779)	1	27.0	42.0	1.6
Tromba xanthura (Godman, 1901)	1	20.9	48.2	2.3
Anthoptini				
Anthoptus epictetus (Fabricius, 1793)	6	11.9 (± 0.8)	12.9 (± 0.4)	1.1 (± 0.08)
Anthoptus insignis (Plötz, 1882)	1	12.0	12.2	1.0
Corticea lysias lysias (Plötz, 1883)	7	12.4 (± 0.9)	12.6 (± 1.1)	1.0 (± 0.04)
Moncini				
Apaustus gracilis gracilis (C. Felder & R. Felder, 1867)	6	9.0 (± 0.7)	6.4 (± 0.7)	0.7 (± 0.07)
Arita arita (Schaus, 1902)	1	18.8	27.4	1.5
Callimormus radiola radiola (Mabille, 1878)	6	9.9 (± 0.4)	9.0 (± 0.5)	0.9 (± 0.06)
Cymaenes alumna (A. Butler, 1877)	7	12.9 (± 0.9)	15.9 (± 0.9)	1.2 (± 0.09)
Cymaenes tripunctus theogenis (Capronnier, 1874)	1	16.9	20.3	1.2
Flaccilla aecas (Stoll, 1781)	1	15.1	20.0	1.3
Lerema ancillaris (A. Butler, 1877)	1	16.0	20.5	1.3
Mnasilus allubita (A. Butler, 1877)	3	11.2 (± 0.02)	12.8 (± 0.6)	1.1 (± 0.1)

Species	N	Body length [mm]	Proboscis length [mm]	Relative proboscis length
Mnasitheus chrysophrys (Mabille, 1891)	1	10.1	9.3	0.9
Morys geisa (Möschler, 1879)	39	14.6 (± 1.2)	20.2 (± 1.4)	1.4 (± 0.09)
Morys micythus (Godman, 1900)	8	15.6 (± 0.9)	19.1 (± 1.2)	1.2 (± 0.07)
Papias phaeomelas (Hübner, [1831])	21	14.5 (± 1.3)	19.3 (± 4.0)	1.3 (± 0.2)
Papias phainis Godman, 1900	2	13.3 (± 0.6)	16.3 (± 0.2)	1.2 (± 0.1)
Papias subcostulata (Herrich-Schäffer, 1870)	29	17.3 (± 1.2)	24.8 (± 2.6)	1.4 (± 0.1)
Vehilius stictomenes illudens (Mabille, 1891)	6	12.4 (± 1.0)	13.1 (± 0.9)	1.1 (± 0.05)
Vettius marcus (Fabricius, 1787)	1	14.6	21.4	1.5
Hesperiini				
Pompeius pompeius (Latreille, [1824])	14	15.5 (± 1.0)	14.5 (± 0.8)	0.9 (± 0.06)
Quinta cannae (Herrich-Schäffer, 1869)	7	18.8 (± 1.2)	21.7 (± 1.1)	1.2 (± 0.06)