



Phylogeny of *Dynastor* and *Brassolis* butterflies (Lepidoptera: Nymphalidae): a tough nut to crack

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Abstract

This study examines the phylogenetic relationships among species of the butterfly genera *Dynastor* and *Brassolis* using 57 characters from adult morphology and wing coloration. We provide evidence for the monophyly of both genera. The relationships among *Dynastor* species are well resolved, but we were unable to find informative characters that could resolve the relationships inside *Brassolis*. We provide diagnoses for *Dynastor* and *Brassolis* and all species included in these genera, including illustrations that show geographical variation in wing color. The status of one subspecies is changed to species; *Brassolis dinizi* d'Almeida, 1956, **NEW STATUS**.

Key words: Brassolini, morphological homogeneity, *dinizi*

Introduction

The idea of a close association between *Brassolis* and *Dynastor* dates back to the early 20th century catalogues. The classification by Stichel (1904) listed *Brassolis* and *Dynastor* sequentially, and in works of that time this normally indicated either morphological or evolutionary affinities. Stichel (1925, 1932) revised his earlier classification and segregated *Brassolis* and *Penetes* into the subtribe Brassolidi, while *Dynastor* and eight other genera were included in the Caliginidi. Stichel's association of *Brassolis* and *Penetes* was based on wing color: species of both genera have a broad, colorful dorsal forewing postmedial band on a contrasting dark brown background, and the hindwing eyespots are small in *Brassolis* and absent in *Penetes* (the latter being unique within Brassolina *sensu* Casagrande 2004). Fruhstorfer (1912) did not follow Stichel's (1904) classification. Instead, he grouped *Brassolis*, *Dynastor* and *Penetes* under his Brassolininae based on a premature generalization that caterpillars in these three genera lack head scoli and caudae, which is true only for *Brassolis*. Casagrande (1995, 2004) included *Brassolis* and *Dynastor* (plus 13 other genera) within the subtribe Brassolina, but did not discuss their relationships. The study by Freitas & Brown (2004) indicated that *Brassolis* and *Dynastor* are closely related, although not sister taxa. Penz' (2007) analysis of Brassolini suggested that these two genera are sister taxa, and distantly related to the *Opsiphanes*-group, including *Penetes*.

Species of *Dynastor* are the only members of Brassolini known to use bromeliads (Bromeliaceae) as larval host plants (Penz *et al.* 1999 and references therein). Females lay eggs sparingly – 12 eggs in three days for captive *D. darius darius* (Fabricius) (Aiello & Silberglied 1978), and 42 eggs in six days for *D. darius stygianus* Butler (Romero *et al.* 2004). Caterpillars have well-developed head scoli and caudae, conforming to a characteristic brassoline morphology (Casagrande 1995). Adult *Dynastor* are crepuscular, and it is likely that these butterflies have a short lifespan; *D. darius* females lasted about one week in captivity (P. DeVries, C. Penz, unpubl. observations). The proboscis of *Dynastor* is typical of fruit-feeding butterflies (Krenn *et al.* 2001), and although rarely attracted to fruit-baited traps (e.g., Moss 1935, DeVries 1988) they have been

observed to feed both in the field and in captivity (Romero *et al.* 2004). *Dynastor* butterflies are predominantly dull brown, except for the orange-rimmed *D. napoleon* Doubleday, the largest and most spectacular member of the genus (Fig. 1). The geographical distribution of the three *Dynastor* species spans South and Central America to Mexico, and largely overlaps with that of *Brassolis* (e.g., Casagrande 2004).

Within Brassolini, species of *Brassolis* share unique life history characteristics; females lay clusters of 200–300 eggs on palms (Arecaceae), and the gregarious caterpillars rest communally inside a case during the day (e.g., Dunn 1917, Cleare & Squire 1934). Müller (1886) suggested that this lifestyle likely led to a reduction of both the head scoli and caudae, otherwise common in brassolines owing to their ancestors (Charaxinae and early Satyrinae; see Freitas & Brown 2004, Peña *et al.* 2006). These characteristics of early stage morphology and life history are conserved within the genus. *Brassolis* butterflies have reduced probosces, do not feed, and have a short adult life – 6–12 days for *B. sophorae* (Linnaeus) (Carvalho *et al.* 1998). Fruhstorfer (1912) considered *Brassolis* as differing most widely from the “normal Brassolid (sic) habitus ... almost recalling the Heterocera”, and these butterflies are indeed homogeneous in their coloration (Fig. 2, 3). *Brassolis* species are distributed throughout South and Central America (e.g., Casagrande 2004, Bristow 2008).

The purpose of this study is to expand upon previous knowledge of species-level phylogenetic relationships of *Dynastor* and *Brassolis*. We examined 57 morphological characters for both males and females of all currently recognized species in these genera. These characters constituted the basis for our phylogenetic analysis, revised generic definitions, and for elevating one subspecies to full species. Illustrations, diagnostic characters, and distribution are provided for species of both genera.

Materials and methods

Specimens. We examined specimens from the following institutions: Milwaukee Public Museum (MPM); Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity (MGCL); Museu Anchieta, Porto Alegre (MAPA); and The Natural History Museum, London (BMNH). Male and female legs and abdomens were prepared by soaking in hot 10% KOH solution, and stored in a 3:1 solution of glycerol and 70% ethanol. Observations and illustrations were made using a stereomicroscope equipped with a camera lucida. Terminology for adult external morphology and genitalia follows Kristensen (2004).

Cladistic analysis. This study follows the taxonomic checklist by Casagrande (2004) and recent changes by Bristow (2008). The nominal subspecies were used to score characters for *Dynastor napoleon*, *D. macrosiris* (Westwood) and *D. darius*. Within *Brassolis*, we studied *B. sophorae*, *B. haenschi* Stichel, *B. isthmia* Bates, *B. granadensis* Stichel, and *B. astyra* Godart. Particularly in the case of *B. sophorae*, we attempted to examine specimens from a broad range of localities to verify the consistency of our characters (structural and color), leading to a re-examination of the status of *B. sophorae dinizi* D’Almeida, 1956 (see results). *Elymnias hypermnestra* (Linnaeus) (Satyrinae), *Bia actorion* (Linnaeus) (Brassolini, Biina) and *Narope pannicululus* (Stichel) (Brassolini, Naropina) were used as outgroups. The examined species, locality data and number of dissected individuals per species are in Appendix 1. The character list and matrix (Appendices 2 and 3) include 57 characters, of which 46 are binary and 11 multistate; 13 were adapted from Penz (2007).

The character matrix was analyzed under implied weights, which weights characters according to their amount of homoplasy following a concave function (Goloboff 1993). We had noticed conflicts in characters during matrix construction, and therefore expected that many of our characters would be homoplasious. When levels of homoplasy are high, implied weights performs better than an analysis using equal weights or successive weighting, given that the latter may produce trees that are not optimal under the weights they imply (Goloboff 1993). TNT (Goloboff *et al.* 2007) was used for all analyses. Heuristic searches were performed with all characters set as non-additive, and consisted of 300 RAS+TBR replicates followed by 50 iterations of ratchet (Nixon 1999) and holding four trees per replication. A wide exploration of concavity values (K=1–20)

was conducted to search for the optimal K that produces highest number of well supported groups (Goloboff 1997, Goloboff *et al.* 2008). Our analyses used two search strategies; one in which internal branches of longitude zero were collapsed (collapse rule 4) and the resulting trees were condensed and the duplicates discarded (condense; unique), and another without collapsing zero length branches (collapse 0 option). Group support and stability were assessed through jackknife resample (36% as exclusion percentage), and Relative Bremer support (retaining up to 2000 suboptimal trees, 7 steps longer than the optimal). We used MacClade 4.08 (Maddison & Maddison 2005) for character optimization, and for matrix and tree editing.

Results

Species Identification

Genus *Dynastor* Doubleday

Robust-bodied, ranging from medium (*darius* FW length 97.9–109.8 mm, *macrosiris* 94.6 mm) to large (*napoleon* 116.7–131.7 mm). Antennae mildly clubbed. Dorsal FW brown; postmedial band cream-white, always distal to the discal cell in both sexes, broken (Fig. 1). Costal FW margin ripple-patterned in both sexes. Dorsal HW marginal line usually thin and cream-white (thick and bright orange in *napoleon*); postmedial band usually absent (except *darius*). Ventral surface of both wings either mottled or ripple-patterned (*macrosiris*). Ventral HW usually with three eyespots, in cells Sc+R1 (elongated), M1, and Cu1 (C-shaped). Extra eyespots may be present. Monomorphic for wing color and shape, males smaller than females. Male gnathos bifurcated, varying in shape between species; phallus short, with few small spines on the shaft; valva narrow apically, with a sclerotized costal margin bearing small to large spines (Fig. 8E). Female lamella antevaginalis absent (Fig. 9B), corpus bursa with paired signa.

Dynastor napoleon Doubleday

(Fig. 1A–B; 8H, J; 9G)

Type species.

Diagnosis: Both sexes can be recognized by five characters: (1) dorsal FW costal margin orange; (2) dorsal HW with a broad orange marginal band; (3) dorsal HW postmedial band absent; (4) ventral pattern cryptic, light brown mottled with dark brown; (5) ventral HW veins from the cubital sector thick and dark, contrasting the background.

Distribution: Southeastern Brazil, Rio de Janeiro (Casagrande 2004).

Subspecies: None (Casagrande 2004).

Dynastor macrosiris (Westwood)

(Fig. 1C–D, 8G)

Diagnosis: Both sexes can be recognized by four characters: (1) dorsal FW postmedial band continuous from costal margin to cell M2, stopping at M3 or Cu1; (2) dorsal HW postmedial band absent; (3) ventral FW with large yellow and green eyespots in cells M1 and M2; (4) conspicuous ripple-pattern ventrally on both wings.

Distribution: Central and northern South America, French Guiana, Colombia, Bolivia, Guatemala (Casagrande 2004). There are records of *D. macrosiris* in high elevations sites in Colombia and Ecuador (Moss 1935). It would be interesting to compare specimens collected in high versus lower elevations.

Subspecies: Casagrande (2004) listed four subspecies: nominal *macrosiris* (type locality: French Guiana), *hannibal* Oberthür (Colombia), *pharnaces* Stichel (Bolivia), and *strix* (Bates) (Guatemala). Examined males from El Salvador and French Guiana differ in both wing color and genitalia, and work in progress will address this issue.

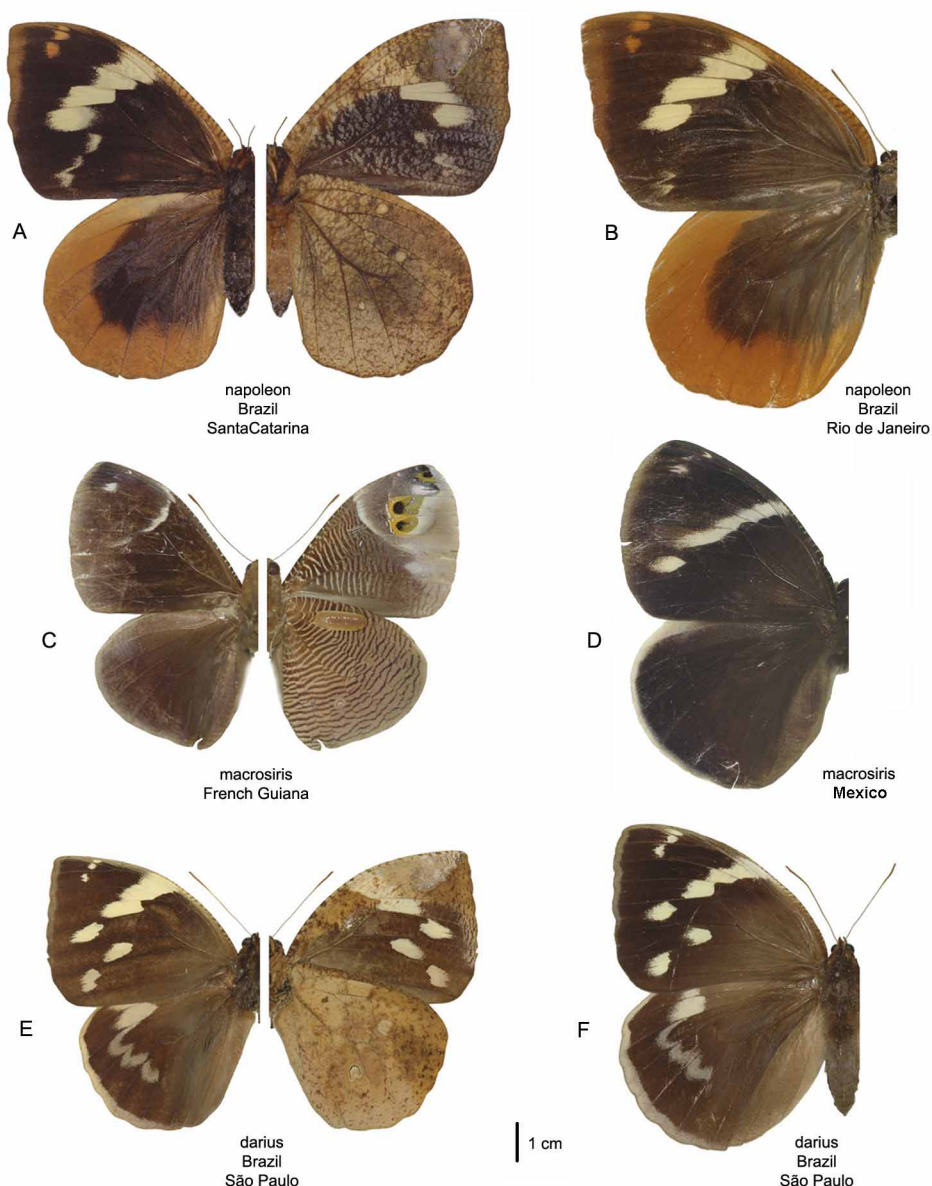


FIGURE 1. *Dynastor* species in dorsal (left) and ventral (right) views. (A) Male *D. napoleon* from Santa Catarina (Brazil). (B) Female *D. napoleon* from Rio de Janeiro (Brazil). (C & D) Male and female *D. macrosiris* from French Guiana and Mexico, respectively. (E & F) Male and female *D. darius* from São Paulo (Brazil).

Dynastor darius (Fabricius)

(Fig. 1E–F; 8C, E; 9A, B)

Diagnosis: Both sexes can be recognized by three characters: (1) dorsal FW postmedial band continuous from costal margin to cell M2, broken into dots at cells M3, Cu1 and Cu2; (2) dorsal HW postmedial band present, stronger above M1, faded and wavy below that vein; (3) ventral coloration cryptic, light brown mottled with dark brown.

Distribution: Central and South America, Costa Rica, Surinam, French Guiana, Brazil and Paraguay (Casagrande 2004).

Subspecies: Casagrande (2004) listed five subspecies: nominal *darius* (type locality: Brazil, [Rio de Janeiro]), *anaxarete* (Cramer) (Surinam), *faenius* Fruhstorfer (Brazil, Rio Grande do Sul), *ictericus* Stichel (Paraguay), and *stygianus* Butler (Costa Rica). Examined males from Paraguay and Brazil (São Paulo) differ

slightly in genitalic morphology but have nearly identical wing pattern, and work in progress will address this issue.

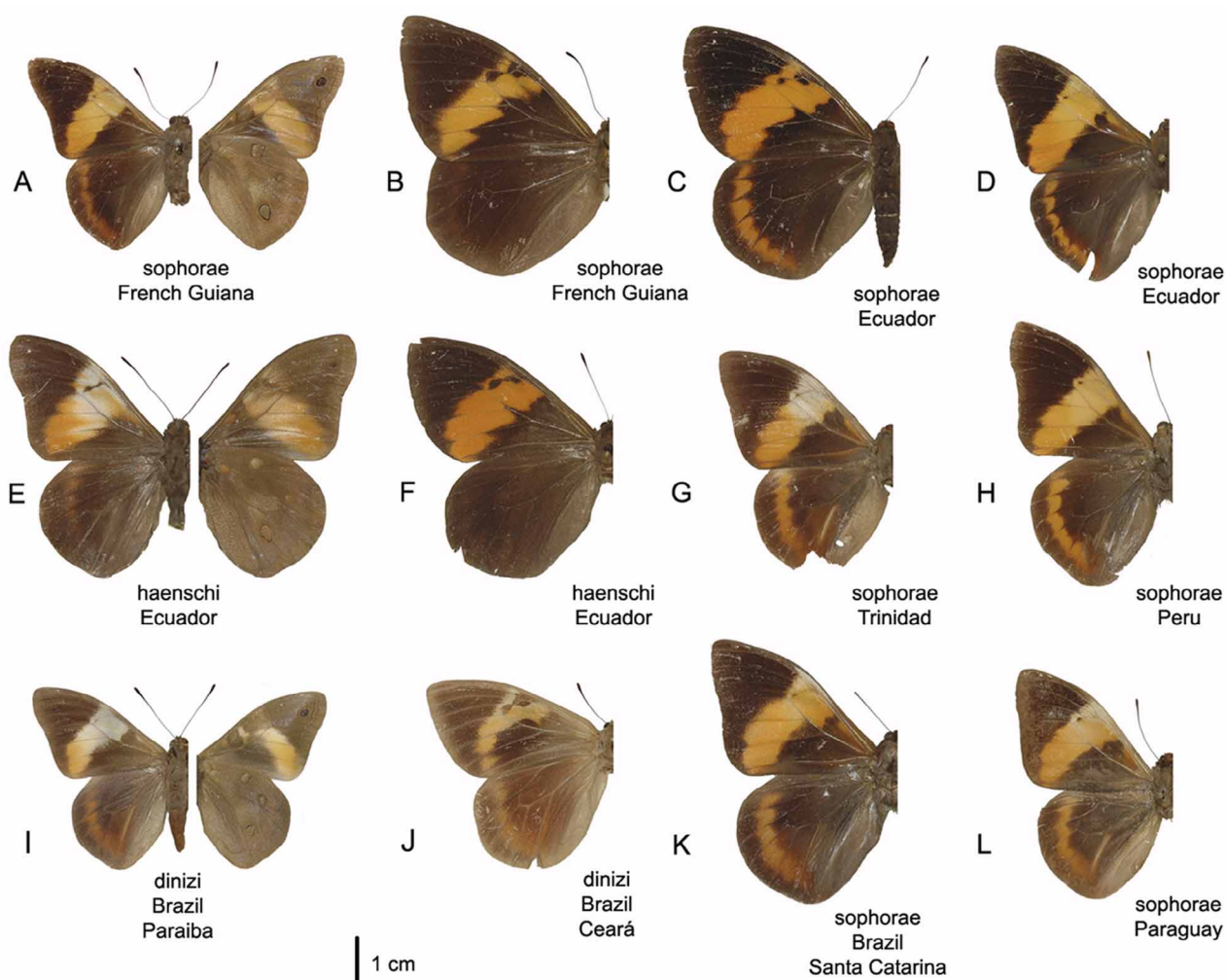


FIGURE 2. *Brassolis* species in dorsal (left) and ventral (right) views. (A & B) Male and female *B. sophorae* from French Guiana. (C & D) Female and male *B. sophorae* from Ecuador. (E & F) Male and female *B. haenschi* from Ecuador. (G) Male *B. sophorae* from Trinidad. (H) Male *B. sophorae* from Peru. (I & J) Male and female *B. dinizi* from Paraiba and Ceará respectively (Brazil). (K) Male *B. sophorae* from Santa Catarina (Brazil). (L) Male *B. sophorae* from Paraguay.

Genus *Brassolis* Fabricius

Robust-bodied, medium size (male FW length from 60.5 mm (*dinizi*) to 82.7 mm for (*astyra*); Fig. 2, 3). Antennae short, strongly clubbed. Reduced, non-functional proboscis (Fig. 3E). Tibial spurs absent in both sexes. Dorsal FW brown with an orange, or orange and white postmedial band, depending on the species. Dorsal HW brown with or without an orange postmedial band, depending on the species. Males with a small, narrow patch of androconial scales below vein Cu2 (Fig. 7B, character 16). Sexes similar in color, males smaller than females. FW basal, costal margin in-curved in males, bowed in females. Ventral HW brown stippled with white; eyespots in cells Sc+R1 and Cu1 variable in size. Male and female genitalia remarkably uniform across species. Male gnathos absent (unique within *Brassolini*); valva broad, distally curved and with apical serration (Fig. 8F); phallus with minute spines along the shaft and usually two to three setae on the edge of the vesica. Female sterigma projected as a flap posteriorly (Fig. 9C, D, E); anterior section of sterigma (lamella antevaginalis) thin and generally continuous, forming a 'loop'. Corpus bursa lacking signa.

***Brassolis sophorae* (Linnaeus)**

(Fig. 2A–D, G–H, K–L; 8B, F)

Type species.

Diagnosis: Recognized by a combination of two characters: (1) in males, dorsal FW postmedial band normally orange and nearly entire (small brown spot at crossvein m2–m3), in females, this band is nearly bifurcated into two branches at the distal edge of the discal cell; (2) in both males and females, dorsal HW postmedial band well defined (Fig. 2).

Distribution: *B. sophorae* is a widespread polytypical species, reported to occur from Colombia to Paraguay (Casagrande 2004).

Subspecies: Casagrande (2004) listed seven subspecies: nominal *sophorae* (type locality America), *ardens* Stichel (Peru), *dinizi* d'Almeida (Brazil, Paraíba) elevated here to full species status (see below), *laurentii* Stichel (Brazil, Minas Gerais), *luridus* Stichel (Colombia), *philomela* Stichel (Ecuador), and *vulpeculus* Stichel (Paraguay). Bristow (2008) synonymized *philomela* under *luridus*. We examined specimens from locations that potentially represented most of these subspecies, plus Bolivia (Fig. 2). Given that Hans Stichel described several of these subspecies, it is possible that he recognized the color pattern variation within *B. sophorae sensu lato* that we encountered during this study (see Phylogenetic analysis and Discussion).

Remarks: We encountered much variation in color in our examined specimens, and some of this variation overlaps with diagnostic characters for other *Brassolis* species. For example, in some specimens dorsal FW postmedial band was orange and white (as in *B. dinizi* and *B. haenschi*). In some females the dorsal HW postmedial band was faded (as in *B. haenschi*, *B. isthmia*, and *B. astyra astyra*). Dorsal color of abdomen is usually brown, but it is faded orange in specimens from the Brazilian Atlantic coast. See the Phylogenetic analysis section for characters that are polymorphic within *B. sophorae*, and Discussion for implications of this variation.

***Brassolis dinizi* d'Almeida, 1956, NEW STATUS**

(Fig. 2I–J, 7A, 9E)

Diagnosis: Recognized by a combination of seven characters: (1) small size (male FW length 53.3 – 62.5 mm); (2) in both sexes, dorsal background coloration ashen brown; (3) in both sexes, ventral surface of both wings markedly pale and contrasting a diffuse dark area proximal to the FW postmedial band, below the discal cell; (4) in males, dorsal FW postmedial band completely white above Cu1, with a pale orange tinge posteriorly, usually below Cu1 (Fig. 7A, character 12:0); (5) in females, dorsal FW postmedial band nearly bifurcated into two branches at the distal edge of the discal cell (Fig. 2J); (6) in both sexes, dorsal HW postmedial band pale orange and well defined; (7) in both sexes, abdomen faded orange dorsally.

Distribution: Northeastern Brazil (d'Almeida 1956).

Justification for new status: It is likely that d'Almeida (1956) considered *dinizi* a subspecies of *B. sophorae* because it has a well-defined HW postmedial band. However, when compared to *B. sophorae* from several localities across its range (Appendix 1, Fig. 2), *B. dinizi* shows a distinctively pale dorsal and ventral coloration, nearly completely white male FW postmedial band, and smaller wing-length. In combination, characters listed above provide a positive and reliable diagnosis for *dinizi*. Furthermore, the tree in Fig. 4A shows four character changes for this species; a number comparable to *haenschi*, and larger than what was found for other *Brassolis*. While *dinizi* can be clearly distinguished from *sophorae*, other *Brassolis* species are more difficult to separate (e.g., *isthmia* and *granadensis*). Therefore, based on the diagnostic characters listed here, we propose a change in the taxonomic status of *dinizi* from subspecies to species.

***Brassolis haenschi* Stichel**

(Fig. 2E–F, 7C, 8L, 9H)

Diagnosis: Recognized by a combination of seven characters: (1) in males, dorsal FW postmedial band mostly orange, interspersed with white, and distal edge of discal cell usually highlighted by a brown line; in females, postmedial band dark orange, distal edge of discal cell highlighted by a wider brown line (orange postmedial band bifurcated); (2) in males, ventral FW thin brown submarginal lines usually absent; (3) in males, small ventral FW eyespot in cell M1 lacking a pupil; (4) dorsal HW postmedial band very faint or absent, in males, absent in females; (5) in females, wings are darker and rounder than in other species of *Brassolis*; (6) in lateral view, male tegumen taller and broader than other *Brassolis*; (7) in ventral view, posterior flap of the female sterigma round, more heavily sclerotized than other *Brassolis*.

Distribution: From Venezuela to Peru (Casagrande 2004).

Subspecies: Casagrande (2004) listed three subspecies: nominal *haenschi* (type locality Ecuador), *maritimus* Stichel (Venezuela), and *rufescens* Rothschild (Peru).

Remarks: In Venezuela, males may have one incomplete ventral FW thin submarginal line (A. Neild pers. comm.).

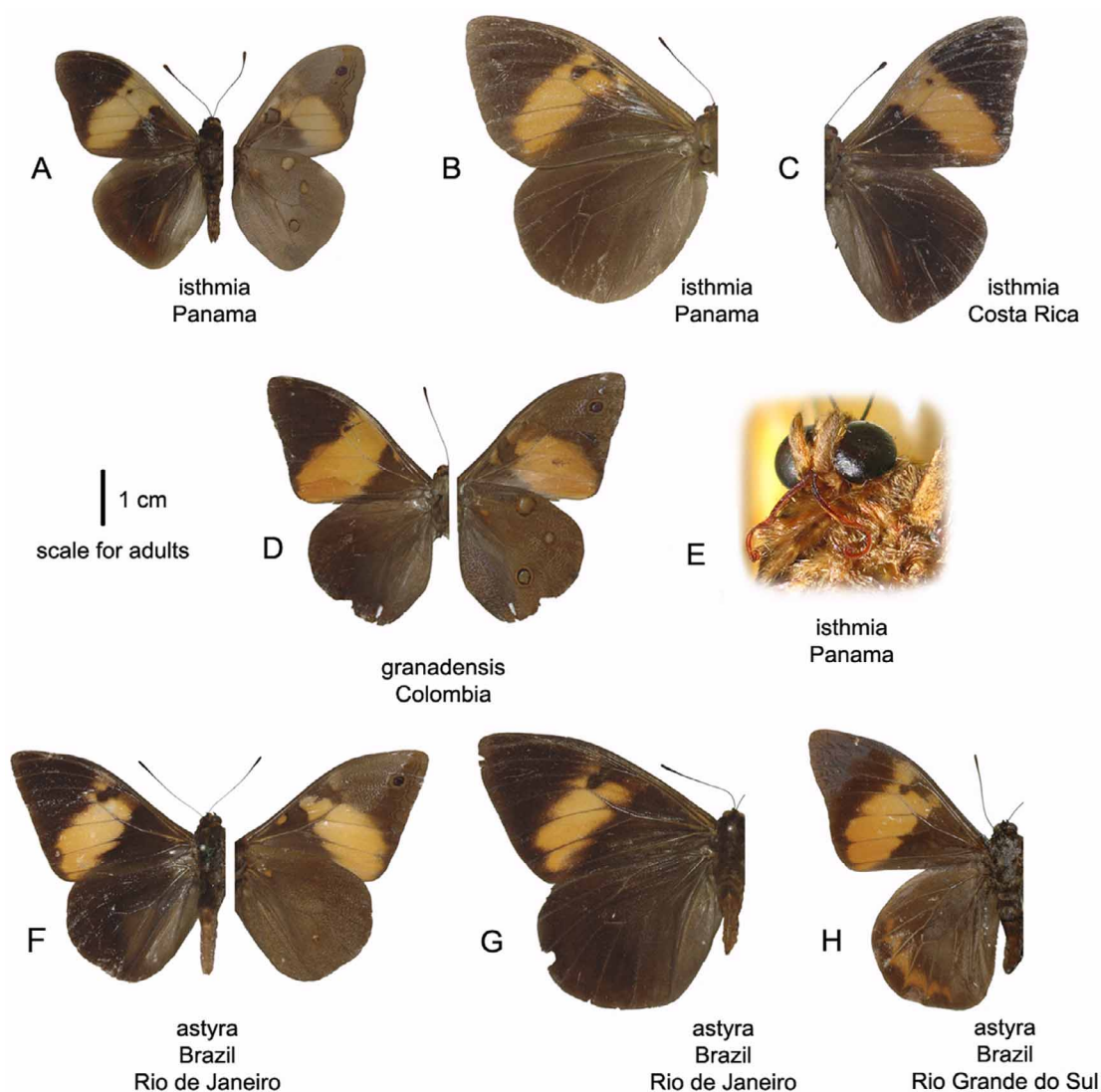


FIGURE 3. *Brassolis* species, in dorsal (left) and ventral (right) views (except for C). (A & B) Male and female *B. isthmia* from Panama. (C) Male *B. isthmia* from Costa Rica. (D) Male of *granadensis* from Colombia. (E) Detail showing head and proboscis of *B. isthmia* from Panama. (F & G) Male and female *B. astyra* from Rio de Janeiro (Brazil). (H) Male *B. astyra* from Rio Grande do Sul (Brazil).

***Brassolis isthmia* Bates**

(Fig. 3A–C, 9C)

Diagnosis: Recognized by a combination of four characters: (1) in males, dorsal FW postmedial band orange and nearly entire (small brown spot at crossvein m2–m3); in females, this band is nearly bifurcated into two branches at the distal edge of the discal cell; (2) both sexes usually lack a dorsal HW postmedial band (faint, barely visible in some males); (3) in males, androconial patch below vein Cu2 light colored, contrasting the wing background color. In *B. granadensis* this androconial patch is brown and matches the wing background color; (4) abdomen usually brown dorsally in both sexes (sometimes with an orange tinge at tip).

Distribution: Panama and Bolivia (Casagrande 2004).

Subspecies: Casagrande (2004) listed three subspecies: nominal *isthmia* (type locality Panama), *boliviana* Rothschild (Bolivia), and *granadensis* Stichel (Colombia, Ecuador). Bristow (2008) elevated *granadensis* to full species (see below), and in light of this taxonomic change, the status of *B. isthmia boliviana* should be verified. Furthermore, Bristow (2008) described two subspecies; *wallengreni* Bristow, 2008 (Ecuador, Isla Puna), and *daisye* Bristow, 2008 (Colombia, Chicorral).

***Brassolis granadensis* Stichel**

(Fig. 3D, 8M)

Diagnosis: Males can be recognized by a combination of five characters: (1) dorsal FW postmedial band orange and nearly entire (small brown spot at crossvein m2–m3); (2) dorsal FW postmedial band wider below discal cell than in *B. isthmia*; (3) lack a dorsal HW postmedial band; (4) brown androconial patch below vein Cu2, matching the wing background color. In *B. isthmia* this androconial patch is lighter than the wing background color; (5) abdomen brown dorsally. According to Bristow (2008) females can be recognized by the absence of dorsal HW postmedial (submarginal) band, by the deep-orange dorsal FW band, and by the flame-like shape of the spots that range across the upper part of the FW discal cell.

Distribution: Colombia and Ecuador (Casagrande 2004, Bristow 2008).

Subspecies: None.

Remarks: Females were not available for examination. The female from the MGCL (Colombia, Tolima, Payande, Mina Vieja area, 800–950 m. 1974, genitalia preparation CMP 07-141) listed by Bristow (2008) as *granadensis* actually corresponds to *isthmia* (R. Bristow pers. comm.)

***Brassolis astyra* Godart**

(Fig. 3F–H; 8D, I; 9D)

Diagnosis: Recognized by a combination of five characters: (1) in both sexes, dorsal FW postmedial orange band clearly bifurcated anteriorly (above M3). In females this band is faded above M3 and inside the discal cell; (2) specimens from the northern end of the distribution (*astyra astyra*) lack a dorsal HW postmedial band, but this band varies from faded to well developed in specimens from southern localities (*astyra philocala*). Dorsal HW postmedial band generally narrower and more jagged in *B. astyra philocala* than in *B. sophorae* and *B. dinizi*; (3) in both sexes, abdomen orange dorsally from third segment onward; (4) in posterior view, male valva usually with a small point at apex (Fig. 8D); (5) in ventral view, anterior section of the female sterigma interrupted at mid point, sclerotized ‘loop’ originates from a fold closer to the midline than in other species.

Distribution: Southeastern Brazil (Casagrande 2004).

Subspecies: Casagrande (2004) listed two subspecies: nominal *astyra* (type locality Brazil), and *philocala* Stichel (Brazil, Rio Grande do Sul).

Cladistic analysis

Implied weights searches under $K=1$ and 2 found two most parsimonious trees. Higher values of K ($K=3$ to 20) consistently yielded the same three most parsimonious trees, one of which is the topology of the strict consensus of these three trees (Fig. 4A). The other two are the same trees found under $K=1$ and 2 (Fig. 4B, C). Trees had a fit of 5.2 . The three most parsimonious trees show *Dynastor* and *Brassolis* as monophyletic sister genera, but differed in the relative positions of *B. sophorae*, *B. haenschi*, *B. dinizi*, and *B. isthmia*, which had an effect on the resolution of the strict consensus (compare topologies in Fig. 4). Unambiguous character transformations for the nodes and terminals were optimized in the strict consensus tree using “hard” polytomy option and are described below (Fig. 4A).

Four synapomorphies supported the *Dynastor* + *Brassolis* clade: last segment of labial palpus shorter than the distal width of second segment (character 1:2, Fig. 8B), reversed to state 1 in *B. haenschi* (approximately the same length as distal width of second segment); valva not projecting beyond uncus tip (30:1, Fig. 8E); groove at the articulating point between valva and appendices angulares limited to the base of valva (34:1); distal opening of phallus located dorsolaterally (38:1). *Dynastor* + *Brassolis* had a low Relative Bremer support and a moderate value of jackknife recuperation (30 and 59; Fig. 4A).

The monophyly of the genus *Dynastor* was supported by seven synapomorphies and one homoplasious transformation. The synapomorphies were: dorsal forewing costal margin striped (4:1, Fig. 7D), dorsal forewing postmedial band broken (8:1, Fig. 7D), female foreleg distal tarsomere with ventral spines between the rows of sensilla (24:1, Fig. 9A), dorsal edge of juxta continuous (37:1), sclerotized tip of phallus forming a small coecum that projects beyond the distal opening (44:1, Fig. 8H), lateral uncus wings merging to form a single dorsal keel (47:1) and distal portion of uncus tall (48:1, Fig. 8G). The homoplasious transformation was the ventral outline of phallobase evenly arched (45:0, Fig. 8H). Relative Bremer support and Jackknife recuperation values for *Dynastor* were high (100 and 99; Fig. 4A).

We found *D. darius* and *D. napoleon* to be sister taxa, and two homoplasious transformations supported this clade: the presence of midleg tibial spurs (21:1), also present in *N. panniculus*; and last segment of labial palpus approximately the same length as distal width of second segment (1:1, Fig. 8C), present also in *B. haenschi*. This clade had moderated values of Relative Bremer support and jackknife recuperation (50 and 52; Fig. 4A).

The monophyly of *Brassolis* was supported by 13 synapomorphies and three homoplasious transformations. The synapomorphies of *Brassolis* were: absence of sensilla styloconica at the proboscis tip (2:0, Fig. 3E); in males, basal third of forewing costal margin slightly concave (3:1, Fig. 7A); male dorsal forewing postmedial band extended through discal cell (6:0, Fig. 7B); presence of a sent organ adjacent to male hindwing vein Cu2 (15:1, Fig. 7A), in males, absence of a dorsal hindwing marginal line (18:0, Fig. 7A); in males, presence of dashed pattern of the distal portion of ventral hindwing discal cell (19:1, Fig. 7C); presence of an anterolateral constriction of the tegumen (26:1, Fig. 8D); internal surface of valva, basal region conspicuously less sclerotized than distal region (33:1); juxta not reaching the edge of the anellus (36:0, Fig. 8I); presence of peg-like setae on semi-sclerotized lobe on left side of phallus (41:1, Fig. 8K); absence of gnathos (49:0); fully sclerotized antrum (55:2); and posterior lobes of the papillae annales more developed ventrally (57:2, Fig. 9H). The homoplasious transformations were: male midleg tarsus longer than tibia (22:0); presence of a semi-sclerotized lobe on the left side of phallus (40:1), which was also found in *D. darius* and in one of the outgroup taxa (*Elymnias hypermnestra*); and the transition between pedunculum and vinculum being straight (28:0, Fig. 8F). Relative Bremer support and Jackknife recuperation values for *Brassolis* were high (81 and 100; Fig. 4A).

Poor resolution of the strict consensus tree reflects the overall morphological similarity within *Brassolis* (Fig. 4A). *Brassolis sophorae*, *B. dinizi*, *B. isthmia* and *B. haenschi* formed an unresolved clade (sophorae-clade) supported by one homoplasious transformation: presence of a dorsal hindwing postmedial band in males (17:1, Fig. 7A). Alternative groupings of these species were represented in the other two trees (Fig. 4B and C). In all resolutions, however, *B. granadensis* was the sister taxon of this clade, supported by one homoplasious transformation: the presence of long setae on a semi-sclerotized lobe on the left side of phallus

(43:1, Fig. 8L). Finally, *B. astyra* appears as sister to all other *Brassolis*.

To identify characters that produced conflicting topologies within the sophorae-clade, we did a search without collapsing zero-length branches, and optimized both ambiguous and unambiguous transformations onto the obtained trees. The results were five alternative topologies for the sophorae-clade (Fig. 5). In these five resolved sub-trees all characters producing ambiguous optimizations (11, 12, 14, 16, 20, 25, 54) but one (54) were coloration characters, and all but one (12) were polymorphic. Trees in Fig. 5 show *B. sophorae* as sister to each of the species in the sophorae-clade (Fig. 5C–E) or as sister to species groups within this clade (Fig. 5A–B).

Given that polymorphic characters supported ambiguous optimizations within the sophorae-clade, an analysis was done excluding nine polymorphic characters (Appendix 3). Characters 11, 13, 14, 16, 20, 25, 43 and 54 were polymorphic for *B. sophorae*, and character 17 was polymorphic for *B. isthmia*, and also for *B. astyra* (outside the sophorae-clade). Two trees were found that differed greatly in resolution, and the strict consensus of these trees showed the sophorae-clade as a polytomy. We therefore concluded that the exclusion of polymorphic characters did not improve our results (trees not illustrated).

As noted above, *B. sophorae* was polymorphic for eight characters, and we therefore asked whether splitting *B. sophorae* into monomorphic terminals would improve tree resolution and would provide a more reliable assessment of relationships. To investigate this, we used male-female pairs (whenever possible) collected in eight countries as terminals. This sampling attempted to represent the type locality (country) of most valid subspecies listed by Casagrande (2004), therefore approximating a range of character variation of *B. sophorae*. Separating *B. sophorae* into eight terminals (putative subspecies) showed that all species of *Brassolis* are associated with one or more subspecies of *sophorae*; i.e., the sophorae-clade was not recovered (Fig. 6).

Discussion

Our study provided evidence supporting the monophyly of *Dynastor* and *Brassolis* with good support values at the genus level, and we confirmed that these two genera are sister groups (Penz 2007). The only synapomorphy of *Dynastor* + *Brassolis* given by Penz (2007) was also found in *Narope panniculus*, but here we provide four additional synapomorphies supporting this group. The diagnoses and illustrations for all species of *Dynastor* and *Brassolis* presented here provide useful tools for species identification and a framework for future taxonomic studies.

Relationships among the three species of *Dynastor* allow us to interpret certain aspects of their distribution and wing coloration. The widespread *Dynastor darius* fully overlaps in geographical range with its two congeners; *D. napoleon* from southeastern Brazil, and *D. macrosiris* from Central America and northern South America. Based on Fig. 4A, we hypothesize that the ancestor of this genus had a northern distribution in South America. Furthermore, *Dynastor* includes a species limited to the Brazilian Atlantic forest, which is biogeographically distinct from the Amazonian region (e.g., Costa 2003). The sister pair *D. darius* and *D. napoleon* share wing pattern elements. Their marbled, cryptic ventral HW pattern differs from the ripple-pattern present in *D. macrosiris* that can be considered plesiomorphic for brassolines based on Satyrinae relationships (Peña *et al.* 2006). Nonetheless, the dorsal orange FW markings, and broad orange HW marginal band of *D. napoleon* represent a contrast to the dull dorsal coloration displayed by *D. darius* and *macrosiris*. Interestingly, crosses of a male *D. napoleon* and a female *D. darius* produced sterile hybrid progeny that lacked orange colored bands (Otero & Casagrande 1992), suggesting a simple pattern of inheritance.

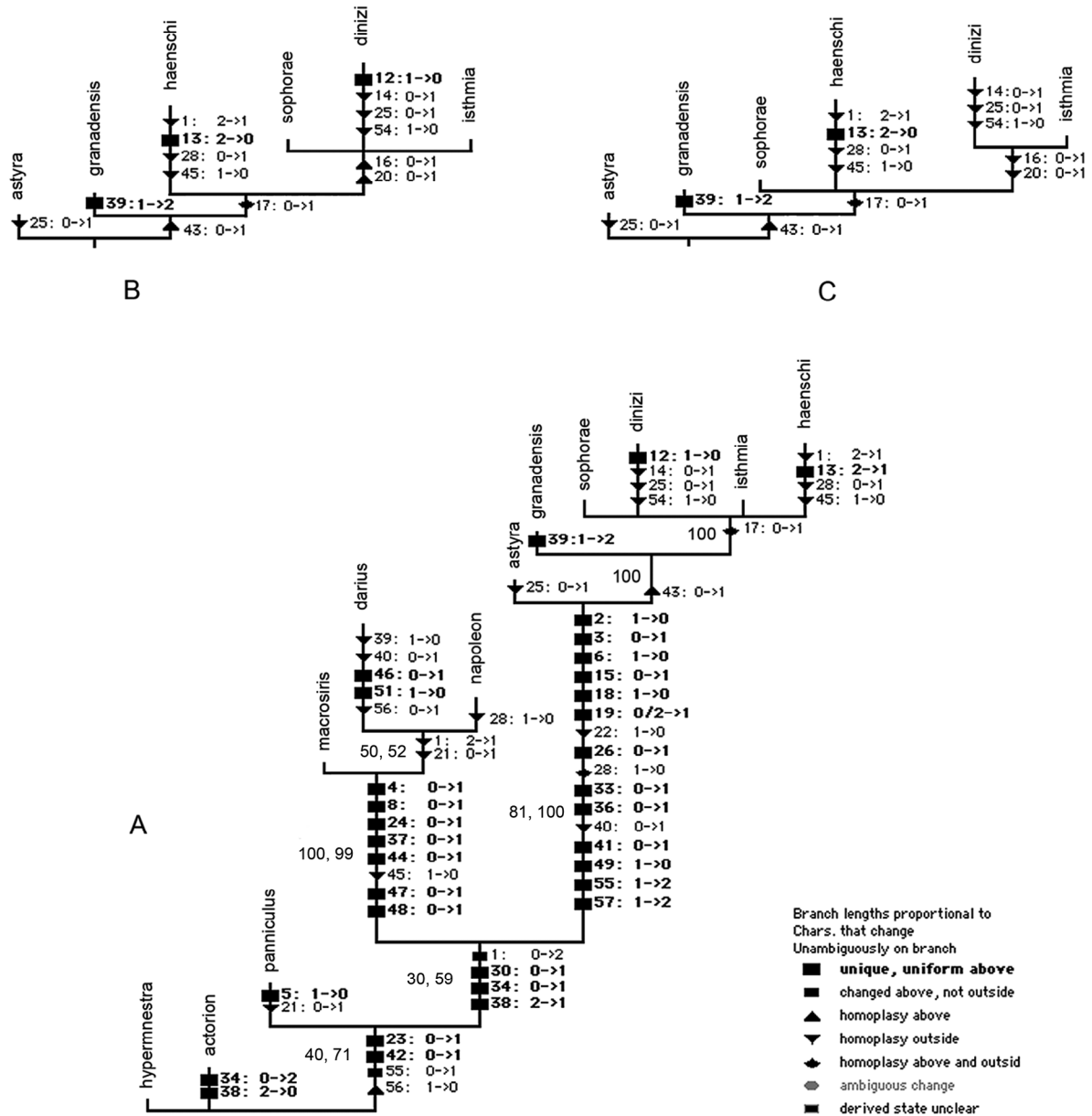


FIGURE 4. (A) Strict consensus tree from the analysis of 57 characters with K=3. (B & C) Two of the most parsimonious trees, the third tree had the same topology of the strict consensus. Relative Bremer support (on the left) and Jackknife values (on the right) are on the left hand of the branches.

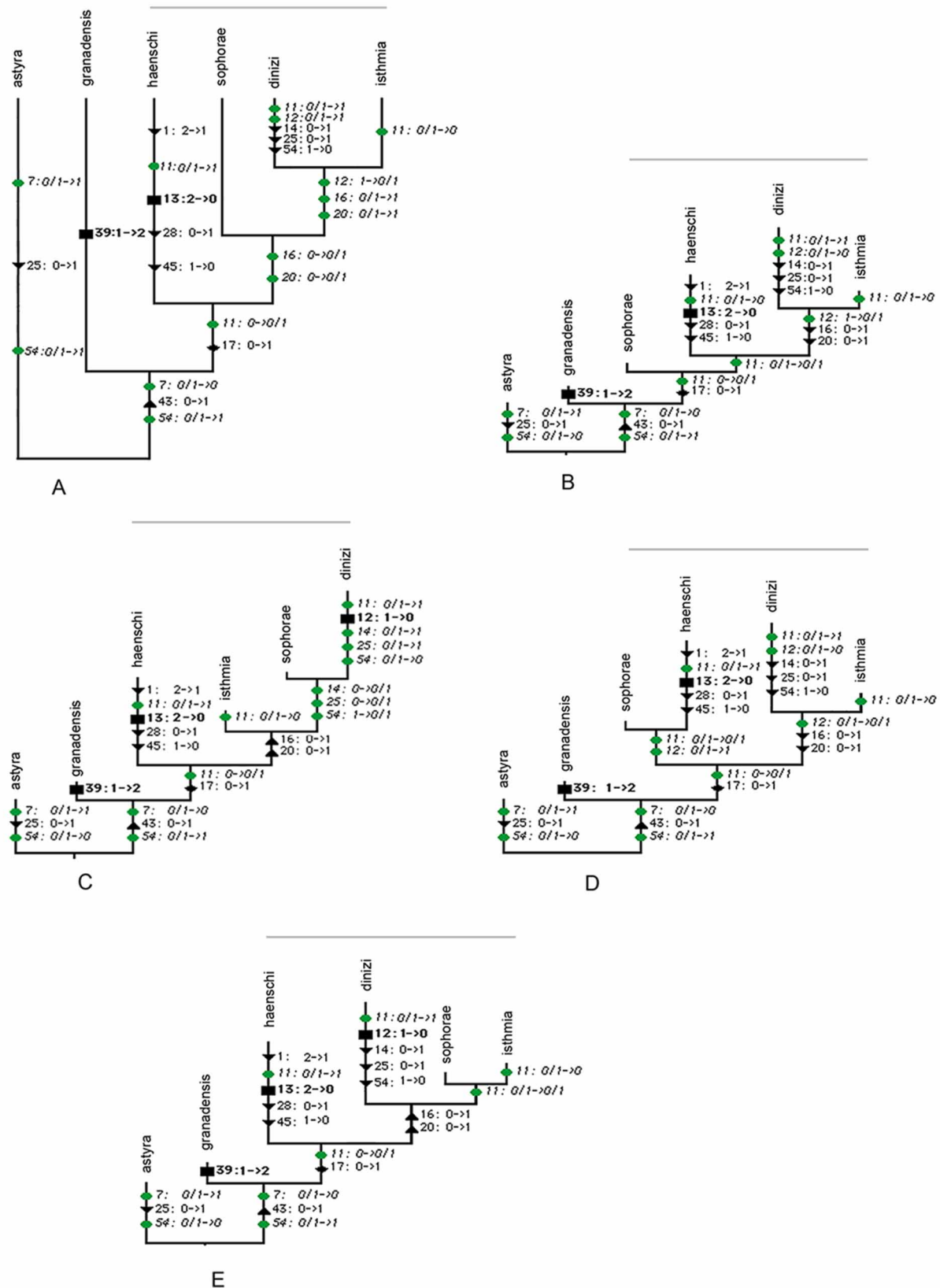


FIGURE 5. (A–E) Five resolutions obtained from a search without collapsing zero-length branches showing optimization of both unambiguous and ambiguous transformations. Symbols follow the legend in Fig. 4. The horizontal bars above the trees indicate the *sophorae*-clade.

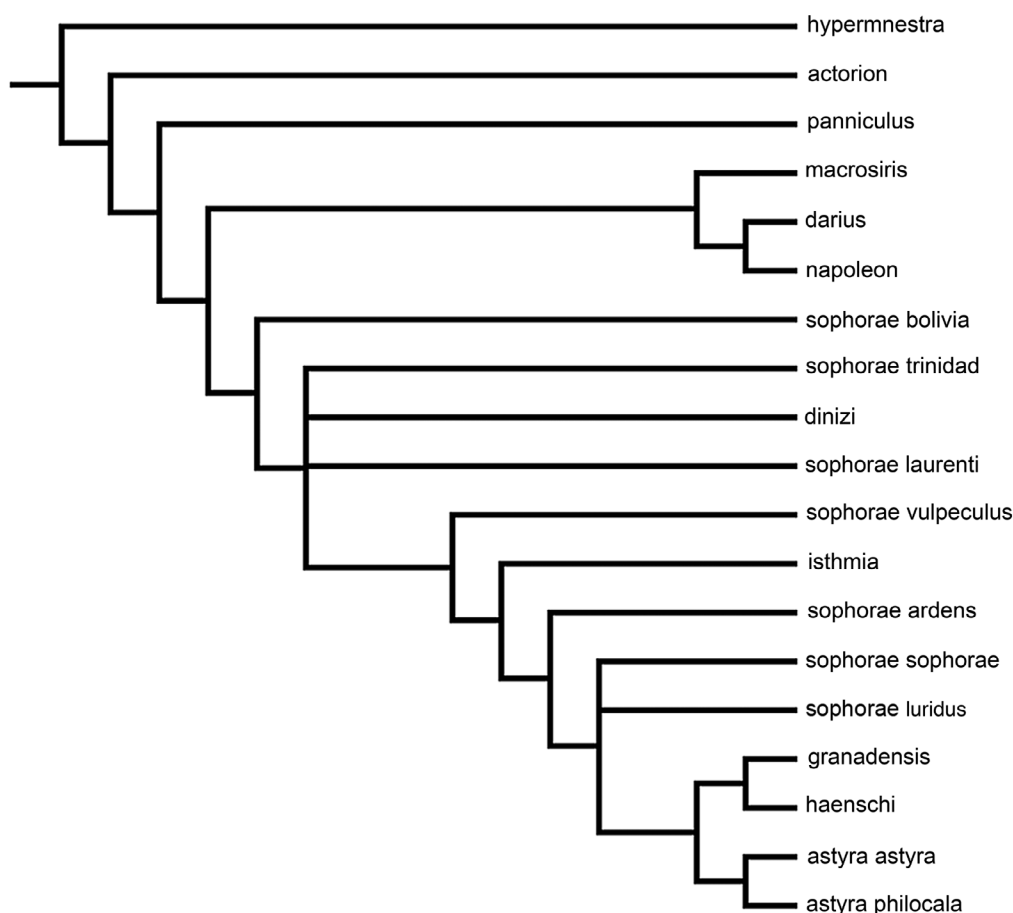


FIGURE 6. Strict consensus of three trees found when *B. sophorae* and *B. astyra* subspecies were used as terminals.

There are at least two possible reasons why we were unable to obtain resolution within *Brassolis*. First, species of *Brassolis* are remarkably uniform in morphology, making it difficult for us to find informative characters. Genitalic morphology may often yield informative characters for phylogeny reconstruction (e.g., Penz & DeVries 2002, Penz 2008); however, interspecific variation in genitalia within *Brassolis* was negligible, as found in other butterfly genera (e.g., Caldas 1997, Hill *et al.* 2002). Second, the few coloration characters that varied among species also varied within species. Seven color characters potentially informative within *Brassolis* were polymorphic for *B. sophorae*. Although polymorphic characters can be used in phylogenetic analyses (e.g., Wiens 1999), in *Brassolis* the high level of polymorphism masked any signal that the color characters might have contained. The approaches we used to deal with polymorphic characters did not significantly increase resolution of the strict consensus tree, nor increase our confidence in the overall topology for the genus as a whole. Color characters that are suitable for species diagnosis did not provide useful information for phylogenetic reconstruction.

Brassolis sophorae has the widest geographical distribution of all species in this genus, ranging from Colombia to southern Argentina and Brazil. Although this polytypic species can be recognized by the shape, color and presence of the FW and HW postmedial bands, our comparative study demonstrates that the variation in color recorded for *B. sophorae* greatly overlaps with that found in other species. Given their short adult lifespan and limited movement (Cleare & Squire 1934, Carvalho *et al.* 1998), there is opportunity for local color pattern variants to arise that would not necessarily contain phylogenetic signal. Early stage morphology can provide key characters for species identification and phylogenetic reconstruction (e.g., Francini *et al.* 2004), but mature caterpillars of *B. sophorae*, *B. isthmia* and *B. astyra* are nearly identical, and a comparative examination did not produce useful characters (C. Penz, pers. obs.). Therefore, what we initially envisioned as a straightforward phylogenetic study of a small group of species turned out to be a fairly difficult endeavor. It would be valuable to investigate whether molecular markers can be used to recover population-level structure and divergence within *Brassolis sophorae*, and relationships among all species in this genus. In the meantime, the phylogeny of *Brassolis* remains unresolved.

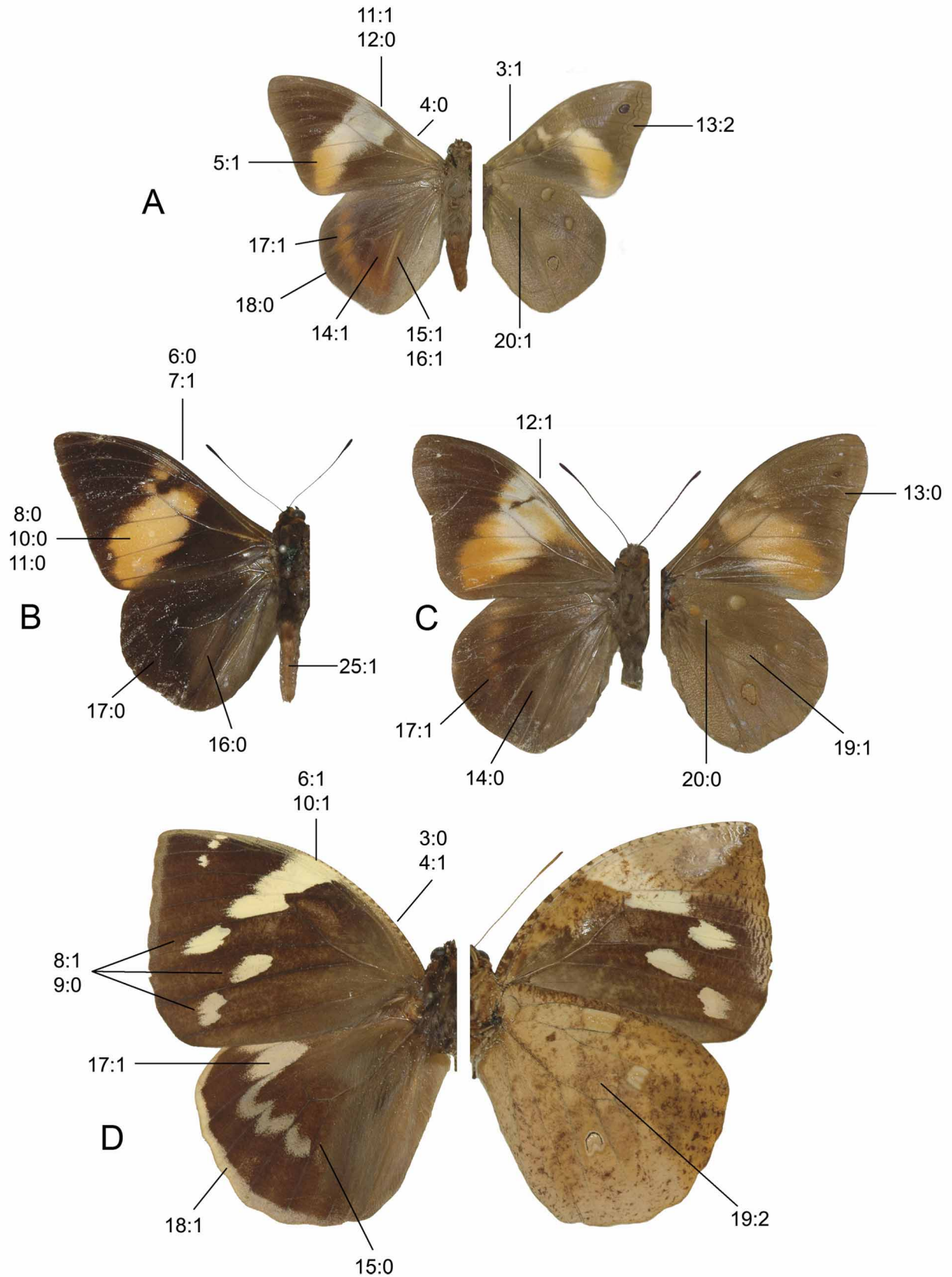


FIGURE 7. Wing characters. (A) *Brassolis dizini*. (B) *B. astyra*. (C) *B. haenschi*. (D) *Dynastor darius*.

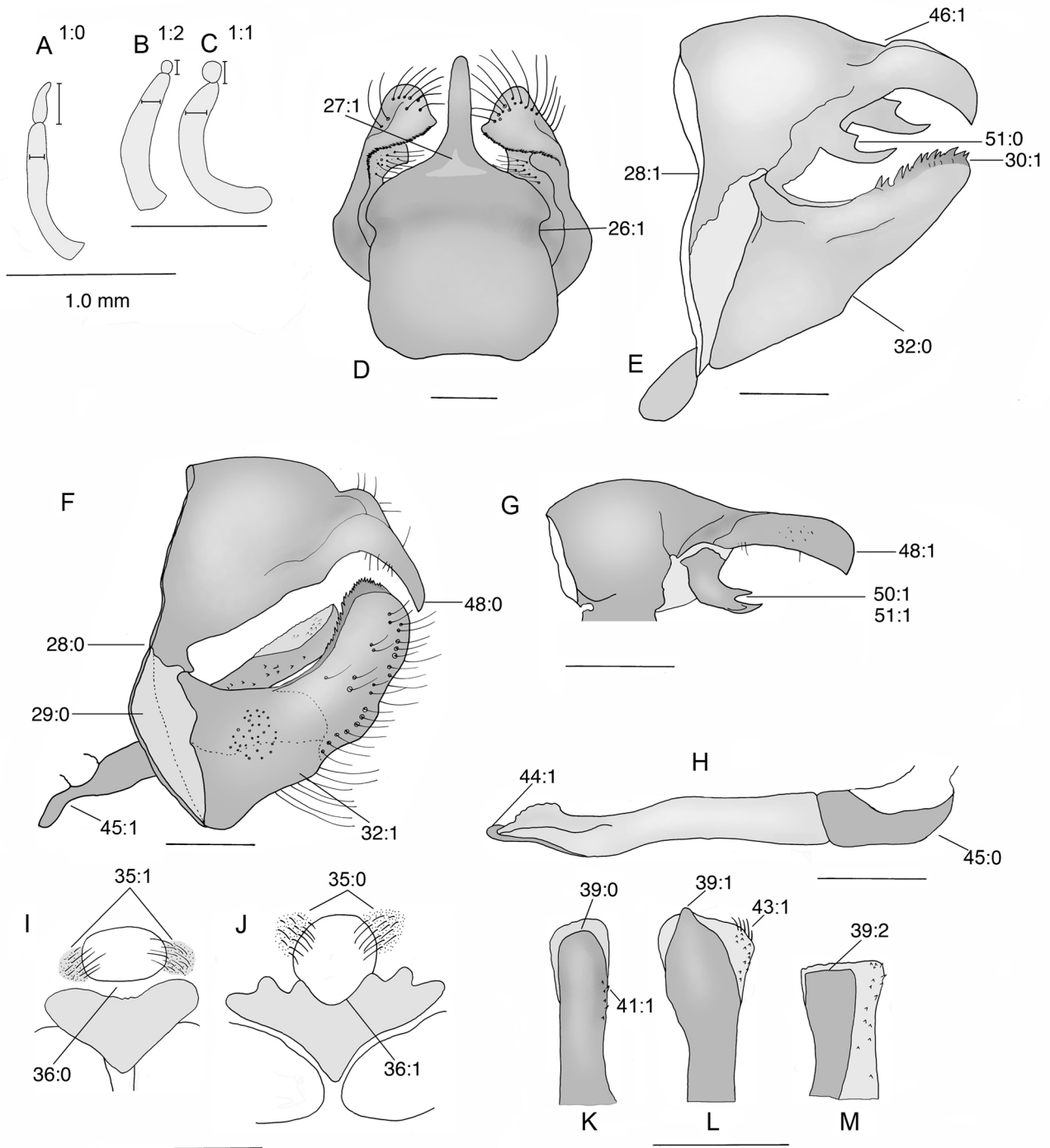


FIGURE 8. Male characters. Scale bars, 1 mm. Labial palp in lateral view. (A) *Bia actorion*. (B) *Brassolis sophorae*. (C) *Dynastor darius*. Tegumen in dorsal view. (D) *B. astyra*. Genital capsule in lateral view. (E) *D. darius*. (F) *B. sophorae*. Tegumen and uncus in lateral view. (G) *D. macrosiris*. Phallus in lateral view. (H) *D. napoleon*. Juxta in ventral view. (I) *B. astyra*. (J) *D. napoleon*. Phallus in ventral view. (K) *D. darius*. (L) *B. haenschii*. (M) *B. granadensis*.

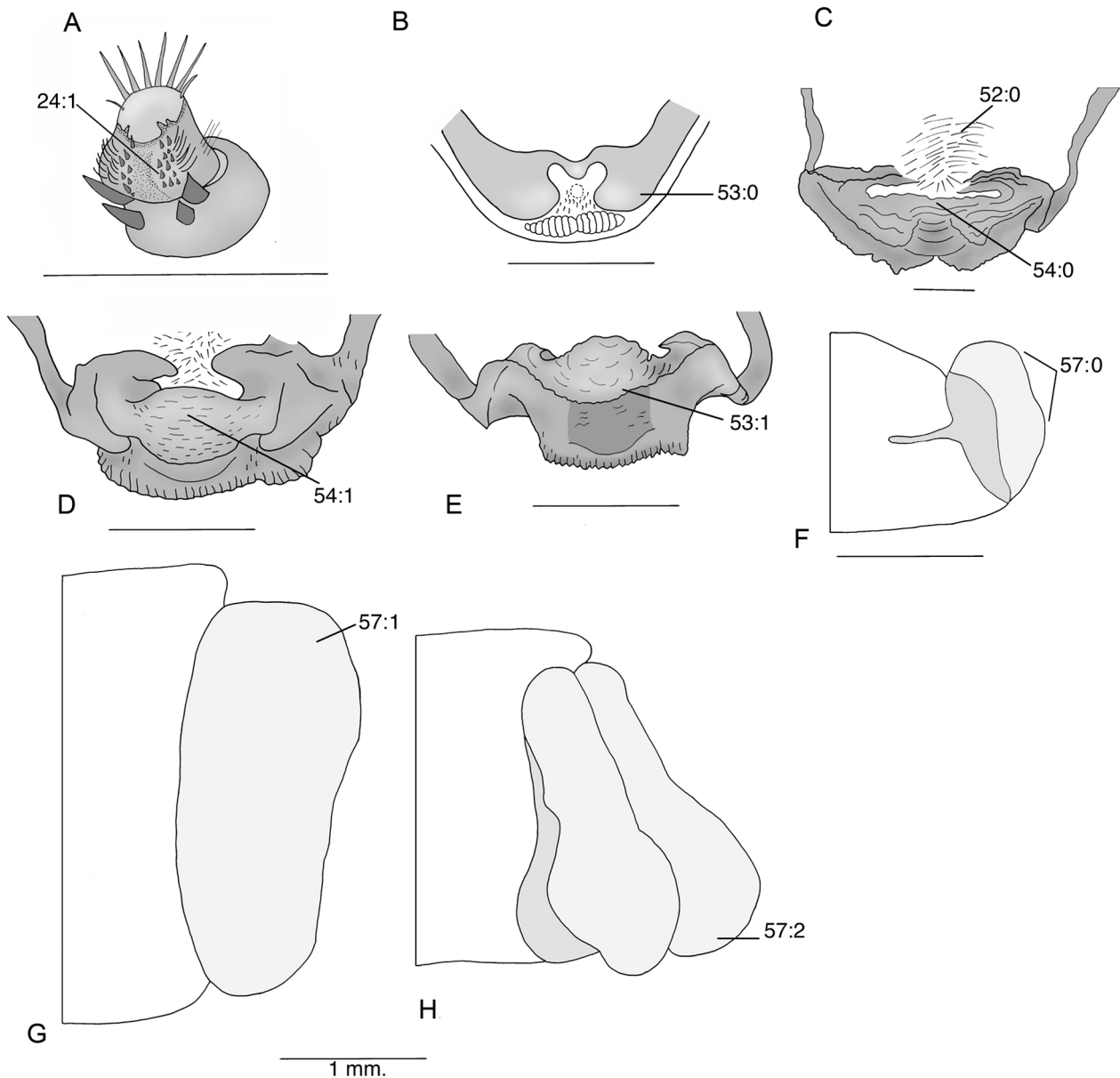


FIGURE 9. Female characters. Scale bars, 1 mm. Female distal tarsomere in ventral view (details of pulvillar process omitted). (A) *Dynastor darius*. Sterigma in ventral view. (B) *D. darius*. (C) *B. isthmia*. (D) *B. astyra*. (E) *B. dinizi*. Posterior lobes of papillae annales in lateral view. (F) *Elymias hypermnestra*. (G) *D. napoleon*. (H) *B. haenschi*. Note that the lamella antevaginalis is not visible in C, D, and E due to the orientation of the drawing.

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Literature cited

- Aiello, A. & Silberglied, R. (1978) Life history of *Dynastor darius* (Lepidoptera: Nymphalidae: Brassolinae) in Panama. *Psyche*, 85, 331–345.
- Bristow, R. (2008) A review of the genus *Brassolis* Fabricius in Colombia and Ecuador with description of two new taxa (Lepidoptera, Nymphalidae). *Zootaxa*, 1806, 47–58.
- Caldas, A. (1997) Notes on male genitalia of the *Anaea ryphea* - *Anaea euryppyle* complex (Nymphalidae), *Journal of the Lepidopterists' Society*, 51, 83–90.
- Carvalho, M.C., Queiroz, P.C.D. & Ruzszyk, A. (1998) Protandry and female size-fecundity variation in the tropical butterfly *Brassolis sophorae*. *Oecologia*, 116, 98–102.
- Casagrande, M.M. (1995) Notas sistemáticas sobre Brassolinae. I tribos (Lepidoptera, Nymphalidae). *Revista Brasileira de Zoologia*, 12, 671–699.
- Casagrande, M.M. (2004) Brassolini. *Atlas of Neotropical Lepidoptera* (ed. By J.B. Heppner), Part 4A Checklist (ed. By G. Lamas), pp. 201–205. Association of Tropical Lepidoptera/ Scientific Publishers, Gainesville, FL.
- Clare, L.D.Jr. & Squire, F.A. (1934) The coconut caterpillar, *Brassolis sophorae* L. (Lep. Brassolidae) in British Guiana. *Agricultural Journal of British Guiana*, 5(3), 166–199.
- Costa, L.P. (2003) The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. *Journal of Biogeography*, 30, 71–86.
- D'Almeida, R.F. (1956) Algumas notas sobre rhopalocera do Brasil (Lep). *Revista Brasileira de Entomologia* 5: 197–202.
- DeVries, P.J. (1988) Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *Journal of Research on the Lepidoptera*, 26, 98–108.
- Dunn, L.H. (1917) The cocoanut-tree caterpillar (*Brassolis isthmia*) of Panama. *Journal of Economic Entomology*, 10, 473–488.
- Francini, R.B., Freitas, A.V.L. & Penz, C.M. (2004) Two new species of *Actinote* (Lepidoptera, Nymphalidae) from Southeastern Brazil. *Zootaxa*, 719, 1–10.
- Freitas, A.V.L. & Brown Jr., K.S. (2004) Phylogeny of the Nymphalidae (Lepidoptera). *Systematic Biology*, 53, 363–383.
- Fruhstorfer, H. (1912) 5. Familie: Brassolidae. In: Seitz, A. (Ed.), *Die Gross-Schmetterlinge der Erde*. Stuttgart, Alfred Kernen. 5, 285–328 (15 May), 329–332 (31 May), pls. 61–67.
- Goloboff, P.A. (1993) Estimating character weights during tree search. *Cladistics*, 9, 83–92.
- Goloboff, P.A. (1997) Self-weighted optimization: tree searches and character state reconstructions under implied transformation cost. *Cladistics*, 13, 225–245.
- Goloboff, P., Farris, J. & Nixon, K. (2007) T.N.T.: Tree Analysis Using New Technology. Program and documentation, available from the authors, and at <www.zmuc.dk/public/phylogeny>.
- Goloboff, P., Carpenter, J.M. Arias, S.J. & Miranda-Esquivel, D.R. (2008) Weithing against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, 24, 758–773.
- Hill, R., Penz, C.M. & DeVries, P.J. (2002) Phylogenetic analysis and review of *Panacea* and *Batesia* butterflies (Nymphalidae). *Journal of the Lepidopterists' Society*, 56(4), 199–215.
- Kristensen, N.P. (2004) Handbook of Zoology, Vol. IV. Arthropoda: Insecta, Part 36, Lepidoptera, moths and butterflies, vol. 2: Morphology, Physiology, and Development. de Gruyter, Berlin, New York.
- Krenn, H.W., Zulka, K.P. & Gatschnegg, T. (2001) Proboscis morphology and food preferences in nymphalid butterflies (Lepidoptera: Nymphalidae). *Journal of Zoology*, 254(1), 17–26
- Maddison, W.P. & Maddison, D.R. (2005) MacClade: version 4.08. Sunderland, MA: Sinauer.
- Moss, A.M. (1935) Some details concerning the brassolid butterfly, *Dynastor macrosiris*, its early stages, life-history and food-plants. *Proceedings of the entomological Society of London*, (A) 9, 97–102.
- Müller, W. (1886) Südamerikanische Nymphalidenraupen. Versuch eines natürlichen Systems der Nymphaliden. *Zoologische Jahrbücher (Systematik)*, 1, 417–678.
- Nixon, K.C. (1999) The Parsimony Ratchet, a New Method for Rapid Parsimony Analysis, *Cladistics*, 15, 407–414.
- Otero, L.S., Casagrande, M.M. (1992) Hibridismo em Brassolinae (Lepidoptera, Nymphalidae). *Revista Brasileira de Entomologia*, 36, 723–728.
- Peña, C., Wahlberg, N., Weingartner, E., Kodandaramaiah, U., Nylin, S., Freitas, A.V.L. & Broker, A.V.Z. (2006) Higher level phylogeny of Satyrinae butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data. *Molecular phylogenetics and Evolution*, 40, 29–49.
- Penz, C.M., Aiello, A. & Srygley, R.B. (1999) Early stages of *Caligo illioneus* and *C. Idomeneus* (Nymphalidae, Brassolinae) from Panama, with remarks on larval food plants for the subfamily. *Journal of the Lepidopterists' Society*, 53, 142–152.
- Penz, C. & DeVries, P.J. (2002) Phylogenetic analysis of *Morpho* butterflies (Nymphalidae: Morphinae): implications for classification and natural history. *American Museum Novitates*, 3374, 1–33.

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- Penz, C.M. (2007) Evaluating the monophyly and phylogenetic relationships of Brassolini genera (Lepidoptera, Nymphalidae). *Systematic Entomology*, 32, 668–689.
- Penz, C.M. (2008) Phylogenetic revision of *Eryphanis* Boisduval, with a description of a new species from Ecuador (Lepidoptera, Nymphalidae). *Insecta Mundi*, 35, 1–25.
- Romero, F.M., Bermudez, P. & Gonzales, J.M. (2004) Notes on the life history of *Dynastor darius darius* (Fabricius) (Nymphalidae: Brassolinae) from Venezuela. *Journal of the Lepidopterists' Society*, 59, 37–39.
- Stichel, H. (1904) Lepidoptera Rhopalocera. Fam. Nymphalidae. Subfam. Brassolinae. *Genera Insectorum*, 20, 1–48 (ed. By P. Wytzman). Brussels.
- Stichel, H. (1925) Zur systematik der Brassolidae (Lep. Rhop.). *Neue Beitrage zur systematischen Insektenkunde*.
- Stichel, H. (1932) Brassolidae. *Lepidopterorum Catalogus*, 51, 1–115.
- Wiens, J. (1999) Polymorphisms in Systematics and Comparative Biology. *Annu. Rev. Ecol. Syst.* 30. 327–362.

Appendix 1. Examined material

Abbreviations: Milwaukee Public Museum (MPM), Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity (MGCL), Museu Anchieta, Porto Alegre (MAPA), and The Natural History Museum, London (BMNH); male (m), female (f); Carla Penz (CMP), Ivonne Garzón-Orduña (IG). Dissected specimens are indicated with an asterisk.

Dynastor napoleon

1 m*, Brazil, Santa Catarina, XI 1954, genitalia preparation CMP 06-08 (MPM); 1 m*, Brazil, Santa Catarina, IX 1964, genitalia preparation CMP 06-09 (MPM); 1 m, Brazil, Santa Catarina, 1956 (MGCL); 1 f*, Brazil, Rio de Janeiro, 1920, genitalia preparation IG 07-09 (MPM); 1 f*, no data, genitalia preparation IG 07-10 (MGCL).

Dynastor macrosiris

1 m*, Guiana Française, genitalia preparation CMP 06-34 (MGCL); 1 m*, El Salvador, Finca El Refugio, Ahuachapan, 250 m, Sept. 2006 (PJD); 1 f*, Mexico, Chiapas, 1973 genitalia preparation CMP 06-35 (MGCL); 1 f*, El Salvador, Finca El Refugio, Ahuachapan, 250 m, Sept. 2006 (PJD).

Dynastor darius

1 m* Paraguay, 1973, genitalia preparation CMP 01-14 (MPM); 1 m*, Nicaragua, Managua dept. 7.5 km S Managua, 1858 genitalia preparation IG 07-15 (MPM); 1 f*, Brazil, Parana, Ponta Grossa, XI 1947, genitalia preparation CMP 01-15 (MPM); 1 f, Brazil, Santa Catarina, "Mansa Humbolt" [sic] (MPM).

Brassolis sophorae

1 m*, Guiana Française, genitalia preparation IG 07-01 (MGCL); 1 m*, British Guiana, Georgetown, 1959, genitalia preparation CMP 07-24 (MPM); 1 m*, Trinidad, genitalia preparation IG 07-02 (MGCL); 1 m*, Ecuador, Napo Prov., Jatun Sacha Biol. Sta., 1988, genitalia preparation IG 07-03 (MGCL); 1 m*, Peru, Loreto, 1961, Pucallpa, genitalia preparation CMP 07-135 (MGCL); 1 m*, Bolivia, Santa Cruz, genitalia preparation CMP 07-142 (MGCL); 1 m, Bolivia, Santa Cruz, 1972 (MGCL); 1 m*, Paraguay, Villarica, 1951, genitalia preparation CMP 07-22 (MPM); 1 m*, Brazil, Sta. Catarina, Nova Teutônia, 1960, genitalia preparation CMP 01-03 (MPM); 1 f*, Guiana Française, genitalia preparation CMP 07-139 (MGCL); 1 f*, Trinidad, Moruga, genitalia preparation CMP 07-40 (MGCL); 1 f, Ecuador, Apuya, 600 m, km 20 Tena-Puyo, Napo Province, 1993; 1 f*, Ecuador, 1000 m. Puyo, Oriente, 1950, genitalia preparation CMP 01-04 (MPM); 1 f*, Peru, Loreto, 1981, 43 mi. up Napo river from San Francisco de Orellana, genitalia preparation CMP 07-136 (MGCL); 1 f, Bolivia, Beni Riveralta, 1986 (MGCL); 1 f*, Bolivia, Sta. Cruz Mineros, 1956, genitalia preparation CMP 01-11 (MPM); 1 f*, Paraguay, Villarica, 1949, CMP 07-138 (MPM); 1 f*, Brazil, Nova Friburgo, Rio de Janeiro, genitalia preparation CMP 01-07 (MPM); 1 f, Brazil, São Paulo, São Carlos, 1979 (MGCL).

Brassolis dinizi

1 m*, Brazil, Ceará, Fortaleza 1958, genitalia preparation CMP 01-08 (MPM); 1 m Brazil, Ceará, Fortaleza, 1959, (MPM); 1 m, North Brazil, 1973 (MPM); 1 m, Paraíba, Brazil, (MPM); 1 m*, Brazil, [Ceará] Fortaleza, 1956, genitalia preparation CMP 07-23 (MPM); 1 f*, Brasil, Paraisa [sic], genitalia preparation CMP 01-09 (MPM); 1 f* Brazil, Ceará Fortaleza, 1959, CMP 07-134 (MPM); 1 f Brazil, Ceará, Fortaleza, 1959.

Brassolis haenschii

1 m*, Ecuador, Balzapamba, genitalia preparation IG 07-04 (MGCL); 1 m*, Ecuador, Balzapamba, genitalia preparation CMP 07-133 (BMNH); 1 f*, Ecuador, Los Rios Province, Rio Palenque, genitalia preparation IG 07-08 (MGCL); 1 f*, Ecuador, Los Rios Province, Rio Palenque, genitalia preparation IG 07-06 (MGCL).

Brassolis isthmia

1 m*, Costa Rica, Limon province, puerto Viejo, 1989, genitalia preparation CMP 07-137 (MGCL); 1 m*, Panama, Canal Zone, 1973, genitalia preparation CMP 07-21 (MPM); 1 m, Panama, Balboa, 1966, (MGCL); 1 f*, Panama, Tocumen, 1976, genitalia preparation IG 07-05 (MGCL); 1 f*, Colombia, Tolima, Payande, Mina Vieja area, 800–950 m. 1974, genitalia preparation CMP 07-141 (MGCL).

Brassolis granadensis

1 m*, Colombia Cali, 1956, genitalia preparation CMP 01-10 (MPM); 1 m, no data (MGCL).

Brassolis astyra

1 m*, Panama, Canal Zone, 1973, [this specimen is likely mislabeled] CMP 07-21 (MPM); 1 m*, Brazil, 1939, genitalia preparation CMP 06-39 (MPM); 1 m*, Brazil, Pará, Obidos, 1952, genitalia preparation CMP 07-20 (MPM); 1 m, Brazil, Rio de Janeiro, Gávea, 1960 (MPM); 1 m, Brazil, Corcovado, Rio [de Janeiro], 800 ft, 1910? (MGCL); 1 m, Brazil, [Santa Catarina], Corupa (MPM); 1 m, Brazil, Santa Catarina (MPM); 1 m*, Brazil, Gravataí, 1966 (MAPA); 1 m, Brazil, Gravataí, 1966 (MAPA); 1 f*, Brazil, 1932, genitalia preparation CMP 06-40 (MPM); 1 f*, [Brazil], Rio [de] Janeiro, genitalia preparation IG 07-07 (MGCL); 1 f, Brazil, Rio de Janeiro, 1960 (MPM); 1 f, Brazil, Corcovado, Rio [de Janeiro], 800 ft, 1910 (MGCL); 1 f, Brazil, Itaci, São Paulo, 1960 (MPM); 1 f, Brazil, Santa Catherina, Rio Tirubo, 1937 (MPM); 1 f*, Brazil, Gravataí, 1966 (MAPA); 1 f, Brazil, Gravataí, 1966 (MAPA).

Narope panniculus

1 m*, Ecuador, genitalia preparation CMP 06-03 (AMNH); 1 f*, Brazil, Minas gerais, genitalia preparation CMP 06-04 (AMNH).

Bia actorion

1 m*, Peru, Loreto, Iquitos, 1986, genitalia preparation CMP 01-01 (MPM); 1 f*, Peru, Satipo, 1950, genitalia preparation CMP 01-02 (MPM).

Elymnias hypermnestra

1 m*, Ceylon 9-7-62 genitalia preparation CMP 02-45 (MPM); 1 f*, E. Pakistan, Bandura, Hashnabad Dacca Dt. 02-66 genitalia preparation CMP 02-46 (MPM).

Appendix 2. Character list

1. Last segment of labial palpus: (0) longer than the distal width of second segment (Fig. 8A), (1) approximately the same length as distal width of second segment (Fig. 8C), (2) shorter than the distal width of second segment (Fig. 8B). Note: Males were examined to score this character.
2. Sensilla styloconica at proboscis tip: (0) absent (Fig. 3E), (1) present.
3. Male forewing costal margin, basal third: (0) convex (Fig. 7D), (1) slightly concave (Fig. 7A).
4. Dorsal forewing costal color pattern: (0) solid color (Fig. 7A), (1) striped (Fig. 7D).
5. Male, dorsal forewing postmedial band: (0) absent, (1) present (Fig. 7A).
6. Male, dorsal forewing postmedial band: (0) extended through discal cell (Fig. 7B), (1) distal from discal cell (Fig. 7D).
7. Male, dorsal forewing postmedial band, as it extends through discal cell: (0) continuous, (1) with a gap at anterior edge of discal cell (Fig. 7B).
8. Male, dorsal forewing postmedial band: (0) continuous (Fig. 7B), (1) broken (Fig. 7D).
9. Male, broken dorsal forewing postmedial band composed of spots in cells: (0) M3, Cu1 and Cu2 (Fig. 7D), (1) M3 and Cu2, (2) M3 only.
10. Male, main color of the dorsal forewing postmedial band: (0) orange (Fig. 7B), (1) pale yellow (Fig. 7D), (2) white.
11. When male dorsal forewing postmedial band contains the color orange, white overlay: (0) absent (Fig. 7B), (1) present (Fig. 7A).
12. When male dorsal forewing postmedial band contains the color orange, white overlay: (0) solid from costal margin through discal cell (Fig. 7A), (1) diffuse from costal margin through discal cell (Fig. 7C).
13. Male, ventral forewing submarginal lines: (0) absent (Fig. 7C), (1) one, (2) two (Fig. 7A). Note: A line was scored as 'present' when it was complete or nearly so.
14. Male, color of the dorsal, medial area of hindwing, posterior to discal cell: (0) brown, same as hindwing background color (Fig. 7C), (1) orange, contrasting hindwing background color (Fig. 7A).
15. Male, dorsal scent organ adjacent to hindwing vein Cu2: (0) absent (Fig. 7D), (1) present (Fig. 7A). Note: Ventrally, male hindwing cell Cu2 also has a distinctive appearance that could be related to the scent organ located dorsally in the same cell.
16. Male, color of the dorsal hindwing scent organ adjacent to vein Cu2: (0) similar to neighboring region of the wing (Fig. 7B), (1) lighter than neighboring region of the wing (Fig. 7A).
17. Male, dorsal hindwing postmedial band: (0) absent (Fig. 7B), (1) present (Fig. 7A,C).
18. Male, dorsal hindwing marginal line: (0) absent (Fig. 7A), (1) present (Fig. 7D).
19. Male, pattern of the distal portion of ventral hindwing discal cell: (0) ripple pattern, (1) dashed (Fig. 7C), (2) marbled (Fig. 7D). Note: The character state 'dashed' refers to small rows of two or three white scales on a dark background.
20. Male, proximal portion of ventral hindwing discal cell, dashed pattern formed by broad white scales: (0) absent (Fig. 7C), (1) present (Fig. 7A).

21. Midleg tibial spurs: (0) absent, (1) present. Note: Character 12 in Penz (2007).
22. Male, midleg tarsus length: (0) longer than tibia, (1) approximately the same length as tibia. Note: No measurements were taken, comparisons were done by eye.
23. Male midleg, dorsal spines on tarsus: (0) absent, (1) present. Note: Character 13 in Penz (2007).
24. Female foreleg, distal tarsomere, ventral spines between the sensillae: (0) absent, (1) present (Fig. 9A).
25. Abdomen, dorsal color: (0) brown, (1) orange (Fig. 7B).
26. In dorsal and dorsolateral views, anterolateral constriction of the tegumen: (0) absent, (1) present (Fig. 8D). Note: Character 16 in Penz (2007).
27. Fenestrula between tegumen and uncus: (0) absent, (1) present (Fig. 8D).
28. In lateral view, transition between pedunculum and vinculum: (0) straight (Fig. 8F), (1) at an angle (Fig. 8E).
29. Anterior apodeme that forms the edge of vinculum: (0) wide (Fig. 8F), (1) narrow.
30. In lateral view, valva: (0) projecting beyond uncus tip, (1) not projecting beyond uncus tip (Fig. 8E).
31. Heavier sclerotization of the dorsal edge of valva: (0) does not extend to the valva tip, (1) extends just to the valva tip. Note: Adapted from character 26 in Penz (2007).
32. In lateral view, ventral posterior region of valva: (0) excavated (Fig. 8E), (1) projected (Fig. 8F), (2) straight.
33. Internal surface of valva, basal region: (0) slightly less sclerotized than distal region, (1) conspicuously less sclerotized than distal region. Note: This region is commonly less sclerotized in all *Brassolini*, however in *Brassolis* it is conspicuously less sclerotized.
34. Groove at the articulating point between valva and appendices angulares: (0) absent, (1) limited to the base of valva, (2) extended distally for ca. one third of the valva length. Note: Character 31 in Penz (2007).
35. Distribution of setae on the diaphragm: (0) with a dense patch dorsally (Fig. 8J), (1) with a dense patch ventrally (Fig. 8I).
36. Juxta: (0) reaching the edge of the anellus (Fig. 8I), (1) not reaching the edge of the anellus (Fig. 8J).
37. Dorsal edge of juxta: (0) notched, (1) continuous. Note: Specimens for which the juxta was nearly transparent and difficult to see were scored as “?”.
38. Distal opening of phallus: (0) dorsal, (1) dorsolateral, (2) ventrolateral. Note: Character 35 in Penz (2007).
39. Shape of sclerotized tip of phallus: (0) rounded (Fig. 8K), (1) pointed (Fig. 8L), (2) squared (Fig. 8M).
40. Semi-sclerotized lobe on left side of phallus: (0) absent, (1) present.
41. Peg-like setae on semi-sclerotized lobe on left side of phallus: (0) absent, (1) present (Fig. 8K).
42. Peg-like setae on phallus shaft: (0) absent, (1) present. Note: Character 37 in Penz (2007).
43. Long setae on semi-sclerotized lobe on left side of phallus: (0) absent, (1) present (Fig. 8L).
44. Sclerotized tip of phallus: (0) flat, allowing vesica to expand distally, (1) forming a small coecum that projects beyond the distal opening (Fig. 8H).
45. In lateral view, ventral outline of phallobase: (0) evenly arched (Fig. 8H), (1) undulated (Fig. 8F).
46. In lateral view, uncus base: (0) straight, (1) projected (Fig. 8E).
47. Lateral uncus wings, as they extend posteriorly into uncus process: (0) vanishing gradually; (1) merging to form a single, prominent dorsal keel. Note: Adapted from character 39 in Penz (2007).
48. In lateral view, distal portion of uncus; (0) short (Fig. 8F), (1) tall (Fig. 8G).
49. Gnathos: (0) absent, (1) present. Note: Character 46 in Penz (2007).
50. Gnathos, dorsal expansion of proximal region: (0) absent, (1) present (Fig. 8G). Note: Adapted from character 47 in Penz (2007), where the expansion is described as ‘posterior’.
51. Gnathos, dorsal expansion of proximal region: (0) more proximal, branching off at half the length of gnathos (Fig. 8E), (1) more distal, branching off beyond half of the length of gnathos (Fig. 8G).
52. Anterior section of sterigma: (0) absent, (1) present.
53. Posterior section of sterigma: (0) flush to the body wall, (1) forming a ‘flap’ (Fig. 9E). Note: This was mistakenly described as ‘anterior section of sterigma’ by Penz (2007, character 66).
54. Dorsal projections of flap formed by the posterior section of sterigma: (0) small (Fig. 9C), (1) large (Fig. 9D). Note: These projections can be seen by pulling down the ‘flap’.
55. Antrum: (0) entirely membranous, (1) with a sclerotized spot, (2) fully sclerotized. Note: Adapted from Penz (2007, character 70).
56. Signa: (0) absent, (1) present. Note: Character 72 in Penz (2007).
57. In lateral view, posterior lobes of papilla annales: (0) more developed dorsally (Fig. 9F), (1) equally developed dorsally and ventrally (Fig. 9G), (2) more developed ventrally (Fig. 9H).

