

PHYLOGENY AND REVISION OF THE GENUS *HERACLIDES* HÜBNER, 1819
(LEPIDOPTERA: PAPILIONIDAE: PAPILIONINAE: PAPILIONINI)

By

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To my lovely wife, Dadria, and our first child

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Abstract of Dissertation Presented to the Graduate School
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REVISION AND PHYLOGENY OF THE GENUS *HERACLIDES* HÜBNER, 1819
(LEPIDOPTERA: PAPILIONIDAE: PAPILIONINI)

By

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This work assessed the information about this economically important group of *Citrus*-feeding swallowtails and the relationships between these species. Surprisingly, we know little about the biology and habits of the majority of these species. With the recent introduction of a *Citrus*-feeding swallowtail to the West Indies from Southeast Asia, *Papilio demoleus*, it becomes crucial to understand the effect this butterfly will have on the ecology of native fauna. This butterfly has spread from the Dominican Republic to Jamaica, and Puerto Rico; potentially dispersing to Florida in the near future. By understanding the relationships within the *Heraclides* and building our knowledge of their biology and habits, we may be better able to sustainably manage this new invasive, while protecting the native fauna of Florida and the region at large.

Evaluation of phylogenetic evidence for subgroups within the *Heraclides* inferred from investigation of support for relationships among subgroups using existing genetic data, and 133 morphological characters, mainly from genitalic and wing pattern elements yielded the proposed group structure. A generalized wing pattern of homologous elements for *Heraclides* is proposed and the formal nomenclature, natural history, and life history of the 28 species revised. Three new synonyms are proposed: *Papilio isidorus nymphius* (Rothschild & Jordan, 1906), *Papilio rhodostictus pacificus* (Rothschild & Jordan, 1906), and *Heraclides chiansiades mossi* Brown,

1994. Additionally, distribution maps for each species and subspecies are included as well as a straightforward identification key based mainly on wing pattern for the group. I hope that the identification of major areas for future investigation will serve as a catalyst for future studies into the biology and morphology of this group. There is a need for detailed studies into the morphology and systematics of *Papilio* (sensu lato) to understand their overall relationships and end controversy about the generic status of the subgroups it contains, including the status of the *Heraclides*.

CHAPTER 1 INTRODUCTION AND LITERATURE REVIEW

Introduction

The recent arrival of an invasive rutaceous-feeding Swallowtail Butterfly, *Papilio demoleus*, in the West Indies has stirred the interest of citrus farmers, agricultural pest managers, and conservation biologists alike. The fact that this species is a rutaceous-feeder suggests that cultivated and native New World Rutaceae may be suitable hosts for this pest. These potential hosts include plants in the genera *Amyris*, *Piper*, *Ptelea*, *Ruta*, and *Zanthoxylum*, host plants for native rutaceous-feeding Papilionidae and other fauna of the West Indies and South Florida. However, its ability to use these hosts is unknown but poses concerns for organism spread and the feasibility of control. Concern about its ability to feed on hosts of native fauna is not trivial, as some of the native Swallowtail butterflies are endangered, threatened, or otherwise quite rare (example: the Schaus Swallowtail, *Heraclides aristodemus ponceanus*).

Central to the management of this new invasive butterfly is an understanding of the impact this butterfly will have on native rutaceous-feeding papilionids. The information that exists on the life histories of some of the rutaceous-feeding papilionid species is sparse, and little done to clarify the evolutionary relationships among these species. As such, knowledge of the phylogenetic relationships within the *Heraclides* is limited. Any new life history information will aid significantly in understanding these relationships. There has been much work on the phylogenetics of swallowtail butterflies in general, but this has focused on phylogenetic relationships at the higher taxonomic levels of family, subfamily, and tribes. To a lesser extent attention has been paid within genera, and among species (see Aubert et al., 1999; Caterino and Sperling, 1999; Caterino et al., 2001; Hancock, 1983; Igarashi, 1984; Miller, 1987; Monroe, 1961; Nazari et al., 2007; Reed and Sperling, 1999; Zakharov et al. 2004).

Historical Classification and Phylogenetics

Classification within the Papilionidae has often proved quite difficult due to the wide diversity of life histories and phenotypic appearances (Monroe, 1961). The earliest attempts at the classification of Papilionidae, based on phenetics (also known as numerical taxonomy), started with Rothschild and Jordan (1906), and Seitz (1907), was improved upon by Le Cerf (1924) and d'Almeida (1966), among others. Phylogenetic attempts started with Ford (1944), and continued with Ehrlich (1958), Monroe (1961), Hancock (1983), Igarashi (1984), Miller (1987), and Tyler et al. (1994). The field of molecular biology, with the use of DNA sequence data, subsequently added significant knowledge. Work by Kristensen (1976), Hancock (1983), Miller (1987), and Tyler et al. (1994) have been most convincing in showing that the monophyly of the family Papilionidae is supported by several synapomorphies, chief of which is the larval osmeterium (Caterino et al., 2001).

Classification below family level has been more controversial, with various schemes proposed. Goose (1881) divided the family based on morphology and male genitalia into the genera *Graphium*, *Pachliopta*, *Papilio*, and *Troides*. He did not include subfamilial or tribal classification. Staudinger (1892) listed *Euryades* and *Cressida* as the most primitive taxa in the family, and Jordan and Stichel (1907) linked *Baronia* and *Parnassius* (Igarashi, 1984). Ford (1944) recognized four subfamilies within Papilionidae based on white and yellow anthoxanthins and red pigments, namely Baroniinae, Papilioninae, Parnassiinae, and Zerynthiinae. He divided Papilioninae into five tribes (Cressidini, Graphiini, Papilionini, Teinopalpini, and Troidini). Monroe (1953) subsequently reduced the tribes to three (Graphiini, Papilionini, and Troidini). Ehrlich (1958) however, only recognized three subfamilies (Baroniinae, Parnassiinae, and Papilioninae), but somewhat concurred with Ford (1944) in recognizing four tribes within Papilioninae (Cressidini, Graphiini, Papilionini, and Teinopalpini) (Hancock, 1983). Recently,

there has been general acceptance on the three subfamilies of Papilionidae (Baroniinae, Parnassiinae, and Papilioninae), and there seems to be consensus and relative acceptance of a monophyletic Papilionini tribe within the Papilioninae, the largest of the three Papilionidae subfamilies (Aubert et al., 1999; Miller, 1987; Tyler et al., 1994). Miller (1987), proposed five synapomorphic characters for the monophyly of this subfamily. These characters are the presence of a pseuduncus on the VIII tergite in males, anal brushes along vein 2a on the ventral surface of male hindwing, which may be homologous to the androconia of other subfamilies, a basal spur on the forewing, a distinct meral suture on the metathorax, and larvae with a white saddle on the abdominal segments.

Divisions within the tribe Papilionini, i.e., at the generic level, have proved to be much more problematic, with no current consensus on the subdivisions. This has been confounded by the fact that one of the most comprehensive cladistic treatments of the tribe, Miller (1987), assigns all but two species in the tribe Papilionini into one genus *Papilio*; he found no justification for the use of subdivisions in *Papilio* (Miller, 1987; Aubert et al., 1999; Zakharov et al., 2004^a). Miller (1987) also proposed that there is no evidence for the generic status of the groups within *Papilio* (sensu lato) and suggested four synapomorphic characters for the monophyly of *Papilio* (sensu lato). These are, scale-less tibiae and tarsi, a lateral process on the vesica of the males, a zipper-like signum in females, and prominent ostial armature in females. Tyler et al. (1994) in their review of the Swallowtail Butterflies of the Americas accepted for the most part the conclusions of Miller (1987) and sought to build on them by showing the monophyly of several groups within Papilionini, including *Heraclides*. Zakharov et al. (2004^a) took a comparative review of some of the major schemes adopted for the species groups that fall under the umbrella *Papilio* (sensu lato), showing that Monroe (1961) included five subsections

under *Papilio* but fell short of designating them as genera or subgenera because of the complexity involved in separating them using adult characters. Hancock (1983), using cladistic methods, found phylogenetic, and inferred evolutionary antiquity, evidence for six genera, and Igarashi (1984) found evidence for seven genera based on immature stages. Other major works adopted for the most part Hancock's (1983) scheme (see Collins and Morris, 1985), but there remains considerable support for Miller's (1987) treatment. Häuser et al. (2005) modified Collins and Morris's (1985) *Papilio* by dividing it into two genera (*Chilasa* and *Papilio*). They then subdivided *Papilio* into nine subgenera (Smith and Vane-Wright, 2008), one of which is *Heraclides*. Lamas (2004), in his checklist of Papilionoidea, one of the latest and most up to date treatment, subdivided *Papilio* into eight groups, *Heraclides* being one of them.

Phylogenetic Placement of *Heraclides*

One of the earliest phylogenetic hypotheses of *Heraclides* was based on 30 characters, and positions *Heraclides* as a sister group of *Eleppone* and *Chilasa*. This group is in turn sister to *Pterourus*. *Papilio* (sensu stricto) and *Princeps* are treated as sister taxa, together these being sister to the *Pterourus-Heraclides-Chilasa-Eleppone* group (Hancock, 1983). Prior to this, several authors, including Munroe (1961) had divided *Papilio* (sensu lato) into groups, one of which contained members of *Heraclides*, but they did not explore relationships. Igarashi (1984) and Miller (1987) followed this trend and recognized only *Papilio* (sensu lato); thus the relationship of the *Heraclides* to the rest of *Papilio* (sensu lato) was not made explicit except that *Heraclides* and *Chilasa* were presumed to be sister groups by Igarashi (1984) (Tyler et al. 1994).

Beginning in the 1990's, attempts to resolve the issues within the Papilionini have focused on the use of molecular data and the computational strength of computer software. To a lesser extent, morphological characters and life history information augment molecular information. These modern phylogenetic treatments largely agree on the monophyly of *Heraclides*. Modern

phylogenetic treatments that include more than one *Heraclides* species include Tyler et al. (1994), Caterino and Sperling (1999), Aubert et al. (1999), Reed and Sperling (1999), Zakharov et al. (2004), and Kunte (2009). Other works that shed light on the placement of *Heraclides* within *Papilio* (sensu lato) include Caterino et al. (2001) and Nazari et al. (2007).

Tyler et al. (1994) in their review of 44 taxa, including five members of *Heraclides*, utilized 155 morphological and behavioral characters (221 character state changes) and employed the Hennig-86 program to show relationships, one of the first such approaches that used the computational strength of computers. They employed a heuristic approach with branch swapping to produce phylogenies that shows some support for Miller (1987). However, they got conflicting results for juveniles versus adults, but the total evidence phylogeny shows *Heraclides* with *Chilasa* as a monophyletic clade.

Using 2.3 kb of sequence data from mitochondrial *Cytochrome Oxidase I* and *II* genes, Caterino and Sperling (1999) included two species of *Heraclides* (*H. cresphontes* and *H. anchisiades*) in their analysis of *Papilio* (sensu lato). Analysis was done using PAUP (Phylogenetic Analysis Using Parsimony and Other Methods ©, version 4) under parsimony and maximum likelihood frameworks; MacClade (version 3.06) yielded various sequence statistics. Amino acid transformations were weighed equally in the parsimony analysis. A heuristic search with 50 random taxon additions and branch swapping algorithms in addition to 1000 bootstrap replicates with simple taxon addition and NNI branch swapping was done. Additionally, the Hasegawa-Kishino-Yano model of sequence evolution was implemented. They found good support for the previously recognized species groups and subgenera. *Heraclides* placed basal to the rest of *Papilio* (sensu lato) under a parsimony framework; there was no support for this placement with maximum likelihood. Their suggested hypothesis for relationships in *Papilio*

(sensu lato) shows *Heraclides* as a monophyletic clade, basal to the remainder of *Papilio* (sensu lato). There is strong support for the monophyly of *Heraclides* (*H. cresphontes* + *H. anchisiades*) when the 2.21 kb of sequence data from *mitochondrial cytochrome oxidase I* and *II* genes (Caterino and Sperling, 1999) were combined with 1.01 kb of sequence data from the nuclear coding gene *elongation factor-1 α* (*EF-1 α*). The relationships between 22 species of *Papilio* (sensu lato) were investigated under a maximum parsimony framework (Reed and Sperling, 1999). Analysis of *EF-1 α* , separate from *COI/COII*, supported monophyly of *Heraclides* (*H. cresphontes* + *H. anchisiades*). However, only in the analysis of *COI/COII* does *Heraclides* (*H. cresphontes* + *H. anchisiades*) come out as basal to the remainder of *Papilio* (sensu lato). In other cases, *Heraclides* was rooted within *Papilio* (sensu lato).

The monophyly of *Heraclides* (using *H. cresphontes* and *H. anchisiades*) was also shown using 1307 bp from sections of the genes for the large ribosomal RNA (LSU) and subunit 1 of NADH-dehydrogenase (ND1)(Aubert et al., 1999). The software used was PAUP and all heuristic searches for optimal trees were done using TBR branch swapping with the option PULPARS. Trees were developed using parsimony, distance (minimum evolution), and maximum likelihood methods. The pooled alignable LSU sites and the 1st and 2nd codon positions of the ND1 sequence all show significant support for the monophyly of *Heraclides* (*H. cresphontes* + *H. anchisiades*). In all cases, *Heraclides* was nested within *Papilio* (sensu lato) being closest related to the *Pterourus* + *Chilasa* group.

Zakharov et al. (2004), in the most comprehensive molecular treatment of the *Heraclides* group to date, looked at seven species of *Heraclides* (*H. anchisiades*, *H. erostratus*, *H. hectorides*, *H. torquatus*, *H. astyalus*, *H. cresphontes* and *H. thoas*) in their analysis of 3.3 kb of sequence of the genes *COI*, *COII* and *EF-1 α* . Analysis was conducted using PAUP (version

4.0b-b10) under maximum parsimony and maximum likelihood frameworks. Bayesian analyses were also done. Selected ecological and morphological traits were included in the analysis which led to phylogenies that support previous hypotheses of five major subdivisions within *Papilio* (sensu lato), namely *Heraclides*, *Pterourus*, *Chilasa*, *Eleppone*, and *Papilio* (sensu stricto). Monophyly of *Heraclides* is strongly supported, and the group falls out as sister taxa to the *Pterourus* + *Chilasa* clade similar to Aubert et al., (1999); all three genera fall out as sister taxa to the remainder of *Papilio* (sensu lato). Similar results were achieved when Kunte (2009) looked at the “Diversity and Evolution of Batesian Mimicry in *Papilio* Butterflies”. In his work, 2.3 kb of mitochondrial genes from *COI*, *COII* and *tRNA-leucine* and ~1.0 kb of nuclear gene *EF-1a* were analyzed under maximum parsimony, maximum likelihood, and Bayesian frameworks. He also used seven taxa from *Heraclides* (*H. anchisiades*, *H. erostratus*, *H. hectorides*, *H. torquatus*, *H. astyalus*, *H. cresphontes* and *H. thoas*).

While showing the monophyly of species groups (especially monophyly of the *Heraclides*) within *Papilio* (sensu lato), these studies seem reluctant to designate such groups as genera, perhaps because of the nature of the studies, being phylogenetic studies instead of taxonomic revisions or reviews. This field has lacked recent generic revisions and reviews, perhaps due to the lack of easily identifiable synapomorphic morphological characters for differentiation of species groups and genera within Papilionini. Until further studies provide reliable characters for differentiation within this tribe, the situation will likely remain the same; it is hoped that this study will take steps in doing so for the *Heraclides*.

Historical Taxonomic Treatment of *Heraclides*

Hübner (1819) described *Heraclides* almost 200 years ago with type species *Papilio thoas* Linnaeus, 1771. Since the description of *Papilio thoas*, roughly five decades had passed (48 years) before this new *Heraclides* genus was proposed. By this time, several species now

recognized to be a part of *Heraclides* were described and with his work in 1819, Hübner moved these taxa under the umbrella of *Heraclides*. Two other genera proposed by Hübner in 1819 were; *Calaides* with type species *Papilio androgeus* Cramer, 1775; and *Priamides* with type species *Priamides hipponous* Hübner, 1819. In 1825, Hübner described the genus *Troilides* with type species *Troilides tros* now recognized as a synonym of *Heraclides torquatus* Cramer, 1777. In 1833, Swainson proposed a new genus called *Thoas* with type species *Papilio thoas* Linnaeus, 1771; subsequently treated as a synonym of *Heraclides*.

Due to the large number of enthusiastic Swallowtail butterfly collectors, and the striking allure of large colorful tropical insects, there had been much collecting and the description of many species by amateur and professional lepidopterists; this has led to much synonymy in groups such as *Heraclides*. Since the description of *Papilio thoas* in 1771 by Linnaeus, approximately 238 years have passed and many have chosen to follow tradition and treat the species and groups in this genus as previous persons have done instead of applying modern techniques in the hopes of clarifying some of the relationships. The two last major treatments of this group were by Miller (1987) and Tyler et al. (1994).

The 28 recognized species of *Heraclides* are in four groups historically. The ***Priamides*** (*anchisiades*) subgroup consisting of *Heraclides anchisiades* Esper, 1788, *Heraclides rogeri* Boisduval, 1836, *Heraclides erostratus* Westwood, 1847, *Heraclides isidorus* Doubleday, 1846, *Heraclides chiansiades* Westwood, 1872, *Heraclides epenetus* Hewitson, 1861, *Heraclides oxynius* (Geyer, 1827), and *Heraclides pelaus* Fabricius, 1775. The ***Troilides*** (*hyppason*) subgroup consisting of *Heraclides hyppason* Cramer, [1775], *Heraclides garleppi* Staudinger, 1892, *Heraclides lamarchei* Staudinger, 1892, *Heraclides hectorides* Esper, 1794, *Heraclides himeros* Hopffer, 1865, and *Heraclides torquatus* Cramer, [1777]. The ***Calaides***

(*androgeus*) subgroup consisting of *Heraclides androgeus* Cramer, [1775], *Heraclides thersites* Fabricius, 1775, *Heraclides caiguanabus* Poey, 1852, *Heraclides aristodemus* Esper, 1794, *Heraclides andraemon* Hübner, 1832, *Heraclides machaonides* Esper, 1796, *Heraclides ornythion* Boisduval, 1836, *Heraclides astyalus* Godart, 1819, and *Heraclides aristor* Godart, 1819. The ***Thoas*** subgroup consisting of *Heraclides thoas* Linnaeus, 1771, *Heraclides melonius* Rothschild & Jordan, 1906, *Heraclides paeon* Boisduval, 1836, *Heraclides homothoas* Rothschild & Jordan, 1906, and *Heraclides cresphontes* Cramer, [1777]. *Papilio peleides* Esper, 1793 is considered a ‘*Nomen dubium*’ or an ‘*artifact*’ and *Papilio tasso* Staudinger, 1884 is considered a possible valid species but will be treated here as a *torquatus* aberration until additional investigations reveal otherwise (Johnson and Matusik, 1987). These two taxa are not included among the recognized species. The four recognized subgroups, 28 recognized species, as well as the numerous subspecies that have been described in *Heraclides* needs to be revisited to test if they will be supported under the scrutiny of a modern systematic treatment.

Research Objectives and Questions

Only seven species of *Heraclides*, namely, *Heraclides anchisiades*, *H. astyalus*, *H. cresphontes*, *H. erostratus*, *H. hectorides*, *H. thoas*, and *H. torquatus*, have been treated in morphological and/or molecular based phylogenetics previously (Aubert et al., 1999; Caterino and Sperling, 1999; Caterino et al., 2001; Nazari et al., 2007; Reed and Sperling, 1999; Zakharov et al. 2004^a; Zakharov et al. 2004^b). I decided to test the phylogenetic relationships among these rutaceous-feeding butterflies using morphological and molecular methods. Previous studies within Papilionidae relied on morphology, as well as sequenced segments of mtDNA Cytochrome Oxidase subunits I and II (*COI* and *COII*), segments of nuclear genes elongation factor-1 alpha (*EF-1 α*), wingless (*w(g)*), and to a lesser extent segments of nuclear ribosomal DNA *16S* and *28S*

and mitochondrial gene NADH-dehydrogenase subunit 1 and 5 (*ND1* and *ND5*) (Aubert et al., 1999; Caterino and Sperling, 1999; Caterino et al., 2001; Nazari et al., 2007; Reed and Sperling, 1999; Roe and Sperling, 2007; Zakharov et al. 2004^a; Zakharov et al. 2004^(b)). *COI* and *COII* would essentially give the same results (Nazari et al. 2007), being that they are both from conserved regions of the mitochondrial DNA and have very low substitution rates. In addition, the utility of ribosomal genes in resolving phylogenies is well-documented (Caterino et al., 2000; Simon et al., 1994).

The prevailing theory of the presence of four main groups within *Heraclides* is tested using phylogenetic methods. Additionally, I hope to evaluate phylogenetic evidence for subgroups within the *Heraclides* using morphology, as well as previously sequenced genes *COI*, *COII*, tRNA-leu, and EF-1 α . I plan to diagnose synapomorphic characters for the species in the genus *Heraclides*, revise the diagnoses and descriptions of the species and subspecies, review formal nomenclature, provide distribution, natural history, and life history information for each species, and develop identification keys based primarily on wing patterns, for the adults of these species of butterflies.

CHAPTER 2 SPECIES AND SUBSPECIES

The Gordian Knots of Taxonomy

Before Carl Linnaeus (also known as Carolus Linnaeus or Carl von Linné) formalized the definition of a species into a taxonomic rank in his first edition of *Systema Naturae* in 1735, man has been trying to define its parameters. Even the great King Solomon, renowned to have been the wisest man alive, perhaps grappled with this concept. I Kings 4: 33 (KJV) it states that “*He spake of trees, from the cedar tree that is in Lebanon even unto the hyssop that springeth out of the wall: he spake also of beasts, and of fowl, and of creeping things, and of fishes*”. The question of what a species is has been a constant reminder to biologists of the importance of continuous searching and deeper digging into this subject. It has become more evident in recent years that one approach will likely not solve this problem, but that scientists should use all the possible tools at their disposal to tackle this problem. Over the years, many have addressed the problem of how to define a species. Renowned biologists such as Charles Darwin, Ernst Mayr, George Gaylord Simpson, Theodosius Dobzhansky, Sewall Wright, James Mallet and many others grappled with the concept of a species.

The quest to define the species has been the ‘Gordian knot’ symptomatic of taxonomy (Ghiselin, 1974) ever since the development of the species concept by the naturalists Ray and Linnaeus (Mayr, 1949). So far, there has been no ‘Alexandrian solution’ to this problem and there may never be, but as with all science, the absence of a foreseeable solution should not be a hindrance to the continuation of searching. In fact, science thrives on an evolving base of knowledge and understanding. One of the main discussions on the species concept has been on whether the concept of a species was ‘fiction’ or ‘objective’ (Burma, 1949a, 1949b; Mayr, 1949; Simpson, 1951). On one hand, some saw the species concept as merely convenient labels for

arbitrary groups that have little biological significance (Burma, 1949(a)). On the other hand, others agreed with the idea that species are readily observable natural units, and that the idea of a species is an objective concept and not vague or subjective (Mayr, 1949). Ghiselin (1974) suggested a radical solution to the species problem. He suggested that if we begin to view species as individuals and not as classes, we would be able to cut the ‘Gordian knot’ with a single blow from this ‘Alexandrian’ sword. He went as far as to state that one who applies the Heraclitus paradox (of not being able to step in the same river twice) to the species concept is either a lunatic or a philosopher. Three and one half decades later, this problem still plagues taxonomy; apparently, Ghiselin’s sword was dull.

Regardless of which concept one accepts, what is clear is that the underlined concept of a species is only a snapshot or picture in time of what that species is. The fundamental taxonomic concept of a species is somewhat limited by that necessary elementary requirement of designating a type. This type specimen is essentially one individual caught at time X, location Y and which is representative of that species name. Some species concepts allow for future evolution of that species, but most would consider a new name for a species that evolves to no longer live up to the attributes of the original type; it essentially becomes a new species and can be described as such. Influenced primarily by the ‘luck of the draw’ as to which individual in the population the biologists was able to capture, kill and curate from location Y, at time X, the designation of a type, and the description of a species name based on that type is somewhat arbitrary. Numerous attempts have been made to be as inclusive as possible in defining what a species is, but to date there has been no umbrella definition to cater to the diversity of biological organisms. Mallet (2007) is of the opinion that agreement on a unified species concept is possible only if there is agreement and acceptance that species lack a single, interpretable

biological reality over their geographic range and across geologic time. Thus, there seems to be a fundamental problem with the concept of a species as it is seen by many today; a logical flaw in most current species definitions (Mallet, 1995).

What is a Species?

If the term species is viewed in an esoteric sense, two meanings become evident. It can be a taxon, a concrete biological object made up of a classifiable population or groups of populations of organisms. It can also be a category or a rank in the Linnaean class structure that contains all taxa of species rank (Mayr, 1996). Species can also be seen as **evolutionary units** and any philosophical foray into the realms of biology and evolution requires an understanding of this meaning (Mayr, 1996). Much debate surrounds identifying the unit responsible for driving evolution, with possible candidates being genes, cells, individuals, groups, and species. This evolutionary unit is subject to natural selection and in this context is the species.

Systematic biology, being one of the oldest scientific disciplines, has the species as one of its central concepts. This central role of the species has made it the fundamental unit of comparison in virtually all of the biological sciences (de Queiroz, 2005; Mallet, 2007), in particular taxonomy, evolution, and molecular biology. Being in such a central role has placed the species concept under much scrutiny and various concepts continue to be proposed. The reconciliation of various concepts into a unified species concept has proven quite difficult as invariably, compromises would have to be made and various central themes of different concepts would have to be rejected (de Queiroz, 2005). At least 24 named species concepts can be identified (Mayden, 1997; de Queiroz, 2005), many of which fall under the modern synthesis of the species concept and are in fact types of the 'Metapopulation Lineage Concept'. This concept is often confused with Mayr's concept, and both known as the 'Biological Species Concept', but there is a clear differentiation in Mayr's early writings (de Queiroz, 2005). Different species

concepts lead to differences in species recognition; this is due to differences in the species boundaries that are proposed. These differences lead invariably to different numbers of recognized species and pose a serious problem for the biological sciences, especially taxonomy, systematics and evolution (de Queiroz, 2005). Examples of some of the more popular definitions of species follow. This is not aimed at being comprehensive; as King Solomon himself stated, “of making many books there is no end; and much study is a weariness of the flesh” Ecclesiastes 12:12. For recent treatments of the major species concepts, see Mallet (2007, 2008).

One of the earliest species concepts identifies the **typological species** (essentialist species) as a group of organisms with individuals that sufficiently match up to certain fixed attributes. Variation or different phenotypes among specimens would set the boundaries of the species. This concept has its roots in the philosophies of Plato and Aristotle and is the concept adapted by Linnaeus but which modern scholars have rejected mainly because (1) in nature, individuals are found frequently being conspecific with other individuals despite sexual dimorphism, polymorphism, age demographic and other types of differences; (2) the existence of **sibling species** (described later). The **morphological species** is a population or group of populations that differs morphologically from other populations. This was perhaps the first concept to be in use, but it is very limited in its scope in that it does not take into effect mimicry or polymorphism. It most likely was the base on which the typological species concept was developed, and is rejected for similar reasons. The **nominalistic species** is an individual. Bessey (1908) best describes this concept when he states that nature only produces individuals, and that species have no real actual existence but that they are only mental concepts. Bessey’s concepts perhaps influenced the works of Ghiselin (1974) and his definition of a species. His views are not widely accepted, and the proposal of the biological species concept by Ernst Mayr best refutes them.

The modern synthesis of species concepts is based on the **metapopulation lineage concept**. This definition holds that species are metapopulations (sets of connected subpopulations or maximally inclusive populations) whose lineages are governed by the limits of interbreeding. Virtually all modern definitions are variants of this concept (de Queiroz, 2005).

The **biological species** proposed by Mayr is a group or groups of potentially interbreeding natural populations reproductively isolated from other groups of potentially interbreeding natural populations. In its most basic definition, a biological species is a protected gene pool. Ernst Mayr is often credited with the development of this concept that draws on some of the attributes of the typological and nominalistic species concepts. Mayr (1996), states that a species is the segregation of nature's total genetic variability into isolated parcels separated from each other by reproductive obstacles. This separation hinders the production of too large a number of gene combinations that are incompatible and disharmonious. This is by far the most accepted and inclusive modern concept of a species, but it is not without its critics and is not all-inclusive. The **evolutionary species** is an entity made up of organisms that maintain their identity from other such entities through time and space and has their own evolutionary fate. As the species evolves, some members may diverge from the attributes of the main population and evolve into a subspecies; maintaining some kind of isolation may eventually lead to the formation of a new full species. The **phylogenetic species** is very similar to the evolutionary species in that they are both concerned with lineage, but differs in that here, the parent species goes extinct and two new species formed. It is the least inclusive taxon recognized in a formal phylogenetic classification (Mayr, 1969, 1996; Mallet, 1995; Adams, 2002). Mallet (1995) proposed the **genotypic cluster species** definition as an alternative to the biological species definition. He envisions a species definition that incorporates the following: 1) species as distinguishable groups of individuals that

have few or no intermediates when in contact; 2) attributes of polytypic species (i.e., more than one subgroup is present at the next lower taxonomic level); and 3) knowledge from morphology and genetics (Mallet, 1995). This definition is in use by many biologists even though they do not call it such. For a more detailed look at this concept, see Mallet (1995). It is essentially the same as the biological species concept in practice but differs in that genotypic cluster species can remain distinct even while violating one or more attributes of the biological species concept.

The importance of understanding the species problem cannot be overemphasized. One should aim to put aside personal preferences and biases and keep in mind various definitions of a species when dealing with this problem. This is especially relevant to the fields of taxonomy and systematics where decisions are made constantly on what species are. A study that uses one species concept to define a taxa will yield very different results from a study that use another species concept (de Queiroz, 2005); the best option may be to use as many species concepts as are compatible and relevant to the field of study, but this may prove confusing (Mallet, 1995). The evolutionary species concept was adopted for this study and proved to be flexible enough to deal with the many geographic variations observed in the species of this study group.

The Subspecies

The subspecies was initially proposed as a separate category and was seen as the solution to geographic variation by Karl Jordan and Ernst Hartert (Mallet, 1995). Mallet (1995) feels that the subspecies category is needed to avoid the dangers of over subdivision when using the phylogenetic species concept, and lumping due to strict application of the biological species concept. However, many systematists are of the opinion that the subspecies cannot be defined objectively and thus should be eliminated. Subspecies have been considered to be sacred units of taxonomy reflecting discrete categories of geographical variation or even incipient speciation by some, whilst others see them as artifacts realized only in museums with use only to those who

delight in playing with nomenclature (Wiens, 1982). The Frenchman François-Marie Arouet, known by the pen name Voltaire, once stated: "*Si Dieu n'existait pas, il faudrait l'inventer*", which translated means "If God did not exist, it would be necessary to invent him". Sourakov (2008) paraphrased Voltaire by stating that if subspecies did not exist, it would be necessary for them to be invented. It would be wise to bear in mind that butterflies do not care what we think a species or subspecies should be. They have their own rules and do not much care for the rules imposed on them. With this in mind, I purposed to find out the opinions of these butterflies on what a species or subspecies should be through the limited eyes of systematics.

Initially called a 'variety' with no distinction between individual and geographic variation, the term subspecies has come to be used as the common term for geographic varieties. Distinct natural populations not sufficiently different to be called separate species were also previously designated as subspecies, but this practice, because it was based on morphological differences, saw the naming of **sibling species** (reproductively isolated groups that are very similar in appearance, behavior and other characteristics) as subspecies. Thus, the yardstick for determining subspecies moved from a purely morphological criterion, to geographic representation, and the subspecies was seen not merely as slightly different local populations but as members of polytypic species. Darwin considered the subspecies as an **incipient species** or **semi-species** (a subspecies which is in the process of changing to a true species, aided by geographic isolating mechanisms which separate it from other subspecies), but it was realized that this designation is true only of isolates and not of continental subspecies with continuous distribution (Mayr, 1982). Semi-species must have evolved from previously interbreeding subspecies (Mallet, 2007) and can be seen as a second step in the process of speciation. Continental subspecies with continuous distributions, **clines** (forms that display gradual genetic

and/or phenotypic variation over a geographical area), typically result from environmental heterogeneity.

Those who object to the use of the subspecies category often point to use of poorly conceived trinomials, and to the fact that subspecies rarely can be justified on the basis of multiple characters. However, many subspecies separated by zones of hybridization show significant differences morphologically, behaviorally, and genetically (Mallet, 2007). Purely environmentally induced differences should not be cause for use of the sub-specific category, even if these differences are consistent. If the range of variation from one population includes or overlaps with the variation found in another population, especially if these differences are small, then these are simply two populations and nothing more (Adams, 2002). If these populations are **sympatric**, with ranges that are identical or overlap or they occur together at least in some places (**parapatric**), they cannot be subspecies. Reproductively isolated sympatric or parapatric groups are separate species. One of the criteria for designating subspecies is that subspecies are **allopatric** with other subspecies of the nominal group, meaning that their ranges are entirely separate; they do not occur in any one place together. Where there are only a few specimens known, most likely the range boundaries of any population would be unknown, and as such, subspecies should not be named until the samples are large enough to show possible range overlaps. Two allopatric taxa should be treated as subspecies especially if their general wing pattern and genitalic characteristics are constant. Sourakov (2008) showed that significant variation can exist within a butterfly species; one female can give rise to offspring that end up being described as two separate subspecies. These subspecies can breed and produce individuals described as a third subspecies. This clear evidence of phenotypic plasticity is just one of many that do occur, and which fly in the face of a morphological description of subspecies, even one

supported by significant geographic distances between described subspecies. What is evident is that a clear understanding of the biology of an organism will aid in the designation of populations as subspecies, and this knowledge should be sought before such a task is embarked upon.

It is with these concepts in mind that a revision of the genus *Heraclides* has been attempted. It is hoped that, as much as possible, changes to the treatment of species and subspecies will reflect the philosophy outlined here. Every attempt has been made to refrain from subjectively splitting taxa (with the hopes of naming my own), or from excessively clumping previously described taxa together with no underlying concept in attempts at over-simplifying the classification within this genus. The systematic criteria outlined here will be applied to the taxa in an objective and consistent manner as is possible. It is hoped that this review of the systematics of this group will serve to stimulate the field anew into seeing each butterfly, not as an opportunity to position one's name in history as the describer of a new taxon, but as a piece of the puzzle as we search for answers to our questions. The describing of new taxa is important, but not of the utmost importance; of utmost importance is seeing one's self as a custodian of the natural world, a return to true natural history where the taxon comes first. The ambitions of the researcher should be a distant second.

CHAPTER 3 MATERIALS AND METHODS

Sources of Material Examined

All materials used for this study are currently part of the collections at the McGuire Center for Lepidoptera and Biodiversity at the Florida Museum of Natural History. This includes material formerly a part of the Allyn Museum (AME), incorporated into the McGuire Center collections (MGCL), in 2004. The collection material used in this study also includes specimens formerly a part of the Department of Plant Industry, Florida State Collection of Arthropods (DPI, FSCA) collections. Additionally, the acquisition of the Kent Wilson Collection in August 2009 significantly aided this study. This last collection includes material used for the book *Swallowtail Butterflies of the Americas: A Study in Biological Dynamics, Ecological Diversity, Biosystematics, and Conservation* by Hamilton Tyler, Keith S. Brown Jr., and Kent Wilson (1994). Another significant acquisition that yielded valuable specimens for this project is the Dietz collection of world Papilionidae, acquired by the McGuire Center in December of 2009.

Specimen Preparation

Wings were examined for conformity to the general *Heraclides* plan (Figure 3-1). Terminology for wing venation follows Tyler et al. (1994). Forewing length was measured from the base to the tip of the wing using a transparent ruler divided into 1 millimeter increments. Photographs of adult butterflies were taken using a Canon® G10 and processed in Adobe Photoshop Elements® and Adobe Photoshop®. Genitalia preparations were done by removing the entire abdomens of male and female butterflies and placing them in a 10% solution of potassium hydroxide (KOH). After maceration, scales were removed and photographs taken at various stages of genitalia removal. Pelts and genitalia were stored in 70% alcohol. Genitalia were photographed with a mounted, computer controlled remote capture camera system

equipped with a Canon® EOS 50D camera and processed in Adobe Photoshop Elements® and Adobe Photoshop®.

Terminology for male and female genitalia follows Miller (1987; Figure 3-2) and Smith and Vane-Wright (2008). Materials photographed to produce figures of adults were labeled; the original photographs done in RAW format and converted to other file types as needed. All dissected material were labeled and photographed in RAW for posterity, and converted to other file formats as needed. A catalogue of dissected material was developed; all dissected materials were placed in vials in alcohol with a unique catalogue number written on paper placed inside the vial as well as outside on the cover of the vial (Table 3-1). Species determinations were made by comparison of the type specimen photographs to the material in the collection. Terminology for wing pattern was developed by a comparison of dorsal and ventral wing surface patterns of all members of *Heraclides* with the outgroup taxa to develop homologous pattern elements. These pattern elements were organized into the generalized wing pattern used for descriptive and phylogenetic purposes (Figure 3-3). Terminology was developed independently of other schemes, but was informed by Beldade and Brakefield (2002), and Nijout (1991, 2001, 2003).

Images of type specimens were obtained from the Lamas collection of type photographs of neotropical butterflies, digitized by the Tropical Andean Butterfly Diversity Project with funding from the Darwin Initiative and the kind cooperation of Gerardo Lamas. Data on specimen labels were recorded as much as possible as they appear. Bold face, italicized and handwritten text is not reproduced but represented as normal text. All information pertaining to a specimen is enclosed by double quotes (“”), with additional notes in square brackets ([]) within the quotes. Information on different labels is separated by two forward slashes (//) while information from

separate lines on each label is separated by one forward dash (/). There are exceptions but only in cases where necessary.

Distribution maps were produced by first recording the names of the collecting localities from specimen labels of the material examined and then converting that information into longitude and latitude coordinates with the help of Biogeomancer (<http://bg.berkeley.edu/latest/>) and Google Maps (<http://maps.google.com/maps?hl=en&tab=wl>) (see Appendix). The resulting data sheet was then converted into a tab delineated text file and imported into DIVA-GIS (a free computer program for mapping and geographic data analysis). The data was then manipulated to produce the requisite maps. Unreliable specimen data were omitted if no obvious location could be ascertained.

Taxon Sampling

The external morphology of all available members of the genus *Heraclides* was examined for this project. Males and females of all species as well as males and females of all subspecies were dissected, with the exception of 8 subspecies where only one sex was represented in the collections, and 4 subspecies where no individuals were immediately available for dissections.

In-group Taxa. A total of 28 species representing the totality of the in-group taxa was used in this study. Sequences for seven species, representing 25% of the species in *Heraclides*, were available and were downloaded from GenBank; their accession numbers are given in Table 3-2. Three of the previously recognized subgroups within *Heraclides* were represented by two species each and one subgroup was represented by a single species. Morphological analysis was done on all 28 species represented in this genus.

Out-group Taxa. Four additional species from among the remaining genera of *Papilio* sensu lato were chosen as the out-group taxa for the molecular analysis; *Pterourus* (*Papilio*) *glaucus*, *Papilio* (*Papilio*) *machaon*, *Princeps* (*Papilio*) *constantinus*, and *Princeps* (*Papilio*)

demoleus; their accession numbers are given in table 3-1. These taxa were included in this study so that comparisons could be made to previous molecular studies that included one or more *Heraclides*. *Pterourus (Papilio) glaucus*, *Papilio (Papilio) machaon*, *Princeps (Papilio) constantinus* were not included in the analysis of morphological characters; *Princeps (Papilio) demoleus* only was used as the outgroup taxa because it is a recently introduced rutaceous-feeder to this region that can potentially outcompete *Heraclides*.

Genes and Alignment of Molecular Sequence Data

Downloaded GenBank sequences were modified to yield 2.292 kilo bases (kb) of mitochondrial genes COI, tRNA-leu and COII, and 1.234 kilo bases (kb) of the nuclear gene EF-1 α . The combined molecular data was 3.526 kilo bases (kb). Sequences were aligned by eye using the Alignment Explorer in MEGA4. The mitochondrial genes were aligned against the complete mitochondrial genome of the Giant Silkworm Moth, *Eriogyna pyretorum* (Jiang et al. 2009) in order to partition the three genes it contained accurately.

Phylogenetic Reanalysis of Molecular Data

MEGA (v4) was used for Maximum Parsimony (MP) analysis, PHYML (v2.4.4) was used for Maximum Likelihood (ML) analysis, Hierarchical Likelihood Ratio (hLRTs) and Akaike Information Criterion (AIC) tests were done with Modeltest as implemented in PAUP (evaluation of evolutionary models) and MrBayes (v3.1.2) was used for Bayesian analysis. To get an estimation of the phylogenetic relationships within *Heraclides* that was as accurate as possible given the limited nature of the available data, the following strategies were implemented. Prior to any phylogenetic tree reconstruction, the data for individual partitions as well as the concatenated data were checked for nucleotide bias using the test of the homogeneity of substitution patterns between sequences (disparity index) as implemented in MEGA using a Monte Carlo test with 1000 replicates to estimate p-values. This was done in order to understand

substitution rate patterns in the data. A partitioned homogeneity test (incongruence-length difference test) was run on the partitioned concatenated data to test for possible incongruence in one or more genes. This test was implemented in PAUP as a heuristic search with 100 initial replicates to estimate p-values.

Maximum Parsimony Analyses. All codon positions were used with complete deletion of gaps and missing data. All MP analyses were conducted in MEGA and utilized heuristic searches: Starting trees were determined by 100 random additions of sequences, the Close-Neighbor-Interchange algorithm with search level 3 was used. The robustness of the MP analyses was tested with bootstrap analyses - 1000 repetitions. The 50% default cut-off value for the consensus tree of the most parsimonious trees was used. Trees were visualized and edited in MEGA. Analysis was conducted on the individual and concatenated data separately.

Maximum Likelihood Analyses. To determine how well competing substitution models fit the data, all data were subjected to hLRTs as well as an AIC test as implemented in the program Modeltest. The models tested range from the simplest Jukes-Cantor (JC) model to a parameter rich general time reversible (GTR) model. Individual and concatenated data were analyzed in PHYML. The best model chosen by hLRTs was implemented with each data set. Suggested values for gamma (Γ), and the proportion of invariable sites (I) for each set of data, were used. The robustness of the ML analyses was tested with bootstrap analyses – 1000 repetitions. The starting tree was estimated using the BIONJ method, a variant of the Neighbor Joining (NJ) method. The 50% default cut-off value for the consensus tree was used. Trees were visualized and edited in MEGA.

Bayesian Analyses. Partitioned and combined data were evaluated under a Bayesian framework using MrBayes. The same model chosen for ML (GTR+ Γ +I) was used. As part of

the analyses, the specific nucleotide substitution model parameters were estimated. Four Markov chains were run simultaneously, one cold and three heated; the default heat of each chain was used. A random tree was used as the starting point for each chain; each chain was set to run for 10^6 generations, sampling every 100th cycle, and printing every 1000th cycle. Stationarity was determined by plotting the log likelihood scores against generation time in the program Tracer (v1.4.1). Sample points before stationarity were discarded as burn-in samples (10^4 generations/100 trees). All data was run twice, each beginning with a different starting tree. MrBayes supports only one taxon as the out-group; *Papilio demoleus* was designated the out-group taxon but the other species were still included in the analysis (*P. machaon*, *P. constantinus*, and *P. glaucus*). After the burn-in was removed, the remaining data was used to generate the majority rule consensus tree with posterior probabilities as measure of support. Posterior probabilities > 95% are considered as significant support. The partitioned concatenated data was run with the same model across the four partitions (GTR+ Γ +I) but allowing for the partitions to evolve separately (prset applyto=all; ratepr=variable).

Phylogenetic Analysis of Morphological Data

The morphological data was managed using Mesquite: A modular system for evolutionary analysis (v2.72); this allowed for easy organization of taxa and characters. The morphological data (matrix of characters; Table 3-3) was exported as a nexus file from Mesquite and evaluated under a MP framework using PAUP. The matrix plus the trees created by PAUP were then imported into Winclada and manipulated to map characters and character changes onto the final tree.

Maximum Parsimony Analyses. Several heuristic searches were done using PAUP. A total of 133 characters from juvenile and adult stages (including male and female genitalia) were used (Table 3-3). For all analyses except MP analysis #1, a successive reweighing scheme

according to a rescaled consistency index was applied in order to obtain a better resolution or best fit of the characters on any of the trees obtained (Farris, 1969; Civeyrel et al., 1998). The outgroup taxon in all cases was *P. demoleus*; all trees were rooted on the outgroup taxon. All characters were unordered with multistate characters interpreted as uncertainty and all trees were obtained by stepwise addition. Two trees were held at each step during stepwise addition and Maxtrees was set at 5000. The steepest descent and mulltrees option was in effect, and the tree-bisection-reconnection (TBR) algorithm was used for branch swapping. A strict consensus tree was produced from the number of trees retained and 10,000 bootstrap replicates were run on the trees held in memory to produce a 50% majority-rule consensus tree.

MP Analysis #1 – Unconstrained topology with equally-weighted characters. For this analysis, 38 characters were parsimony uninformative whilst 95 characters were parsimony informative. No topological constraints were enforced. The number of replicates done for the heuristic search was 10; characters were equally-weighted.

MP Analysis #2 – Unconstrained topology. In this analysis, 38 characters were parsimony uninformative whilst 95 characters were parsimony informative. No topological constraints were enforced. The number of replicates done for the heuristic search was 10. Characters were reweighed by the maximum value of the rescaled consistency indices and the heuristic search re-run until the tree length remained unchanged.

MP Analysis #3 – Production of the topological constraint. In this analysis, only 8 taxa were included in this analysis. These were the 7 taxa for which DNA material was available plus *P. demoleus* as the outgroup taxon. The molecular data available for these species was concatenated with the morphological data for these species to produce data containing 3659 characters. Of this total, 2974 were constant and excluded from the analysis. The remaining 685

characters included 365 characters that were parsimony uninformative and 329 characters that were parsimony informative. No topological constraints were enforced. The number of replicates done for the heuristic search was 100. Characters were reweighed by the maximum value of the rescaled consistency indices and the heuristic search re-run until the tree length remained unchanged.

MP Analysis #4 – Constrained topology. In this analysis 38 characters were parsimony uninformative whilst 95 characters were parsimony informative. The number of replicates done for the heuristic search was 1. The strict consensus tree produced from the concatenated molecular and morphological data for the 8 taxa in MP analysis #3 was used as a topological constraint on the backbone of the tree. Only trees compatible with the backbone constraint tree were kept. Characters were reweighed by the maximum value of the rescaled consistency indices and the heuristic search re-run until the tree length remained unchanged. A constrained topology was chosen to avoid Long Branch attraction that would have occurred if the genetic data for only seven species were concatenated to the morphology data for the 28 species.

Hypothesis testing. The Templeton or Wilcoxon signed-ranks (as well as wining-sites) tests were implemented in PAUP. Three tests were conducted: 1) on the unconstrained tree with reweighted characters vs. the unconstrained tree with equally-weighted characters; 2) on the constrained tree with reweighted characters vs. the unconstrained tree with equally-weighted characters; and 3) on the constrained tree with reweighted characters vs. the unconstrained tree with reweighted characters. The null hypothesis for the Templeton test is that the tree lengths of the retained trees before and after are equal ($H_0: \theta = 0$). There is significant difference if the test statistic is less than 0.05 ($P < 0.05$).

Morphological Characters

Table 3-3 shows the corresponding character matrix for *Heraclides* species. Where possible, characters are figured on the images of the adults, (Figures 6-1 to 6-68), or referenced from previous works. When figured on the images of the adults, character states are indicated in brackets beside the character number.

Immature

1. Egg surface with longitudinal grooves: 0 = absent, 1 = present (Tyler et al., 1994; plate 26A). Igarashi (1984) and Tyler et al. (1994; character 2) found the structure of the surface of the eggs a useful character. They however focused on the texture of the surface, and the arrangement of the granulations. I have found that in this group there are no granulations and thus have modified this character to represent the variation observed; that of longitudinal grooves as in *H. anchisiades*.

2. Color of freshly laid eggs: 0 = cream, pale yellow, or pale green, 1 = ochreous. There are several cases where the color of freshly laid eggs have been described as whitish, pale green, pale yellow, or cream colored. I have found that there is much subjectivity in the use of colors to describe eggs. I propose that eggs described as whitish could also be cream colored, or pale yellow and perhaps even pale green. I have used the term ochreous to describe a darker reddish orange or reddish yellow color. This color is more of an earthy color also described as rust color.

The host plant family primarily used for oviposition of eggs was used by Tyler et al. (1994; character 3). They referred to the use of a similar character by Hiura (1983) and Igarashi (1984). The original character coding proved problematic. Several plant families were grouped together with no clear rationale as to why this was being done. In addition, this character was coded for a wider cross-section of genera. I have chosen to recode this character into the

following four characters in an attempt to be more objective, given that some species use several plant families. When the plant order used was investigated, no clear trend arose in how the species uses them. The majority of species use Rutaceae as well as Piperaceae. It was tempting to combine these two, but because there were at least two species that were recorded on Piperaceae and not Rutaceae, as well as the fact that these two plant families are in different orders, I decided to keep them separate. I coded the use of a host plant family by a species as unknown (?) instead of absent (0) in cases where there is little information available about the species or in cases where the species were uncommon. This way I avoid making erroneous statements about the use of plant families as host plants given the paucity of available information for some of species treated.

3. Rutaceae used as host plant: 0 = absent, 1 = present.
4. Piperaceae used as host plant: 0 = absent, 1 = present.
5. Umbelliferae/Apiaceae used as host plant: 0 = absent, 1 = present.
6. Araceae used as host plant: 0 = absent, 1 = present.
7. Host plant placement of eggs: 0 = ventral surface of leaf, 1 = dorsal surface of leaf (Tyler et al., 1994; plate 26A). Tyler et al. (1994; character 4) used a similar character and referred to previous use by Igarashi (1984); however, their coding did not give a rationale for grouping the placement of eggs on the leaf with whether or not the eggs were placed on or off the plant. As such, I decided to recode this character to make it more objective and representative of the taxa in question.
8. Eggs laid as a group: 0 = absent, laid solitarily or in a loose group, 1 = present, laid in a tight bunch of many ordered eggs (Tyler et al., 1994; plate 26A). Tyler et al. (1994; character 5) found this character useful and referred to its use by Igarashi (1984). *H. anchisiades* and similar

species place their eggs together in ordered rows. This character is very consistent and seems to be linked to the gregarious behavior observed in larvae. Eggs laid in a tight bunch of many ordered eggs give rise to gregarious larvae, and eggs laid solitarily or as a loose group give rise to solitary larvae. I have chosen not to include a separate character describing the behavior of larvae whether solitary or gregarious, as this behavior seems to be directly linked to how the eggs are laid.

9. 1st instar larva with a whitish or yellowish saddle-like (or 'V'-shaped) patch over A3-A4: 0 = absent, 1 = present (Tyler et al., 1994; plate 26A and 27A). This character was used by Hiura (1983; character 3), Miller (1987; character 21), and Tyler et al. (1994; character 12). I have reused this character but chose to not to differentiate between a whitish or yellowish color as color is a highly subjective descriptive tool, and the difference in whitish or yellowish seems dubious.

10. Mature larva (4th – 5th instar) with a whitish saddle-like (or 'V'-shaped) patch on the dorsal surface of A4, A5, and sometimes a small section of A6, running down to the sides laterally and anteriorly going over to the lateral sides of A3: 0 = absent, 1 = present (Tyler et al., 1994; plate 26A, 26B, 27A and 27B). This character is related to that used by Tyler et al. (1994; character 34) and Hiura (1983; character 4). Tyler et al. (1994) described this character as an absent, complete, or broken 'X' in conjunction with the white on A8 – A10. I believe this character to be somewhat linked to the previous, but distinct enough to be kept separate given that the presence or absence of a saddle-like patch in the first instars seems to have little effect on its development in later instars. In *H. caiguanabus*, as well as *H. aristodemus*, the white patches on the sides do not meet dorsally. However, I treated this character as present in these species because I believe these patches to be homologous to the patches that meet dorsally to form a V-

shape in other species. I had originally included a separate character dealing with the absence or presence of a whitish collar at T1 of mature larvae. I found that this character was closely associated with the saddle-like patch and decided not to treat it separately. The larvae of *Heraclides* are often referred to as mimicking bird droppings; I believe previous authors were collectively referring to the patterns expressed here.

11. Short fleshy projections on the dorsal surface of all body segments of the 1st instar larva: 0 = absent, 1 = present. This character has been modified from that used by Tyler et al. (1994; character 14 & 15). This has also been used by Igarashi (1984), and Miller (1987; character 70). I chose to modify this character, as previous versions were coding for differences at the generic or family levels and higher, whilst this work seeks to look at differences at the species level.

12. Round bumps on the 5th instar: 0 = absent (smooth surface), 1 = present (Tyler et al., 1994; plate 26A, 26B, 27A and 27B). There are two pairs of these bumps on the dorsal surface of the thoracic segments, and one pair on each abdominal segment. The functions of these are unknown but seem to be homologous to long projections in other groups. A similar character was used by Hiura (1983; character 48), Igarashi (1984), Miller (1987; characters 70, 86, and 103), Tyler et al. (1994; character 38), and Nazari et al. (2006; character 225). I have modified the coding and the states of this character to be more representative of the taxa in question. The presence or absence of long red or yellow tubercles on mature larvae was also used by Hiura (1983; character 49), Igarashi (1984), Miller (1987; character 103), Tyler et al. (1994; character 39). The taxa included here do not have long tubercles but I believe these bumps to be homologous with those tubercles.

13. Color of mature larva (4th to 5th instar): 0 = predominantly green, 1 = predominantly mottled, dark brown with white or pale yellow markings.

The cephalic profile (dorsal view) of the pupa was used by Igarashi (1984) and Tyler et al. (1994; character 54). Igarashi (1984), Miller (1987; character 69), and Tyler et al. (1994; character 56) also looked at the length of dorsal horns on the thorax. I believe these characters warrant a more objective treatment and propose the following four characters as representing the variation observed in this group.

14. Cephalic profile: 0 = circular, 1 = horn-like (Tyler et al., 1994; plate 26B and 27B). This area can be deeply divided into a pair of horns or the entire area may be more circular, with little to no division or cleft between the two sides.

15. Thoracic projection: 0 = short, 1 = long (Tyler et al., 1994; plate 26B and 27B). This is located at T2 on the pupa and may be present as a short bump or as a projection that is longer than the width of any two abdominal segments combined.

16. Pupa strongly bent dorsally at thorax/abdominal junction: 0 = absent, 1 = present (Tyler et al., 1994; plate 26B and 27B). This character has not been recoded from that used by Tyler et al. (1994; character 63). They also referred to the use of similar characters by Hiura (1983; character 7) and Igarashi (1984).

Igarashi (1984), and Tyler et al. (1994; character 69) used color polymorphism in their look at a wider range of Papilionidae genera. I have found that more variation and objectivity can be brought out if this character is subdivided. I propose the following two characters.

17. Pupal color: 0 = only brown observed, 1 = brown and green present (polymorphic for pupal character).

Adult: Tyler et al. (1994) used mimetic patterns as their character 82. They also referred to the use of a similar character by Hiura (1983; character 15). I have decided to recode this character and represent it as the following two characters.

18. Mimetic patterns: 0 = absent, 1 = present.
19. Mimetic patterns limited to females: 0 = absent, 1 = present.
20. Sexual dimorphism: 0 = absent, 1 = present. In *H. ornythion*, females may sometimes appear similar to males. I have chosen to treat the character as present in this species given that there are females that appear different from the males as well as those that look similar. Evidence of the use of this character for members of this subgroup prior to this has not been found. This is treated as absent in *H. hyppason* due to the closeness of the white spots in the males compared to the females.
21. Red spots on the lateral side of the thorax and abdomen: 0 = absent, 1 = present (Tyler et al., 1994; plate 81). The character states have been modified for consistency from that used by Tyler et al. (1994; character 94). A similar character was used by Miller (1987; character 109). In the *Heraclides*, only red spots are present and thus the character was modified to reflect this. The distribution of these red spots on the body varies and is difficult to describe. In addition, variation among species is not documented well enough to determine if the precise locations or distribution on the body, are diagnostic at the species level. This is present in species closely related to *H. anchisiades*, but absent in *H. hyppason* and the remainder of the *Heraclides*.
22. Antennal color of males: 0 = unicolorous, 1 = with distinctive yellow tips (Figure 6-14a). This character is modified from that originally used by Zakharov et al. (2004) and Smith and Vane-Wright (2008; character 28) to be more representative of the *Heraclides* and the variation present there. Present only in *H. aristodemus*, *H. andraemon*, and *H. machaonides*.

Wings: Most of the following characters are new and are based on the generalized wing pattern plan in Figure 3-3. A few are modified from Tyler et al. (1994), Zakharov et al. (2004), and Smith and Vane-Wright (2006). Because of the presence of sexual dimorphism in this group,

many of the characters are duplicated to reflect instances where the females are different from the males.

23. Dorsal forewing (DFW) with a distinctive “X” formed by the central and SMB bands: 0 = absent (Figure 6-1c), 1 = present (Figure 6-1e). This is present in the “*thoas*” subgroup as well as in some members of *H. aristodemus*. I code it as present in *H. aristodemus* and not as a polymorphic character since in the members where it could be coded as absent, the “X” seems to be modified by the extension of the SMB all the way up the wing.

24. DFW central band in males: 0 = absent (Figure 6-1a), 1 = present (Figure 6-1c). The central band is often the largest band on the wing. In some species, the central band is reduced and is only present as large spots on the wing. The size, width, and extent of this band vary greatly between, and somewhat less within species. This character is coded as absent in *H. aristor* and *H. caiguanabus* due to only the presence of a few spots of the costal branch of the central band. This character is also coded as absent in those species that only possess a spot, such as *H. anchisiades*” and other similar species as well as some females of other species in this subgroup.

25. DFW central band in females: 0 = absent (Figure 6-24b), 1 = present (Figure 6-1d). This character is coded as absent in *H. thersites* because the yellow on the wing appears to be only a very bright suffusion being represented on the dorsal and ventral surfaces and I do not believe it to be homologous to the central band elements.

26. DFW central band/spot element of males present in cell r3-r4 towards the wing apex: 0 = absent (Figure 6-19e), 1 = present (Figure 6-2a). In *H. machaonides* this codes as present because I believe the spot in this location is homologous with the same spot in the other species and not a part of the SMB as it could be easily assumed to be.

- 27.** DFW central band: 0 = narrow (less than 50% of the wing surface; Figure 6-1f), 1 = broad (more than 50% of the wing surface; Figure 6-7a).
- 28.** DFW central band element at r5-m1 the longest: 0 = absent (Figure 6-13a), 1 = present (Figure 6-1c).
- 29.** DFW central band element at r5-m1 triangular: 0 = absent (Figure 6-5b), 1 = present (Figure 6-5c). Present only in *H. paeon*.
- 30.** DFW central band element at r5-m1 notched: 0 = absent (Figure 6-15e), 1 = present (Figure 6-13f). This notch is caused from an incomplete fusing of the apical and costal branches of the central band. In species where both states occur, this character is treated as polymorphic.
- 31.** DFW central band element at cu1-cu2 with distal edge cone shaped: 0 = absent (Figure 6-1f), 1 = present (Figure 6-3c). This is seen most often in *H. cresphontes*.
- 32.** DFW central band or spot elements in males: 0 = white (Figure 6-24c), 1 = yellow (Figure 6-1d). Typically, the central band of *Heraclides* is yellow. Occasionally this may be white and in species closely related to *H. anchisiades*, it is typically as a white spot. This character is coded as yellow in *H. aristor* and *H. caiguanabus* because of the presence of a few of the spots of the costal branch of the central band.
- 33.** DFW central band or spot elements in females: 0 = white (Figure 6-24d), 1 = yellow (Figure 6-1b).
- 34.** DFW central band in males as a spot: 0 = absent (Figure 6-7c), 1 = present (Figure 6-21c).
- 35.** DFW central band in females as a spot: 0 = absent (Figure 6-6b), 1 = present (Figure 6-21f).

- 36.** DFW central band spot touching the anal edge of the wing in cell 1a-2a: 0 = absent (Figure 6-24f), 1 = present (Figure 6-30d). The presence of this has been observed only in *H. chiansiades* and *H. hyppason* males.
- 37.** DFW central band spot of males located in the tornal area around cells cu1-cu2 and cu2-1a: 0 = absent (Figure 6-30c), 1 = present (Figure 6-24a). Present primarily in *H. anchisiades*.
- 38.** DFW central band spot of females located in the tornal area around cells cu1-cu2 and cu2-1a: 0 = absent (Figure 6-30d), 1 = present (Figure 6-17b). This is seen in the females of *H. garleppi* and some females of *H. torquatus*.
- 39.** DFW central band spot in males located centrally around cells m2-m3 and m3-cu1: 0 = absent (Figure 6-27a), 1 = present (Figure 6-29b). Present primarily in *H. isidorus*.
- 40.** DFW central band spot in females located centrally around cells m2-m3 and m3-cu1: 0 = absent (Figure 6-27b), 1 = present (Figure 6-28b). Present primarily in some females of *H. androgeus* and *H. torquatus*.
- 41.** DFW central band interrupted by a bar at vein M2: 0 = absent (Figure 6-15f), 1 = present (Figure 6-18c). Present in *H. garleppi* (except the nominate subspecies) and *H. torquatus* only.
- 42.** DFW central band as a narrow bar running from the middle of the costal edge of the wing to the anal angle: 0 = absent (Figure 6-22c), 1 = present (Figure 6-22e). Present only in *H. pelaus*.
- 43.** DFW central band missing elements in cells cu1-cu2, cu2-1a, and 1a-2a, but having the costal branch: 0 = absent (Figure 6-6a), 1 = present (Figure 6-6c). This is treated as present in *H. aristor* and *H. caiguanabus* due to the presence of a few spots of the costal branch of the central band. In *H. caiguanabus*, these spots are reduced and often appear to be absent.

- 44.** DFW central band apical branch (from cell r4-r5 to the apical tip of the wing): 0 = absent (Figure 6-15c), 1 = present (Figure 6-2c).
- 45.** DFW central b and costal branch (around the distal edge of the discal cell): 0 = absent (Figure 6-16c), 1 = present (Figure 6-4c).
- 46.** DFW central b and costal b ranch with elements invading the corner where R 4 and R 5 meet: 0 = absent (Figure 6-19e), 1 = present (Figure 6-17c). This spot is present primarily in *H. garleppi* and is useful in separating it from *H. torquatus*.
- 47.** DFW discal cell spot formed from an invasion of the discal cell by the central b and elements: 0 = absent (Figure 6-11b), 1 = present (Figure 6-8c).
- 48.** DFW discal spot bar shaped, across the entire cell: 0 = absent (Figure 6-2d), 1 = present (Figure 6-15d). Present only in *H. machaonides* and *H. andraemon*.
- 49.** DFW sub-marginal spots: 0 = absent (Figure 6-20c), 1 = 1 to 4 (Figure 6-2f), 2 = 5 to 8 (Figure 6-6e).
- 50.** DFW with the outer edges of the central band in a linear pattern: 0 = absent, 1 = present. In the out-group, *P. demoleus*, the outer edges of the spots of the central band are not in a straight line, and are irregular.
- 51.** Suffusion present instead of wing pattern elements: 0 = absent (Figure 6-8e), 1 = present (Figure 6-31d). Present mainly in some species closely related to *H. anchisiades*.
- 52.** Hindwing M3 elongate and forms tail (or at least a well-marked tooth): 0 = absent or rudimentary (less than $\frac{1}{4}$ hindwing length not including fluting; Figure 6-24e), 1 = present (greater than $\frac{1}{4}$ but less than $\frac{1}{2}$ the hindwing length not including fluting; Figure 6-3b). Also used by Nazari et al. (2006; character 102), Zakharov et al. (2004), and Smith and Vane-Wright

(2006; character 25). I have modified this character to reflect the taxa in question. All the *Heraclides* have the tail, or the largest fluted tooth, at the same position.

53. Hindwing tail with club: 0 = absent (Figure 6-17a), 1 = present (Figure 6-2c). Also used by Zakharov et al. (2004), Smith and Vane-Wright (2006; character 26) and Miller (1987; characters 91, 105, and 157).

54. Hindwing tail with spot: 0 = absent (Figure 6-10e), 1 = centrally located (Figure 6-3a), 2 = touching the distal edge of the tail (Figure 6-15c). The tail spots in *H. himeros* and *H. machaonides* touch the distal edge of the tail.

55. Yellow stripe along the outer margin of the tail formed from an extension of the marginal spot m2-m3: 0 = absent (Figure 6-16c), 1 = present (Figure 6-16a). Present only in *H. himeros*.

56. Hindwing with secondary tails at Cu1 and Cu2 deeply fluted (as long as or longer than the width of the cells m3-cu1 and cu1-cu2): 0 = absent (Figure 6-16f), 1 = present (Figure 6-16e).

57. Dorsal hindwing (DHW) central band in males: 0 = absent (Figure 6-22a), 1 = present (Figure 6-3c).

58. DHW central band in females: 0 = absent (Figure 6-22b), 1 = present (Figure 6-4d).

59. DHW central band: 0 = narrow, less than 50% of the wing surface (Figure 6-16c), 1 = broad, more than 50% of the wing surface (Figure 6-7c).

60. DHW central band inner margin running parallel to the wing inner margin up to cell cu1-cu2: 0 = absent (Figure 6-15a), 1 = present (Figure 6-15c).

61. DHW central band decreases in width from the costal margin to a point at the inner margin: 0 = absent (Figure 6-12a), 1 = present (Figure 6-12c). Present only in *H. andraemon*.

62. DHW central band color in females: 0 = white (Figure 6-16e), 1 = yellow (Figure 6-12d).

- 63.** DHW proximal post-discal spots in males: 0 = absent (Figure 6-2e), 1 = present (Figure 6-32a).
- 64.** DHW proximal post-discal spots in females: 0 = absent (Figure 6-2f), 1 = present (Figure 6-20b).
- 65.** DHW proximal post-discal spots in males: 0 = red, 1 = white.
- 66.** DHW proximal post-discal spots in females: 0 = red, 1 = white.
- 67.** DHW inner post-discal spots in males: 0 = absent (Figure 6-4c), 1 = present (Figure 6-14a). The inner post-discal spots in the *Heraclides* are blue and iridescent, but can at times be iridescent green. This character was also used by Hiura (1983; character 27), Miller (1987; character 40 and 114), and Tyler et al. (1994; character 83).
- 68.** DHW inner post-discal spots in females: 0 = absent (Figure 6-4d), 1 = present (Figure 6-13b and 6-7d). In *H. androgeus*, these spots are greatly expanded to almost covering the dorsal surface of the hindwings.
- 69.** DHW sub-marginal spots: 0 = absent (Figure 6-22b), 1 = present (Figure 6-4e).
- 70.** DHW sub-marginal spots in males: 0 = red (Figure 6-22e), 1 = yellow (Figure 6-8e).
- 71.** DHW sub-marginal spots in females: 0 = red (Figure 6-22f), 1 = yellow (Figure 6-5f), 2 = white (Figure 6-6f).
- 72.** DHW proximal post-discal spots merge with the sub-marginal spots in males: 0 = absent (Figure 6-8c), 1 = merges at cells cu1-cu2, m3-cu1, and sometimes m2-m3 (Figure 6-24c). The number of cells occupied by the merge is highly variable within species.
- 73.** DHW proximal post-discal spots merge with the sub-marginal spots in females: 0 = absent (Figure 6-8f), 1 = merges at cells cu1-cu2, m3-cu1, and sometimes m2-m3 (Figure 6-18b), 2 = merges at almost all cells on the hindwing where elements are present (Figure 6-19b).

- 74.** DHW cell sc-rs with eyespot: 0 = absent, 1 = present. This character is modified from that used by Zakharov et al. (2004) and Smith and Vane-Wright (2008; character 12). Seen only in *P. demoleus*.
- 75.** DHW cell cu-1a with an eyespot: 0 = absent (Figure 6-21a), 1 = present (Figure 6-3e). Also used by Zakharov et al. (2004) and Smith and Vane-Wright (2008; character 13). The completeness of the eyespot is very variable within species and I thought it best to represent it by presence or absence only.
- 76.** Ventral hind wing (VHW) proximal post-discal spots in males: 0 = absent (Figure 6-15c), 1 = present (Figure 6-17c).
- 77.** VHW proximal post-discal spots – shape: 0 = following the shape of the inhabited cell (Figure 6-1f), 1 = crescent shaped (Figure 6-11b), 2 = oval (Figure 6-32b).
- 78.** VHW proximal post-discal spots - arrangement: 0 = as discrete spots (Figure 6-9e), 1 = fused into a block of color (Figure 6-14b).
- 79.** VHW proximal post-discal spots – distribution: 0 = in cells m2-m3, m3-cu1 (sometimes present in m1-m2; Figure 6-2f), 1 = in all cells except sc-rs and rs-m1 (Figure 6-18e), 2 = in all cells except sc-rs (Figure 6-11e).
- 80.** VHW discal cell invaded by elements of the proximal post-discal spots as well as elements of the inner post-discal spots: 0 = absent (Figure 6-1c), 1 = present (Figure 6-5c). In *H. torquatus tolmides* females, as well as *H. torquatus atsukoae* females, the merged proximal post-discal and sub-marginal spots often invade the discal cell. Because this does not occur in the nominate subspecies and other subspecies I treat this as absent. This is coded as present only in *H. paeon*.

- 81.** VHW inner post-discal spots in females: 0 = absent (Figure 6-17d), 1 = present (Figure 6-3f).
- 82.** VHW inner post-discal spots in males – shape: 0 = diffused (broad) (Figure 6-13c), 1 = compacted into crescent shaped spots (Figure 6-8c).
- 83.** VHW inner post-discal spots in females – shape: 0 = diffused (broad) (Figure 6-13d), 1 = compacted into crescent shaped spots (Figure 6-8d).
- 84.** VHW sub-marginal spots in males: 0 = red (Figure 6-27c), 1 = yellow (Figure 6-11b), 2 = white (Figure 6-27e).
- 85.** VHW sub-marginal spots in females: 0 = red (Figure 6-27d), 1 = yellow (Figure 6-11c), 2 = white (Figure 6-28d).
- 86.** VHW cell sc-rs with eyespot: 0 = absent, 1 = present. Seen only in *P. demoleus*.
- 87.** VHW cell cu-1a with an eyespot: 0 = absent (Figure 6-24a), 1 = present (Figure 6-15d). The completeness of the eyespot is very variable within species and I thought it best to represent it by presence or absence only.
- 88.** VHW with a red spot at the base of the wing in cell cu2-1a: 0 = absent (Figure 6-21b), 1 = present (Figure 6-21e). Present only in *H. hyppason*.
- 89.** Marginal spots: 0 = narrow, barely visible at the edge of the wing, or visible but as small spots (Figure 6-21a), 1 = broad, length almost $\frac{1}{2}$ the width of a cell (Figure 6-22d).

Genitalia

- 90.** Male genitalia with the rim of the valve: 0 = rounded (Figure 6-36c7), 1 = with a posterior-ventral expansion (Smith and Vane-Wright, 2008; figure 20). The posterior-ventral expansion is found only in *P. demoleus*. Zakharov et al. (2004) and Smith and Vane-Wright (2008; character 29) used a similar character. I have changed the coding of the character they

used to reflect the rounded valve rim seen in all the *Heraclides*. Nazari et al. (2006; character 179) looked at the valve tip, whether it was rounded, narrowed, with a blunt tip, or narrowed, with a pointed tip. I found that this character did not fully represent the variation seen in the *Heraclides* and the outgroup taxon; furthermore they appeared to have been coding for two characters, shape of valve rim shape, and the presence or absence of a pointed tip.

Hiura (1983; character 40), Miller (1987; characters 54, 60, 81, 116, 132, 155, and 156), Tyler et al. (1994; character 131), Zakharov et al. (2004), Smith and Vane-Wright (2008; character 35) and Nazari et al. (2006; character 183) coded for the presence or absence of the harpe (or clasper) as well as if it was simple or complex. They often combined these two characters and did not explicitly state what they meant by the terms “simple” or “complex”. Because of this, I did not reuse the character as they postulated, but instead suggest the following thirteen characters as representative of the taxa being investigated.

91. Male genitalia with harpe shape: 0 = roughly triangular (Figure 6-56c3), 1 = cup-shaped (Figure 6-37c2), 2 = “spoon-shaped” (Figure 6-52c4).

92. Harpe on male genitalia with a tooth-like projection on the dorsal edge: 0 = absent (Figure 6-41c), 1 = present (Figure 6-43c). In *P. demoleus*, this projection is not tooth-like or free but appears as a flange that is contiguous with the rest of the harpe. I treat it as not possessing a tooth-like projection.

93. Tooth-like projection on the dorsal edge of the harpe on the male genitalia serrated: 0 = absent (Figure 6-39c), 1 = present (Figure 6-44c1). In *H. melonius*, the tooth-like projection is not serrated; instead, it appears more sclerotized and blunt.

94. Harpe on the male genitalia with one broad heavily sclerotized spine on the ventral surface: 0 = absent (Figure 6-55c4), 1 = present (Figure 6-44c2).

- 95.** Large spine on the ventral surface of the harpe on the male genitalia with the posterior third and tip: 0 = fused (Figure 6-36c4), 1 = free (Figure 6-44b). In *H. thoas*, the broad heavily sclerotized spine is fused throughout with the rest of the harpe and forms the entire ventral edge of the harpe; the dorsal edge tapers to meet the tip of this spine and is not free from it.
- 96.** Large spine on the ventral surface of the harpe on the male genitalia: 0 = posterior pointing (Figure 6-44b), 1 = ventral pointing (Figure 6-48c3). *H. andraemon* has a ventral pointing spine.
- 97.** Harpe on the male genitalia with 3 to 5 small posterior pointing spines all around the outer edges: 0 = absent (Figure 6-37c1), 1 = present (Figure 6-40c1 to c3). Present only in *H. paeon*.
- 98.** Posterior edge of the harpe on the male genitalia drawn out into a single median spine: 0 = absent (Figure 6-37c2), 1 = present (Figure 6-57c1).
- 99.** The single median spine on the harpe of the male genitalia: 0 = small (Figure 6-41c), 1 = moderate (Figure 6-56c1), 2 = long (more than $\frac{1}{2}$ the length of the rest of the harpe). In *H. aristor* and *H. caiguanabus*, the median spine is only slightly larger than accompanying serrations. In *H. anchisiades* and similar species the median spine is markedly larger than the serrations that may be present, but not as large as the ventral pointing spine seen in the “*thersites*” subgroup. *H. himeros* is the only species in this subgroup with a long median spine.
- 100.** The single median spine on the harpe of the male genitalia: 0 = blunt (Figure 6-49c), 1 = pointed (Figure 6-55c3). *H. machaonides* has a blunt median spine that may or may not have small serrations on the end.

- 101.** Posterior edge of the harpe on the male genitalia drawn out into several small spines: 0 = absent (Figure 6-38c), 1 = present (Figure 6-50c1). Seen only in *H. lamarchei* and *H. hectorides*; these spines are never as large as the posterior pointing ventral spine.
- 102.** Posterior edge of the harpe on the male genitalia rounded, with no spines and no dorsal tooth: 0 = absent (Smith and Vane-Wright, 2008; figure 20), 1 = present (Figure 6-38c).
- 103.** Posterior edge of the harpe on the male genitalia serrated: 0 = absent (Figure 6-54c1), 1 = present (Figure 6-52c5). This is seen only in *H. torquatus* where the posterior edge is rounded and serrated.
- 104.** Male genitalia with pseuduncus tip: 0 = straight (Figure 6-36e2), 1 = bifid (Figure 6-38e). The pseuduncus (also called the superuncus) is the tapered posterior projection of the 8th tergite (Miller, 1987). This is bifid only in *H. homothoas*.
- 105.** Tapering of the pseuduncus on the male genitalia: 0 = narrow (Figure 6-37e), 1 = broad (Figure 6-40e). The pseuduncus can either taper broadly towards the tip (with a broad shoulder), being broad at the base and gradually tapering towards the tip, or it tapers narrowly towards the tip (with a narrow shoulder), being narrow or slim throughout its length.
- 106.** Male genitalia with uncus as paired horn-like processes: 0 = absent (Figure 6-43g), 1 = present (Figure 6-36b). Following Miller (1987), the uncus is the paired process dorsal to the anal tube. This is also adopted by Zakharov et al. (2004) and Smith and Vane-Wright (2008). They went at length to explain the reasons for naming this the uncus and in agreeing with them, I choose the same nomenclature in an attempt to reduce confusion in the field and provide consistency in the naming of homologous structures in the Papilionidae. Nazari et al. (2006; character 167, 171, and 172) also looked at the structure of the uncus. The characters they used did not prove useful to this study group and at times did not appear consistent. I have chosen to

represent the variation in this group by the use of this character, and the following three characters.

107. Paired, horn-like uncal processes on the male genitalia bifid: 0 = absent (Figure 6-40b), 1 = present (Figure 6-37b).

108. Paired, horn-like, bifid uncal processes on the male genitalia with the largest horn: 0 = dorsad (Figure 6-37g), 1 = ventrad (Figure 6-39b).

109. Paired, horn-like uncal processes on the male genitalia with horns very prominent: 0 = absent (Figure 6-40g), 1 = present (Figure 6-41g). In some species, the tips of the horns, as well as most of the horns are very prominent and easily seen. In others, the tips of the horns are quite short, with the rest of the horns short and flat.

Hiura (1983; character 29), Miller (1987; character 43 and 68), Tyler et al. (1994; character 137), and Nazari et al. (2006; character 192) used the shape of the aedeagus. I have chosen to use the following two characters instead of that used previously to improve clarity.

110. Aedeagus on the male genitalia curved: 0 = absent (straight) (Figure 6-36d), 1 = present (Figure 6-44d).

111. Degree of curvature in the aedeagus on the male genitalia: 0 = slightly curved (curved in the middle) (Figure 6-42d), 1 = strongly curved throughout (appearing arch-like throughout) (Figure 6-44d). The “*thersites*” subgroup, as well as *H. aristodemus* and *H. hyppason* have strongly curved aedeagus.

Nazari et al. (2006; character 187), Miller (1987; character 122), Tyler et al. (1994; character 130), and Nazari et al. (2006; character 188) used the shape of the juxta. I have modified the characters previously used to the following two to represent the variation in the taxa being investigated.

112. Male genitalia with juxta (furca) U-shaped: 0 = absent, 1 = present (Figure 6-36f). All *Heraclides* have a U-shaped juxta. This is treated by many as a synapomorphy for the group.

113. Male genitalia with juxta arms: 0 = narrow (or slim) (Figure 6-56f), 1 = broad (or wide) (Figure 6-41f). *H. aristor* and *H. caiguanabus* only have the juxta with wide/broad arms.

When the female genitalia were investigated, no difference was observed in the signae. In fact, a zipper-like signa is proposed as one of the synapomorphies of the Papilionini. As such, I did not show or discuss the signae of this group. Another character in which no differences were observed was the ductus seminalis; this also was not treated here. The female genitalia have never before been treated comprehensively in this group. I found that the lateral view of the genitalia provided little information useful to this group. I opted instead to present and investigate differences from an anal view. This showed significant differences in the structures surrounding the opening of the ostia; I term the structures ‘ostial armature’ to be consistent with previous authors.

114. Opening of the ostium of the female genitalia: 0 = opens anteriorly (Figure 6-61d), 1 = opens centrally (Figure 6-64c).

115. Ostium of the female genitalia: 0 = not supported by a ridge (Figure 6-62a), 1 = supported by a ridge (Figure 6-63e).

116. Structure dorsad of the ostium on the female genitalia: 0 = absent (Figure 6-62d), 1 = present (Figure 6-62f).

117. Shape of the structure dorsad of the ostium on the female genitalia: 0 = broad (Figure 6-61c), 1 = as a small evagination (protrusion) (Figure 6-64g).

118. Broad process on the female genitalia dorsad of the ostium with a ventrally indented midline: 0 = absent (Figure 6-62c), 1 = present (Figure 6-61h).

- 119.** Broad process on the female genitalia dorsad of the ostium with ridged appearance: 0 = absent (Figure 6-61h), 1 = present (Figure 6-62f). Only present in *H. paeon*.
- 120.** Female genitalia with paired peripheral vestibular plates heavily sclerotized: 0 = absent (Figure 6-62a), 1 = present (Figure 6-61g).
- 121.** Female genitalia with peripheral vestibular plates extended laterally (almost wing-like): 0 = absent (Figure 6-67b), 1 = present (Figure 6-67a). This is found only in *H. hyppason*. Also present are spines on each side of peripheral vestibular plates arising from the edges. Because these were seen only in *H. hyppason*, and no other homologous structures could be seen in the other members of this group, it was not coded for separately.
- 122.** Female genitalia with peripheral vestibular plates extended ventrally into processes: 0 = absent (Figure 6-61h), 1 = present (Figure 6-67e).
- 123.** Female genitalia with ventrally extended vestibular processes as a series of conjoined sclerotized spikes (antler-like): 0 = absent (Figure 6-62e), 1 = present (Figure 6-64e).
- 124.** Conjoined sclerotized spikes on the ventrally extended vestibular process of the female genitalia: 0 = short (almost blunt but with small spines) (Figure 6-68e), 1 = long (with very prominent spines) (Figure 6-64a). The number of the spines varies significantly within species.
- 125.** Female genitalia with the paired ventrally extended vestibular processes as raised blunt arms: 0 = absent (Figure 6-63c), 1 = present (Figure 6-62c).
- 126.** Female genitalia with paired ventrally extended vestibular processes ending in a long spine: 0 = absent (Figure 6-62c), 1 = present (Figure 6-62e). Only present in *H. paeon*.
- 127.** Female genitalia with paired structures dorsad of the ostium: 0 = absent (Figure 6-66h), 1 = present (Figure 6-66c). Present only in *H. garleppi*. These structures are a series of raised

conjoined sclerotized spikes similar to but smaller than the ones found on the ventrally extended peripheral vestibular plates in some species.

128. Female genitalia with lateral arms on either side of the ostial opening: 0 = absent (Figure 6-65e), 1 = present (Figure 6-65d). Only found in *H. machaonides*.

129. Female genitalia with a trough between the peripheral vestibular plates and the structure dorsad of the ostium: 0 = absent (Figure 6-64e), 1 = present (Figure 6-61e).

130. Female genitalia with a projection ventrad of the ostial opening: 0 = absent (Figure 6-62d), 1 = present (Figure 6-64i).

131. Ventrad projection of the female genitalia: 0 = knob-like (Figure 6-63f), 1 = hook-like (Figure 6-68g). The "hook-like" ventrad projection is always curved upwards.

132. Female genitalia with a deep trough between the peripheral vestibular plates and a long ridge-like process parallel to the vestibular plates: 0 = absent (Figure 6-65f), 1 = present (Figure 6-65e). This is present only in *H. lamarchei* and *H. himeros*.

133. Broad process above and posterior to the ostia on the female genitalia with a cupped appearance, forming a well-defined deep depression: 0 = absent, 1 = present.

Table 3-1. Material dissected and used in this study (see Appendix for a list of all material examined for this study).

Catalogue #	Genus	Species	Sex	Notes
100125.05	<i>Heraclides</i>	<i>anchisiades anchisiades</i>	M	Peru
100125.03	<i>Heraclides</i>	<i>anchisiades capys</i>	M	Pirachicaba - Brazil
100125.07	<i>Heraclides</i>	<i>anchisiades idaeus</i>	M	Mexico
100125.01	<i>Heraclides</i>	<i>anchisiades philastrius</i>	M	Trinidad
100107.06	<i>Heraclides</i>	<i>andraemon andraemon</i>	M	Cuba
100112.10	<i>Heraclides</i>	<i>andraemon bonhotei</i>	M	N. Andros - Bahamas
100112.12	<i>Heraclides</i>	<i>andraemon tailori</i>	M	Grand Cayman
100107.16	<i>Heraclides</i>	<i>androgeus androgeus</i>	M	Peru
100115.08	<i>Heraclides</i>	<i>androgeus epidaurus</i>	M	Mexico
100115.10	<i>Heraclides</i>	<i>androgeus laodocus</i>	M	Argentina
100107.04	<i>Heraclides</i>	<i>aristodemus aristodemus</i>	M	Hispaniola
100112.02	<i>Heraclides</i>	<i>aristodemus bjorndale</i>	M	Great Inagua - Bahamas
100112.04	<i>Heraclides</i>	<i>aristodemus majasi</i>	M	Crooked Is - Bahamas
100112.08	<i>Heraclides</i>	<i>aristodemus ponceanus</i>	M	FSCA
100112.06	<i>Heraclides</i>	<i>aristodemus temenes</i>	M	Cuba
100107.01	<i>Heraclides</i>	<i>aristor</i>	M	Hispaniola
100107.12	<i>Heraclides</i>	<i>astyalus astyalus</i>	M	Brazil
100115.01	<i>Heraclides</i>	<i>astyalus bajaensis</i>	M	Oaxaca - Mexico
100115.03	<i>Heraclides</i>	<i>astyalus hippomedon</i>	M	Panama
100115.06	<i>Heraclides</i>	<i>astyalus pallas</i>	M	Texas
100115.07	<i>Heraclides</i>	<i>astyalus phanias</i>	M	Brazil
100107.02	<i>Heraclides</i>	<i>caiguanabus</i>	M	Cuba
100127.15	<i>Heraclides</i>	<i>chiansiades chiansiades</i>	M	Juanjuí, San Martin, Peru
100127.16	<i>Heraclides</i>	<i>chiansiades chiansiades</i> (formerly <i>mossi</i>)	M	Manicore - Amazon
91230.09	<i>Heraclides</i>	<i>cresphontes</i>	M	Florida
100101.01	<i>Heraclides</i>	<i>cresphontes</i>	M	Costa Rica
100127.11	<i>Heraclides</i>	<i>epenetus</i>	M	Ecuador
100127.07	<i>Heraclides</i>	<i>erostratus erostratus</i>	M	Mexico
100127.05	<i>Heraclides</i>	<i>erostratus erostratus</i>	M	Guatemala
100127.09	<i>Heraclides</i>	<i>erostratus vazquezae</i>	M	Mexico
100120.10	<i>Heraclides</i>	<i>garleppi garleppi</i>	M	Bolivia
100120.05	<i>Heraclides</i>	<i>garleppi lecerfi</i>	M	F. Guiana
100120.08	<i>Heraclides</i>	<i>hectorides</i>	M	Brazil
100429.01	<i>Heraclides</i>	<i>himeros</i>	M	Brazil
91230.07	<i>Heraclides</i>	<i>homothoas</i>	M	Brazil
100120.01	<i>Heraclides</i>	<i>hyppason</i>	M	Bolivia

Table 3-1. (Continued)

Catalogue #	Genus	Species	Sex	Notes
100128.07	<i>Heraclides</i>	<i>isidorus brises</i>	M	Colombia
100128.06	<i>Heraclides</i>	<i>isidorus brises</i> (formerly <i>nymphius</i>)	M	Colombia
100128.08	<i>Heraclides</i>	<i>isidorus flavescens</i>	M	Ecuador
100128.01	<i>Heraclides</i>	<i>isidorus isidorus</i>	M	Peru
100128.03	<i>Heraclides</i>	<i>isidorus isidorus</i>	M	Costa Rica
100128.04	<i>Heraclides</i>	<i>isidorus isidorus</i> (formerly <i>pacificus</i>)	M	Colombia
100128.02	<i>Heraclides</i>	<i>isidorus tingo</i>	M	Tingo Maria - Peru
100120.07	<i>Heraclides</i>	<i>lamarchei</i>	M	Bolivia
100107.08	<i>Heraclides</i>	<i>machaonides</i>	M	Hispaniola
91230.03	<i>Heraclides</i>	<i>melonius</i>	M	Blue Mt., Jamaica
100107.10	<i>Heraclides</i>	<i>ornythion</i>	M	Mexico
100127.13	<i>Heraclides</i>	<i>oxynius</i>	M	Cuba
100105.15	<i>Heraclides</i>	<i>paeon escomeli</i>	M	Peru
91230.05	<i>Heraclides</i>	<i>paeon paeon</i>	M	Bolivia
100105.13	<i>Heraclides</i>	<i>paeon thrason</i>	M	Venezuela
100128.11	<i>Heraclides</i>	<i>pelaus atkinsi</i>	M	Cuba
100128.13	<i>Heraclides</i>	<i>pelaus imerius</i>	M	Hispaniola
100128.10	<i>Heraclides</i>	<i>pelaus pelaus</i>	M	Jamaica
100128.15	<i>Heraclides</i>	<i>pelaus puertoricensis</i>	M	Puerto Rico
100127.03	<i>Heraclides</i>	<i>rogeri pharnaces</i>	M	Mexico
100127.01	<i>Heraclides</i>	<i>rogeri rogeri</i>	M	Mexico
100107.14	<i>Heraclides</i>	<i>thersites</i>	M	Jamaica
100105.01	<i>Heraclides</i>	<i>thoas autocles</i>	M	Mexico
100105.07	<i>Heraclides</i>	<i>thoas brasiliensis</i>	M	Brazil
100105.09	<i>Heraclides</i>	<i>thoas cinyras</i>	M	Peru
100105.03	<i>Heraclides</i>	<i>thoas neacles</i>	M	Costa Rica
100105.05	<i>Heraclides</i>	<i>thoas oviedo</i>	M	Cuba
100105.11	<i>Heraclides</i>	<i>thoas thoantiades</i>	M	Argentina
91230.02	<i>Heraclides</i>	<i>thoas thoas</i>	M	B. Guiana
100127.17	<i>Heraclides</i>	<i>torquatus atsukoae</i>	M	El Salvador
100121.03	<i>Heraclides</i>	<i>torquatus jeani</i>	M	Colombia
100121.08	<i>Heraclides</i>	<i>torquatus leptalea</i>	M	Ecuador
100121.10	<i>Heraclides</i>	<i>torquatus polybius</i>	M	Bolivia
100121.05	<i>Heraclides</i>	<i>torquatus tolmides</i>	M	Costa Rica
100121.04	<i>Heraclides</i>	<i>torquatus tolus</i>	M	Tamulipas - Mexico
100121.07	<i>Heraclides</i>	<i>torquatus tolus</i>	M	Veracruz - Mexico
100120.03	<i>Heraclides</i>	<i>torquatus torquatus</i>	M	Brazil
100121.01	<i>Heraclides</i>	<i>torquatus torquatus</i>	M	Peru

Table 3-1. (Continued)

Catalogue #	Genus	Species	Sex	Notes
100124.06	<i>Heraclides</i>	<i>anchisiades anchisiades</i>	F	Peru
100125.04	<i>Heraclides</i>	<i>anchisiades capys</i>	F	Brazil
100125.08	<i>Heraclides</i>	<i>anchisiades idaeus</i>	F	Mexico
100125.02	<i>Heraclides</i>	<i>anchisiades philastrius</i>	F	Trinidad
100107.07	<i>Heraclides</i>	<i>andraemon andraemon</i>	F	Cuba
100112.11	<i>Heraclides</i>	<i>andraemon bonhotei</i>	F	N. Caicos Is.
100112.13	<i>Heraclides</i>	<i>andraemon tailori</i>	F	Grand Cayman
100107.17	<i>Heraclides</i>	<i>androgeus androgeus</i>	F	Peru
100115.09	<i>Heraclides</i>	<i>androgeus epidaurus</i>	F	Mexico
100115.11	<i>Heraclides</i>	<i>androgeus laodocus</i>	F	Brazil
100107.05	<i>Heraclides</i>	<i>aristodemus aristodemus</i>	F	Hispaniola
100112.03	<i>Heraclides</i>	<i>aristodemus bjoerndale</i>	F	Great Inagua - Bahamas
100112.05	<i>Heraclides</i>	<i>aristodemus majasi</i>	F	Crooked Is - Bahamas
100112.09	<i>Heraclides</i>	<i>aristodemus ponceanus</i>	F	FSCA
100112.07	<i>Heraclides</i>	<i>aristodemus temenes</i>	F	Cuba
100111.01	<i>Heraclides</i>	<i>aristor</i>	F	Hispaniola
100107.13	<i>Heraclides</i>	<i>astyalus astyalus</i>	F	Brazil
100115.02	<i>Heraclides</i>	<i>astyalus bajaensis</i>	F	Oaxaca - Mexico
100115.05	<i>Heraclides</i>	<i>astyalus hippomedon</i>	F	Panama
100115.04	<i>Heraclides</i>	<i>astyalus pallas</i>	F	Guatemala
100107.03	<i>Heraclides</i>	<i>caiguanabus</i>	F	Cuba
91230.10	<i>Heraclides</i>	<i>cesphontes</i>	F	Florida
100101.02	<i>Heraclides</i>	<i>cesphontes</i>	F	Costa Rica
100127.12	<i>Heraclides</i>	<i>epenetus</i>	F	Ecuador
100127.08	<i>Heraclides</i>	<i>erostratus erostratus</i>	F	Mexico
100127.06	<i>Heraclides</i>	<i>erostratus erostratus</i>	F	Guatemala
100127.10	<i>Heraclides</i>	<i>erostratus vazquezae</i>	F	Mexico
100120.11	<i>Heraclides</i>	<i>torquatus torquatus</i>	F	See photo
100120.04	<i>Heraclides</i>	<i>garleppi interruptus</i>	F	Brazil
100120.06	<i>Heraclides</i>	<i>garleppi lecerfi</i>	F	F. Guiana
100120.09	<i>Heraclides</i>	<i>hectorides</i>	F	Brazil
100429.02	<i>Heraclides</i>	<i>himeros</i>	F	Brazil
91230.08	<i>Heraclides</i>	<i>homothoas</i>	F	Trinidad
100120.02	<i>Heraclides</i>	<i>hyppason</i>	F	Bolivia

Table 3-1. (Continued)

Catalogue #	Genus	Species	Sex	Notes
100128.09	<i>Heraclides</i>	<i>isidorus flavescens</i>	F	See photo
100128.05	<i>Heraclides</i>	<i>isidorus isidorus</i> (formerly <i>pacificus</i>)	F	Colombia
100120.12	<i>Heraclides</i>	<i>lamarchei</i>	F	See photo
100107.09	<i>Heraclides</i>	<i>machaonides</i>	F	Hispaniola
91230.04	<i>Heraclides</i>	<i>melonius</i>	F	See photo
100107.11	<i>Heraclides</i>	<i>ornythion</i>	F	Mexico
100127.14	<i>Heraclides</i>	<i>oxynius</i>	F	Cuba
91230.06	<i>Heraclides</i>	<i>paeon paeon</i>	F	Bolivia: Cochabamba
100105.14	<i>Heraclides</i>	<i>paeon thrason</i>	F	Venezuela
100128.12	<i>Heraclides</i>	<i>pelaus atkinsi</i>	F	Cuba
100128.14	<i>Heraclides</i>	<i>pelaus imerius</i>	F	Hispaniola
100128.17	<i>Heraclides</i>	<i>pelaus pelaus</i>	F	Jamaica
100128.16	<i>Heraclides</i>	<i>pelaus puertoricensis</i>	F	Puerto Rico
100127.04	<i>Heraclides</i>	<i>rogeri pharnaces</i>	F	Mexico
100127.02	<i>Heraclides</i>	<i>rogeri rogeri</i>	F	Mexico
100107.15	<i>Heraclides</i>	<i>thersites</i>	F	Jamaica
100105.02	<i>Heraclides</i>	<i>thoas autocles</i>	F	Mexico
100105.08	<i>Heraclides</i>	<i>thoas brasiliensis</i>	F	Brazil
100105.10	<i>Heraclides</i>	<i>thoas cinyras</i>	F	Peru
100105.04	<i>Heraclides</i>	<i>thoas neacles</i>	F	Costa Rica
100105.06	<i>Heraclides</i>	<i>thoas oviedo</i>	F	Cuba
100105.12	<i>Heraclides</i>	<i>thoas thoantiades</i>	F	Argentina
91230.01	<i>Heraclides</i>	<i>thoas thoas</i>	F	Potaro River, B. Guiana
100127.18	<i>Heraclides</i>	<i>torquatus atsukoe</i>	F	El Salvador
100121.09	<i>Heraclides</i>	<i>torquatus leptalea</i>	F	Ecuador
100121.11	<i>Heraclides</i>	<i>torquatus polybius</i>	F	Brazil
100121.06	<i>Heraclides</i>	<i>torquatus tolmidis</i>	F	Ecuador
100121.02	<i>Heraclides</i>	<i>torquatus torquatus</i>	F	Brazil

Table 3-2. GenBank accession numbers for sequences of the species used in the molecular analysis.

Taxa	Accession Numbers	
	COI - tRNA-Leu - COII genes	EF-1a gene
<i>Heraclides anchisiades</i>	AF044005.1	AF044822.1
<i>Heraclides astyalus</i>	AY457598.1	AY457609.1
<i>Heraclides crespontes</i>	AF044004.1	AF044832.1
<i>Heraclides erostratus</i>	AY457599.1	AY457616.1
<i>Heraclides hectorides</i>	AY457600.1	AY457618.1
<i>Heraclides thoas</i>	AY457601.1	AY457632.1
<i>Heraclides torquatus</i>	AY457602.1	AY457633.1
<i>Papilio constantinus</i>	AF044002.1	AF044836.2
<i>Papilio demoleus</i>	AY569092.1	AF044825.2
<i>Papilio glaucus</i>	AF044013.1	EU136675.1
<i>Papilio machaon</i>	AF044006.1	AF044828.2

Table 3.3. Morphological Character Hypothesis Matrix with missing and inapplicable characters coded as?

Taxa	Characters																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
<i>H. thoas</i>	0	0	1	1	0	1	1	0	1	1	1	0	1	1	0	1	0	0	?	0	
<i>H. cresphontes</i>	0	0	1	0	0	0	1	0	1	1	1	0	1	1	0	1	0	0	?	0	
<i>H. homothoas</i>	0	?	1	?	?	?	1	0	?	?	?	?	?	?	?	?	0	0	?	0	
<i>H. melonius</i>	?	?	1	0	0	0	1	0	?	?	?	?	?	?	?	?	0	0	?	0	
<i>H. paeon</i>	?	0	1	0	1	0	1	0	?	?	?	?	?	?	?	?	0	0	?	0	
<i>H. aristor</i>	?	?	0	?	?	?	1	0	?	?	?	?	?	?	?	?	0	0	?	0	
<i>H. caiguanabus</i>	?	?	0	?	?	?	1	0	?	0	?	?	?	?	?	?	0	0	?	0	
<i>H. thersites</i>	0	0	1	0	0	0	1	0	1	1	?	?	?	?	?	?	0	1	1	0	
<i>H. androgeus</i>	0	0	1	0	0	0	1	0	1	1	1	0	1	0	1	0	0	1	1	1	
<i>H. astyalus</i>	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	0	1	1	1	
<i>H. ornythion</i>	?	?	1	?	?	?	1	0	?	1	?	?	?	?	?	?	0	1	1	1	
<i>H. aristodemus</i>	0	0	1	0	0	0	1	0	?	1	?	?	?	?	?	?	0	0	?	0	
<i>H. andraemon</i>	0	0	1	0	0	0	1	0	0	1	1	0	1	0	?	1	0	0	?	0	
<i>H. machaonides</i>	?	?	1	?	?	?	1	0	?	1	?	?	?	?	?	?	0	0	?	0	
<i>H. lamarchei</i>	?	?	1	?	?	?	1	0	?	?	?	?	?	?	?	?	0	0	?	0	
<i>H. himeros</i>	?	?	1	?	?	?	1	0	?	1	?	1	1	0	1	1	0	0	?	0	
<i>H. hectorides</i>	?	1	1	1	0	0	1	0	0	1	1	1	1	0	1	1	0	1	1	1	
<i>H. garleppi</i>	?	?	1	?	?	?	?	0	?	?	?	?	?	?	?	?	0	1	1	1	
<i>H. torquatus</i>	0	0	1	0	0	0	1	0	1	1	1	1	1	0	0	1	0	1	1	1	
<i>H. hyppason</i>	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	
<i>H. epenetus</i>	?	?	1	?	?	?	?	?	?	0	?	?	?	?	?	?	0	1	0	0	
<i>H. oxynius</i>	1	1	1	?	?	?	?	?	1	?	0	?	?	?	?	?	0	1	0	0	
<i>H. pelaus</i>	1	1	1	0	0	0	0	1	0	0	?	?	?	?	?	?	0	1	0	0	
<i>H. anchisiades</i>	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	
<i>H. isidorus</i>	1	1	1	?	?	?	?	0	1	?	0	?	?	?	?	?	0	1	0	0	
<i>H. chiansiades</i>	1	1	1	?	?	?	?	0	1	?	?	?	?	?	?	?	0	1	?	?	
<i>H. rogeri</i>	1	1	1	?	?	?	?	0	1	0	0	0	1	1	0	0	0	1	0	0	
<i>H. erostratus</i>	1	1	1	?	?	?	?	0	1	?	?	?	?	?	?	?	0	1	0	1	
<i>P. demoleus</i>	?	0	1	?	?	?	?	1	0	1	0	1	0	0	1	0	0	1	0	?	0

Table 3-3 (continued).

Taxa	Characters																			
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
<i>H. thoas</i>	0	0	1	1	1	1	0	1	0	0,1	0	1	1	0	0	?	?	?	?	?
<i>H. cresphontes</i>	0	0	1	1	1	1	0	1	0	0,1	1	1	1	0	0	?	?	?	?	?
<i>H. homothoas</i>	0	0	1	1	1	1	0	1	0	0,1	0	1	1	0	0	?	?	?	?	?
<i>H. melonius</i>	0	0	1	1	1	1	0	1	0	0,1	1	1	1	0	0	?	?	?	?	?
<i>H. paeon</i>	0	0	1	1	1	1	0	1	1	0	0	1	1	0	0	?	?	?	?	?
<i>H. aristor</i>	0	0	0	0	0	0	?	0	0	0	?	1	?	0	0	?	?	?	?	?
<i>H. caiguanabus</i>	0	0	0	0	0	0	?	0	0	0	?	1	?	0	0	?	?	?	?	?
<i>H. thersites</i>	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	?	?	?	?	?
<i>H. androgeus</i>	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0,1	0	?	0	?	1
<i>H. astyalus</i>	0	0	0	1	0	0,1	0,1	0,1	0	0	0,1	1	?	0	0	?	?	?	?	?
<i>H. ornythion</i>	0	0	0	1	0,1	1	0	1	0	0	1	1	1	0	0	?	?	?	?	?
<i>H. aristodemus</i>	0	1	1	1	1	1	0	1	0	1	0	1	1	0	0	?	?	?	?	?
<i>H. andraemon</i>	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	?	?	?	?	?
<i>H. machaonides</i>	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	?	?	?	?	?
<i>H. lamarchei</i>	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	?	?	?	?	?
<i>H. himeros</i>	0	0	0	1	?	1	1	0	0	0	0	1	1	0	?	?	?	?	?	?
<i>H. hectorides</i>	0	0	0	1	0,1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	?
<i>H. garleppi</i>	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	?	1	?	0
<i>H. torquatus</i>	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0,1	0	?	1	?	1
<i>H. hyppason</i>	0	0	0	0	0	0	?	0	0	?	?	0	0	1	0,1	1	0	0	0	0
<i>H. epenetus</i>	1	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>H. oxynius</i>	1	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>H. pelaus</i>	1	0	0	1	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?
<i>H. anchisiades</i>	1	0	0	0	0	0	?	0	0	?	?	0	0	0,1	0,1	0	1	1	0	0
<i>H. isidorus</i>	1	0	0	0	0	0	?	0	0	?	?	0	0	0,1	0,1	0	0	0	1	0
<i>H. chiansiades</i>	1	0	0	0	?	0	?	0	0	?	?	0	?	1	?	1	0	?	0	?
<i>H. rogeri</i>	1	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>H. erostratus</i>	1	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?
<i>P. demoleus</i>	0	0	0	1	1	1	0	0	0	0	1	1	1	0	?	?	?	?	?	?

Table 3-3 (continued).

Taxa	Characters																			
	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>H. thoas</i>	0	0	0	1	1	0,1	0,1	0	1	1	0	1	1	1	0	0	1	1	0	0
<i>H. cresphontes</i>	0	0	0	1	1	0,1	0	?	1	1	0	1	1	1	0	0	1	1	0	0
<i>H. homothoas</i>	0	0	0	1	1	0	0	?	1	1	0	1	1	1	0	0	1	1	0	0
<i>H. melonius</i>	0	0	0	1	1	0	0	?	1	1	0	1	1	1	0	0	1	1	0	0
<i>H. paeon</i>	0	0	0	1	1	0,1	0	?	1	1	0	1	0	0	0	0	1	1	0	0
<i>H. aristor</i>	?	?	1	0	1	0	0	?	2	1	0	1	0	0	0	0	0	0	?	?
<i>H. caiguanabus</i>	?	?	1	0	1	0	0	?	2	1	0	1	0	0	0	0	0	0	?	?
<i>H. thersites</i>	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	1	0	1	0
<i>H. androgeus</i>	0	0	0	1	1	1	1	0	0	1	0,1	0,1	0	0	0	0	1	0	1	0
<i>H. astyalus</i>	0	0	0	1	1	1	1	0	2	1	0	1	0	0	0	0	1	0	0,1	0
<i>H. ornythion</i>	0	0	0	1	1	1	0	?	2	1	0	1	0	0	0	0	1	0,1	0	0
<i>H. aristodemus</i>	0	0	0	1	1	0,1	0	?	2	1	0	1	0	0	1	0	1	1	0	0
<i>H. andraemon</i>	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0
<i>H. machaonides</i>	0	0	0	0	1	0,1	1	1	2	1	0	1	1	2	0	0	1	1	0	1
<i>H. lamarchei</i>	0	0	0	1	1	0,1	0	?	0	1	0	1	0	0	0	1	1	1	0	0
<i>H. himeros</i>	0	0	0	1	1	0	0	?	0	1	0	1	0	2	1	0	1	1	1	0
<i>H. hectorides</i>	0	0	0	1	0	?	0	?	0	1	0	1	0	0	0	1	1	1	0	0
<i>H. garleppi</i>	0,1	0	0	0	1	1	0	?	0	1	0	1	0	0	0	0	1	0	1	0
<i>H. torquatus</i>	1	0	0	0	1	0	0	?	0	1	0	1	0	0	0	0	1	0	1	0
<i>H. hyppason</i>	?	?	?	?	?	?	0	?	0	?	0	0	?	?	?	0	0	0	?	?
<i>H. epenetus</i>	?	?	?	?	?	?	0	?	0	?	1	0	?	?	?	0	0	0	?	?
<i>H. oxynius</i>	?	?	?	?	?	?	0	?	0	?	0	1	0	0	0	0	0	0	?	?
<i>H. pelaus</i>	0	1	0	0	1	0	0	?	0	?	0	1	0	0	0	0	0	0	?	?
<i>H. anchisiades</i>	?	?	?	?	?	?	0,1	0	0	?	0,1	0	?	?	?	0	0	0	?	?
<i>H. isidorus</i>	?	?	?	?	?	?	0,1	0	0	?	0,1	0	?	?	?	0	0	0	?	?
<i>H. chiansiades</i>	?	?	?	?	?	?	0	?	0	?	1	0	?	?	?	0	0	?	?	?
<i>H. rogeri</i>	?	?	?	?	?	?	0	?	0	?	1	0	?	?	?	0	0	0	?	?
<i>H. erostratus</i>	?	?	?	?	?	?	0	?	0	?	0	1	0	0	0	0	0	0	?	?
<i>P. demoleus</i>	0	0	0	1	1	1	1	0	2	0	0	0	?	?	?	0	1	1	0	0

Table 3-3 (continued).

Taxa	Characters																			
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
<i>H. thoas</i>	0	1	0	0	?	?	0	0	1	1	1	0	0	0	1	1	0	0	0	0
<i>H. cresphontes</i>	0	1	0	0	?	?	0	0	1	1	1	0	0	0	1	1	0	0	0	0
<i>H. homothoas</i>	0	1	0	0	?	?	0	0	1	1	1	0	0	0	1	1	0	0	0	0
<i>H. melonius</i>	0	1	0	0	?	?	0	0	1	1	1	0	0	0	1	1	0	0	0	0
<i>H. paeon</i>	0	1	0	0	?	?	0	0	1	1	1	0	0	0	1	1	0	1	1	1
<i>H. aristor</i>	?	?	0	0	?	?	0	0	1	1	1	0	0	0	1	1	0	0	0	0
<i>H. caiguanabus</i>	?	?	0	0	?	?	0	0	1	1	2	0	0	0	1	1	0	0	0	0
<i>H. thersites</i>	0	?	0	1	?	?	0	0	1	1	1	0	0	0	1	1	1	0	1	0
<i>H. androgeus</i>	0	?	0	1	?	?	0,1	1	0,1	1	1	0	0	0	1	1	1	0	2	0
<i>H. astyalus</i>	0	?	0	1	?	?	0	0	1	1	1	0	0	0	1	1	1	0	2	0
<i>H. ornythion</i>	0	1	0	0	?	?	0	0	1	1	1	0	0	0	1	1	1	0	2	0
<i>H. aristodemus</i>	0	1	0,1	0,1	0	0	1	1	1	1	1	0	0	0	1	1	0	1	2	0
<i>H. andraemon</i>	1	1	0	0	?	?	1	1	1	1	1	0	0	0	1	1	0	1	0	0
<i>H. machaonides</i>	0	1	0	0	?	?	1	1	1	1	1	0	0	0	1	0	?	?	?	0
<i>H. lamarchei</i>	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	1	2	0	1	0
<i>H. himeros</i>	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	1	2	0	1	0
<i>H. hectorides</i>	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	2	0	1	0
<i>H. garleppi</i>	0	?	0	1	?	0	0	0	1	1	0	0	1	0	0	1	2	0	1	0
<i>H. torquatus</i>	0	?	0,1	1	0	0	0	0	1	1	0	0	1,2	0	0	1	2	0	1	0
<i>H. hyppason</i>	?	?	1	1	0	0	0	0	1	0	0	1	1	0	0	1	2	0	1	0
<i>H. epenetus</i>	?	?	0	0	?	?	0	0	0	?	?	0	0	0	0	1	2	0	1	0
<i>H. oxynius</i>	?	?	1	1	1	1	0	0	0	?	?	0	0	0	0	1	2	0	1	0
<i>H. pelaus</i>	?	?	0	0	?	?	0	0	1	0	0	0	0	0	0	1	2	0	1	0
<i>H. anchisiades</i>	?	?	1	1	0	0	0	0	1	0	0	1	1,2	0	0	1	2	0	1	0
<i>H. isidorus</i>	?	?	1	1	0	0	0	0	1	0,2	0,2	1	1,2	0	0	1	2	0	1	0
<i>H. chiansiades</i>	?	?	1	?	0	?	0	?	0	0	?	1	?	0	0	1	2	0	1	0
<i>H. rogeri</i>	?	?	1	1	0	0	0	0	0,1	0	0	0	0	0	0	1	2	0	1	0
<i>H. erostratus</i>	?	?	1	1	0	0	0	0	1	1	0	0	0	0	0	1	2	0	1	0
<i>P. demoleus</i>	0	?	0	0	?	?	0	0	1	1	1	0	0	1	1	1	0	0	2	1

Table 3-3 (continued).

Taxa	Characters																			
	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
<i>H. thoas</i>	1	1	1	1	1	0	1	0	0	0	0	?	1	0	0	0	0	?	?	
<i>H. cresphontes</i>	1	1	1	1	1	0	1	0	0	0	1	0	?	0	?	?	0	0	?	?
<i>H. homothoas</i>	1	1	1	1	1	0	1	0	0	0	1	0	?	0	?	?	0	0	?	?
<i>H. melonius</i>	1	1	1	1	1	0	1	0	0	0	0	1	0	0	?	?	0	0	?	?
<i>H. paeon</i>	1	1	1	1	1	0	1	0	0	0	1	0	?	0	?	?	1	0	?	?
<i>H. aristor</i>	1	1	1	1	1	0	1	0	0	0	0	0	?	0	?	?	0	1	0	1
<i>H. caiguanabus</i>	1	1	1	1	1	0	1	0	0	0	0	0	?	0	?	?	0	1	0	1
<i>H. thersites</i>	1	1	1	1	1	0	1	0	0	0	1	1	1	1	1	0	0	0	?	?
<i>H. androgeus</i>	1	1	1	1	1	0	1	0	0	0	1	1	1	1	1	0	0	0	?	?
<i>H. astyalus</i>	1	1	1	1	1	0	1	0	0	0	1	1	1	1	1	0	0	0	?	?
<i>H. ornythion</i>	1	1	1	1	1	0	1	0	0	0	1	1	1	1	1	0	0	0	?	?
<i>H. aristodemus</i>	1	0	0	1	1	0	1	0	0	0	1	1	1	1	1	0	0	0	?	?
<i>H. andraemon</i>	1	0	0	1	1	0	1	0	0	0	1	1	1	1	1	1	0	0	?	?
<i>H. machaonides</i>	1	0	0	1	1	0	1	0	0	0	0	0	?	0	?	?	0	1	1	0
<i>H. lamarchei</i>	1	1	1	1	1	0	0	0	0	0	2	0	?	0	?	?	0	0	?	?
<i>H. himeros</i>	1	1	1	1	1	0	0	0	0	?	2	0	?	0	?	?	0	1	2	1
<i>H. hectorides</i>	1	1	1	0	0	0	0	0	0	0	2	0	?	0	?	?	0	0	?	?
<i>H. garleppi</i>	0	1	?	1	0	0	0	0	0	0	0	0	?	1	1	0	0	1	1	1
<i>H. torquatus</i>	0	1	?	1	0	0	0	0	0	0	2	0	?	0	?	?	0	0	?	?
<i>H. hyppason</i>	0	1	?	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	?	?
<i>H. epenetus</i>	0	1	?	0	0	0	0	0	1	0	0	0	?	0	?	?	0	1	1	1
<i>H. oxynius</i>	0	1	?	0	0	0	0	0	1	0	0	0	?	0	?	?	0	1	1	1
<i>H. pelaus</i>	0	1	?	0	0	0	0	0	0	0	0	0	?	0	?	?	0	1	1	1
<i>H. anchisiades</i>	0	1	?	0	0	0	0	0	0	0	0	0	?	0	?	?	0	1	1	1
<i>H. isidorus</i>	0	1	?	0,2	0,2	0	0	0	0	0	0	0	?	0	?	?	0	1	1	1
<i>H. chiansiades</i>	0	1	?	0,2	0,2	0	0	0	0	0	0	0	?	0	?	?	0	1	1	1
<i>H. rogeri</i>	0	1	?	0	0	0	0	0	0	0	0	0	?	0	?	?	0	1	1	1
<i>H. erostratus</i>	0	1	?	0	0	0	0	0	0	0	0	0	?	0	?	?	0	1	1	1
<i>P. demoleus</i>	1	1	1	1	1	1	1	0	0	1	1	0	?	0	?	?	0	0	?	?

Table 3-3 (continued).

Taxa	Characters																
	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117
<i>H. thoas</i>	0	0	0	0	1	1	1	1	1	0	?	1	0	0	1	1	0
<i>H. crespontes</i>	0	1	0	0	0	1	1	0	1	0	?	1	0	0	0	1	0
<i>H. homothoas</i>	0	1	0	1	1	1	0	?	0	1	0	1	0	0	0	1	0
<i>H. melonius</i>	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	?
<i>H. paeon</i>	0	0	0	0	1	1	0	?	0	1	0	1	0	0	1	1	0
<i>H. aristor</i>	0	0	0	0	1	1	1	1	1	1	0	1	1	0	0	1	0
<i>H. caiguanabus</i>	0	0	0	0	1	1	1	0	1	1	0	1	1	0	0	1	0
<i>H. thersites</i>	0	0	0	0	1	0	?	?	?	1	1	1	0	1	1	1	1
<i>H. androgeus</i>	0	0	0	0	1	0	?	?	?	1	1	1	0	1	1	1	1
<i>H. astyalus</i>	0	0	0	0	1	0	?	?	?	1	1	1	0	1	1	1	1
<i>H. ornythion</i>	0	0	0	0	1	0	?	?	?	1	1	1	0	1	1	1	1
<i>H. aristodemus</i>	0	0	0	0	1	0	?	?	?	1	1	1	0	1	1	1	1
<i>H. andraemon</i>	0	0	0	0	1	0	?	?	?	0	?	1	0	0	1	1	1
<i>H. machaonides</i>	0	0	0	0	1	0	?	?	?	0	?	1	0	1	1	1	1
<i>H. lamarchei</i>	1	0	0	0	1	0	?	?	?	1	0	1	0	0	1	1	1
<i>H. himeros</i>	0	0	0	0	1	0	?	?	?	1	0	1	?	0	1	1	1
<i>H. hectorides</i>	1	0	0	0	1	0	?	?	?	1	0	1	0	0	0	1	1
<i>H. garleppi</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. torquatus</i>	0	0	1	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. hyppason</i>	0	0	0	0	1	1	1	1	0	1	1	1	0	1	1	1	0
<i>H. epenetus</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. oxynius</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. pelaus</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. anchisiades</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. isidorus</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. chiansiades</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. rogeri</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>H. erostratus</i>	0	0	0	0	1	0	?	?	?	1	0	1	0	1	1	1	1
<i>P. demoleus</i>	0	1	0	0	?	0	?	?	?	1	0	0	0	0	0	1	0

Table 3-3 (continued).

Taxa	Characters															
	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133
<i>H. thoas</i>	1	0	1	0	0	?	?	0	?	0	0	1	1	1	?	?
<i>H. cresphontes</i>	0	0	0	0	0	?	?	0	?	0	0	0	0	?	?	?
<i>H. homothoas</i>	0	0	0	0	1	0	?	1	0	0	0	0	0	?	?	?
<i>H. melonius</i>	?	?	1	0	0	?	?	0	?	0	0	0	0	?	?	?
<i>H. paeon</i>	0	1	1	0	1	0	?	1	1	0	0	0	0	?	?	?
<i>H. aristor</i>	1	0	1	0	0	?	?	0	?	0	0	1	1	1	?	?
<i>H. caiguanabus</i>	1	0	1	0	0	?	?	0	?	0	0	1	0	?	0	?
<i>H. thersites</i>	?	?	1	0	1	1	1	0	?	0	0	0	0	?	0	?
<i>H. androgeus</i>	?	?	1	0	1	1	1	0	?	0	0	0	1	0	0	0
<i>H. astyalus</i>	?	?	1	0	1	1	1	0	?	0	0	0	1	0	0	0
<i>H. ornythion</i>	?	?	1	0	1	1	1	0	?	0	0	0	1	0	0	0
<i>H. aristodemus</i>	?	?	1	0	1	1	1	0	?	0	0	0	1	0	0	0
<i>H. andraemon</i>	?	?	1	0	1	1	1	0	?	0	0	0	1	1	0	0
<i>H. machaonides</i>	?	?	1	0	0	?	?	0	?	0	1	0	1	0	0	0
<i>H. lamarchei</i>	?	?	1	0	0	1	0	0	?	0	0	0	1	1	1	0
<i>H. himeros</i>	?	?	1	0	0	?	?	0	?	0	0	0	1	1	1	0
<i>H. hectorides</i>	?	?	1	0	0	?	?	0	?	0	0	0	0	?	0	0
<i>H. garleppi</i>	?	?	1	0	1	1	0	0	?	1	0	0	1	1	0	0
<i>H. torquatus</i>	?	?	1	0	0	?	?	0	?	0	0	0	1	1	0	0
<i>H. hyppason</i>	1	0	1	1	0	?	?	0	?	0	0	0	0	?	0	0
<i>H. epenetus</i>	?	?	1	0	1	1	0	0	?	0	0	0	1	1	0	0
<i>H. oxynius</i>	?	?	1	0	1	1	0	0	?	0	0	0	1	1	0	0
<i>H. pelaus</i>	?	?	1	0	1	1	0	0	?	0	0	0	1	1	0	0
<i>H. anchisiades</i>	?	?	1	0	1	1	0	0	?	0	0	0	1	1	0	0
<i>H. isidorus</i>	?	?	1	0	1	1	0	0	?	0	0	0	1	1	0	0
<i>H. chiansiades</i>	?	?	1	0	1	1	0	0	?	0	0	0	1	1	0	0
<i>H. rogeri</i>	?	?	1	0	1	1	0	0	?	0	0	0	1	1	0	0
<i>H. erostratus</i>	?	?	1	0	1	1	0	0	?	0	0	0	1	1	0	0
<i>P. demoleus</i>	0	0	0	0	0	?	?	0	?	0	0	0	0	?	0	1

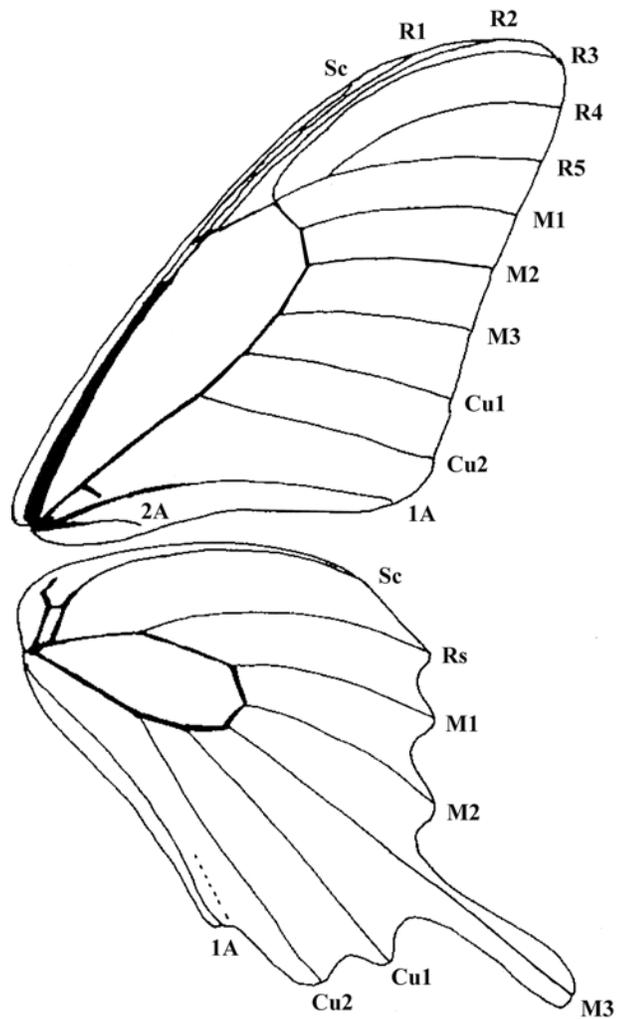


Figure 3-1. *Papilio thoas* wing pattern showing system of nomenclature used for veins (Tyler et al. 1994). Extra-discal cells are named based on their boundary veins (Miller, 1969). **Sc** = subcosta; **R** = radius (numbered 1 through 5); **M** = medius (numbered 1 through 3); **Cu** = cubitus (numbered 1 and 2); **A** = anal vein (with prefix 1 and 2).

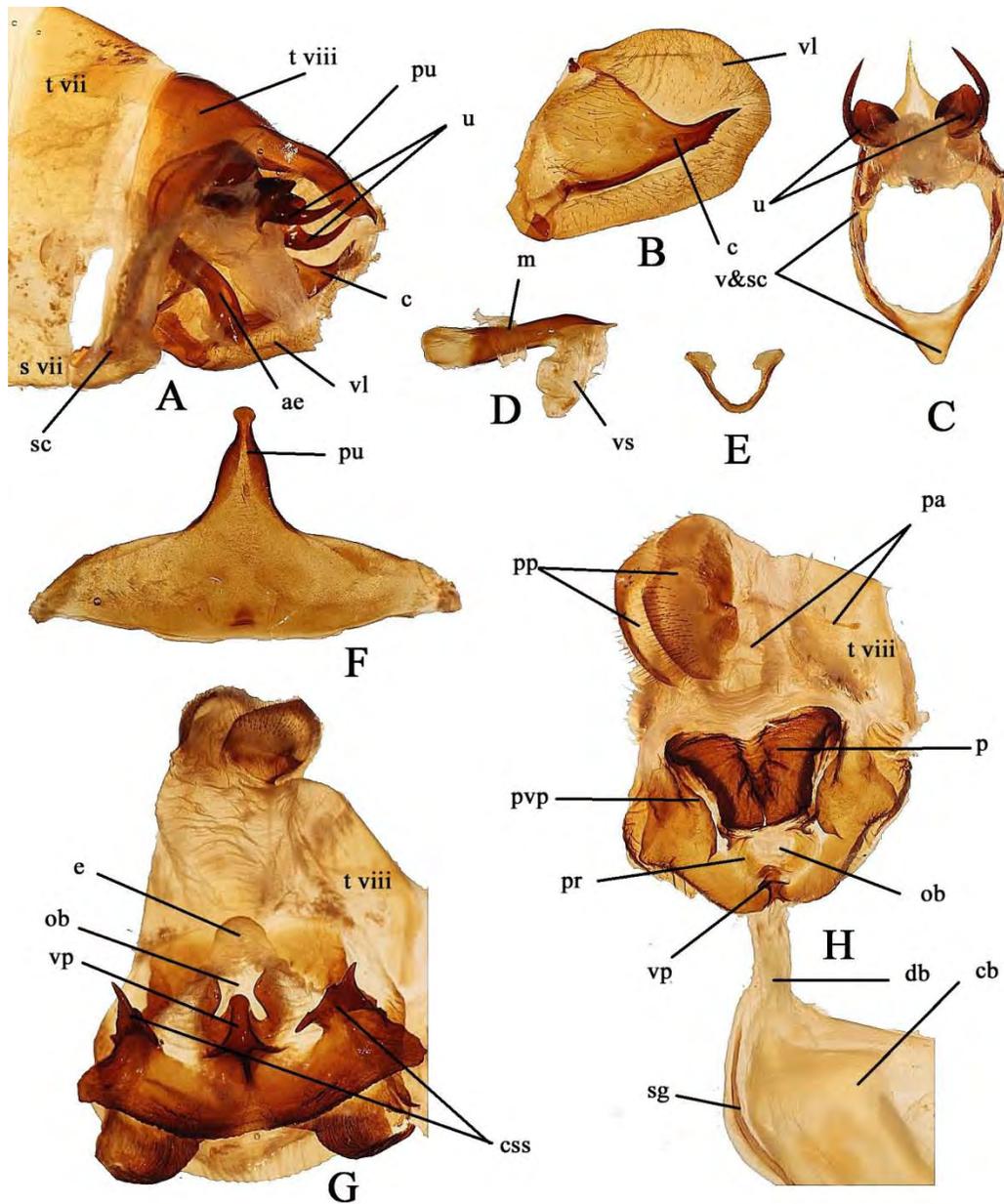


Figure 3-2. Terminology for genitalic nomenclature adapted from the scheme used by Miller (1987). **A.** male in lateral view with left valve removed; **B.** left valve; **C.** uncus, vinculum and saccus; **D.** aedeagus; **E.** juxta in anal view; **F.** dorsal view of the 8th tergite; **G.** anal view of the female genitalia showing ostial armature; **H.** anal view of female genitalia showing ostial armature and corpus bursa. **ae** = aedeagus; **c** = clasper; **cb** = corpus bursae; **css** = conjoined sclerotized spines; **db** = ductus bursae; **j** = juxta; **m** = manica; **ob** = ostium of the bursa; **p** = medial plate; **pa** = posterior apophysis; **pp** = papillae anales; **pr** = proximal vestibular plate; **pu** = pseuduncus; **pvp** = peripheral vestibular plate; **s** = sternite; **sc** = saccus; **sg** = signum; **t** = tergite; **u** = uncus; **vl** = valve; **v** = vinculum; **vs** = vesica.

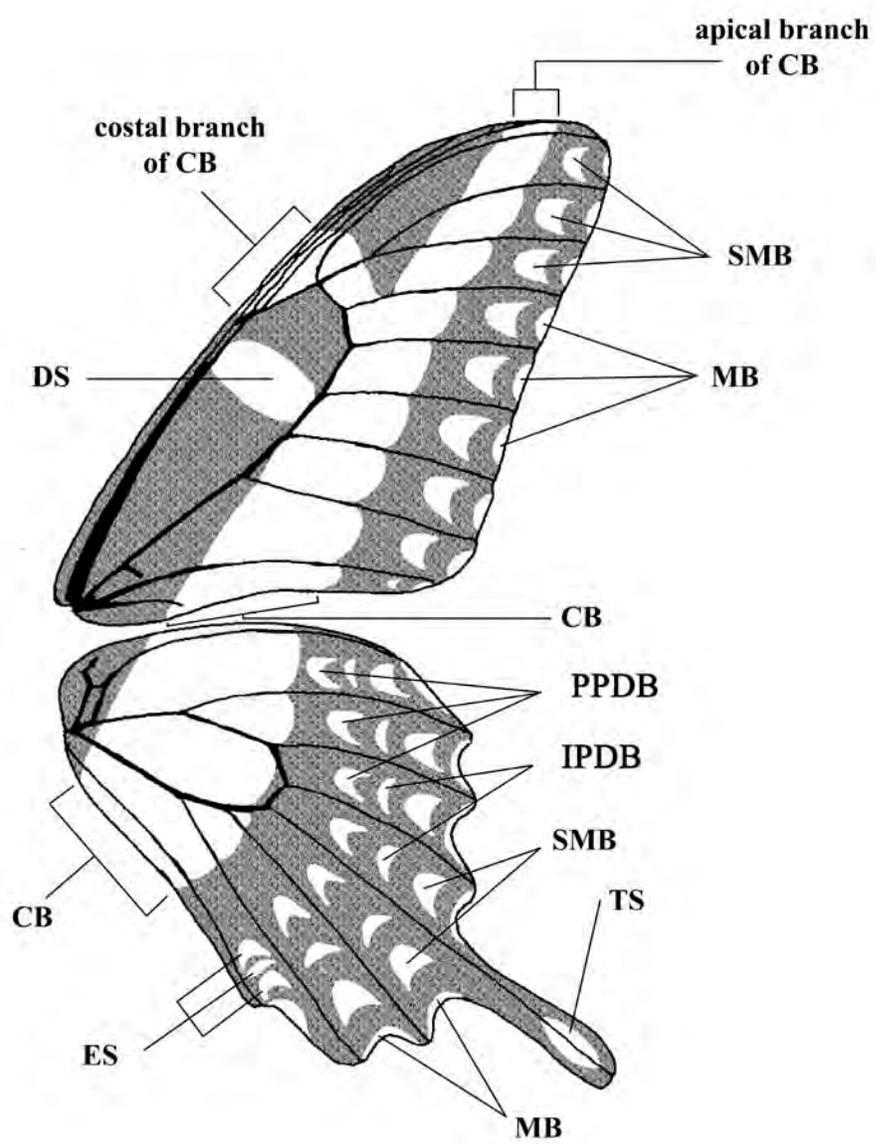


Figure 3-3. Generalized wing pattern of *Heraclides*. **DS** = discal spot; **CB** = central band; **MB** = marginal band; **SMB** = sub-marginal band; **PPDB** = proximal post-discal band; **IPDB** = inner post-discal band; **TS** = tail spot; **ES** = eyespot (often the last elements of PPDB, IPDB, and SMB converge to form an eyespot).

CHAPTER 4 RESULTS

Phylogenetic Reanalysis of Molecular Data

Sequence Alignment and Data Description. The relatively small number of sequences allowed for manual alignment of the sequences. The similarity of the taxa being investigated suggested that differences in sequences would be small and in order to limit the number of insertions that would be introduced this approach was seen as more appropriate. For the mitochondrial sequences, one gap each was introduced at positions 10, 1595, and 1611; the sequence for *P. glaucus* started after all the others (position 32). Alignment against the Giant Silkworm Moth's complete mitochondrial genome yielded three partitions for COI, tRNA-Leu, and COII. For the nuclear sequences, no gaps were introduced but some sequences were shorter necessitating the inclusion of missing data at the ends of these sequences. The EF-1 α sequences for *H. anchisiades* and *H. crespontes* stopped at position 1010, the sequence for *H. hectorides* stopped at position 1045, and the sequence for *H. torquatus* stopped at position 1231. The concatenated sequence had the following partitions: COI (position 1 to 1543), tRNA-leu (position 1544 to 1611), COII (position 1612 to 2292), and EF-1 α (position 2293 to 3526) which were 1542, 68, 681 and 1234 bp in length respectively.

Tests for Best fit Model. Hierarchical likelihood ratio tests (hLRTs) as well as Akaike information criterion (AIC) agreed for the most part on the model to be used. The model chosen for mitochondrial, nuclear, as well as for the concatenated data was predominantly GTR+ Γ +I. One other model was chosen for the nuclear data by hLRTs – Tamura and Nei with gamma distribution and invariable rates (TrN+ Γ +I); this model was not used as the likelihood score was worse than that for the AIC model (GTR+ Γ +I).

Tests for Homogeneity. Tests for the homogeneity of substitution patterns between sequences (disparity index) revealed the probability of rejecting the null hypothesis that these sequences evolved with the same pattern of substitution, as judged from the extent of differences in base composition biases between sequences. P-values smaller than 0.05 are considered significant. The results suggest that these sequences have not evolved with the same pattern of nucleotide substitution when the individual as well as the concatenated data were analyzed. Partitioned homogeneity tests revealed that there was some incongruence in one or a few genes by the low p-value (0.01). It was discovered that the gene responsible for the incongruence was tRNA-leucine. When removed the p-value was 0.51. However, removal of this gene from the analysis had no marked effect on the topology or posterior probabilities of the consensus tree, but suggests that a partitioned Bayesian analysis may yield better results.

Maximum Parsimony Analyses. MP analysis of the mitochondrial genes yielded three most parsimonious trees (Figure 4-1). The consistency index is 0.543536, the retention index is 0.485884, and the composite index is 0.319268 (0.264095) for all sites and parsimony informative sites (in parentheses). The percentage of parsimonious trees in which the associated taxa clustered together is shown next to the branches (values >50% shown). There were 2258 positions in the final dataset, out of which 305 were parsimony informative. MP analysis of the nuclear genes yielded one most parsimonious tree with length = 234 (Figure 4-2). The consistency index is 0.651007, the retention index is 0.704545, and the composite index is 0.547980 (0.458664) for all sites and parsimony informative sites (in parentheses). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches (values >50% shown). There were 1005 positions in the final dataset, out of which 83 were parsimony informative. MP analysis of the

concatenated molecular data yielded one most parsimonious tree with length = 1244 (Figure 4-3). The consistency index is 0.560573, the retention index is 0.530035, and the composite index is 0.360032 (0.297123) for all sites and parsimony informative sites (in parentheses). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches (values >50% shown). There were 3263 positions in the final dataset, out of which 388 were parsimony informative.

Maximum Likelihood Analyses. ML analyses of the mitochondrial genes yielded one tree (Figure 4-4). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches (values >50% shown). ML analysis of the nuclear genes yielded one tree (Figure 4-5). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches (values >50% shown). ML analysis of the concatenated data yielded one tree (Figure 4-6). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches (values >50% shown).

Bayesian Analyses. Bayesian analyses done on all molecular data reached stationarity well before 10,000 cycles. Nonetheless, the first 100 trees were discarded as burn-in samples and the consensus trees were computed from the remaining trees in each analysis. The two independent runs for all data converged on similar log likelihood scores and an identical consensus tree was constructed in each case. The analysis of the mitochondrial gene produced identical trees with unresolved relationships among several taxa (Figure 4-8) whereas the analysis of the nuclear genes was completely resolved with significant support for all nodes except two (Figure 4-8). The best resolution was achieved by concatenating the data and increased support was achieved by partitioning the concatenated molecular data (Figure 4-9).

Phylogenetic Analysis of Morphological Data

Maximum Parsimony Analyses. MP analysis of the unconstrained equally weighted morphological data (MP analysis #1) yielded 159 equally parsimonious trees with tree length of 257. The strict consensus tree is shown in Figure 4-10. Tree number one had a consistency index of 0.5447, retention index of 0.7588, a composite index of 0.4658, homoplasy index of 0.4553, homoplasy index excluding uninformative characters of 0.5342, and a rescaled consistency index of 0.4133. The trees were rooted using outgroup method.

MP analysis of the unconstrained reweighted morphological data (MP analysis #2) yielded 4 most parsimonious trees. The strict consensus tree is shown in Figure 4-11. The 143 best trees before reweighing the characters had tree lengths of 257. The best-reweighted tree had a tree length of 114.36. This tree had a consistency index of 0.7988, retention index of 0.8981, a composite index of 0.6987, homoplasy index of 0.2012, homoplasy index excluding uninformative characters of 0.3013, and a rescaled consistency index of 0.7174.

MP analysis of the concatenated molecular and morphological data for eight taxa (MP analysis #3) yielded two trees with tree length of 1010 before reweighting of characters, and one tree with length 618.33333 after reweighting the characters. This reweighted tree had a consistency index of 0.9725; homoplasy index of 0.0275, consistency index excluding uninformative characters of 0.9232, homoplasy index excluding uninformative characters of 0.0768, retention index of 0.9408, and rescaled consistency index of 0.9149 (Figure 4-12). The tree produced in this analysis was used as the backbone constraint tree for MP analysis of the constrained reweighted data (MP analysis #4).

MP analysis of the constrained reweighted morphological data (MP analysis #4) yielded one tree (Figure 4-13) with tree length 262 before reweighting and 110.70 after reweighting. This tree had a consistency index of 0.8121, homoplasy index of 0.1879, consistency index excluding

uninformative characters of 0.7139, homoplasy index excluding uninformative characters of 0.2861, retention index of 0.9065, and rescaled consistency index of 0.7362. This was the shortest tree and forms the basis for the discussion of character evolution across *Heraclides*.

Hypothesis testing. The Templeton (Wilcoxon signed-ranks) tests failed to reject the following null hypotheses. 1) The unconstrained tree with reweighted characters is of equal length to the unconstrained tree with equally weighted characters ($P = 1.0000$). 2) The constrained tree with reweighted characters is of equal length as the unconstrained tree with equally weighted characters ($P = 0.0896$). 3) The constrained tree with reweighted characters is of equal length as the unconstrained tree with reweighted characters ($P = 0.1444$). Trees created before the introduction of assumptions (reweighting characters and constraining the tree) were not significantly different but better resolution was achieved (as evidenced by the bootstrap values of the nodes) through the implementation of these assumptions.

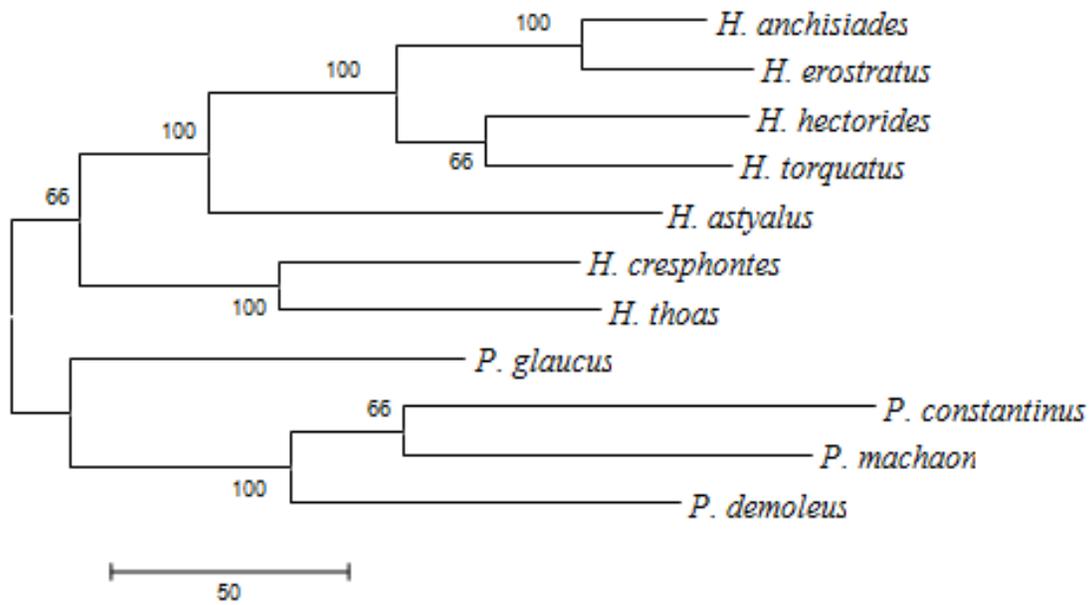


Figure 4-1. The strict consensus tree inferred from 3 most parsimonious trees for mitochondrial genes. Tree rooted at midpoint with bootstrap values above nodes (50% cut-off).

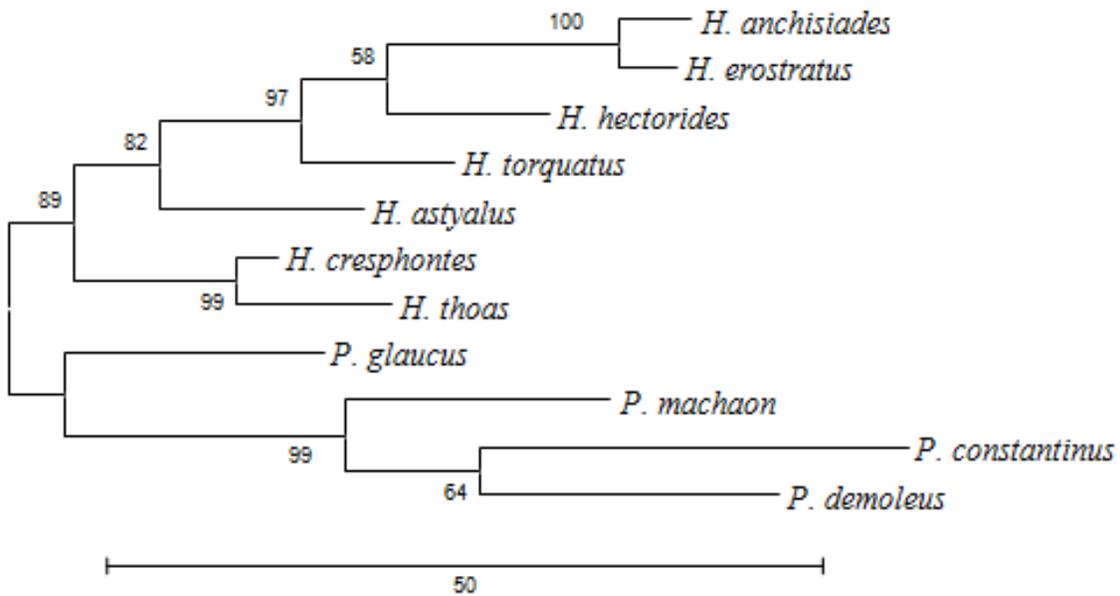


Figure 4-2. The most parsimonious tree for the nuclear genes. Tree rooted at midpoint with bootstrap values above nodes (50% cut-off).

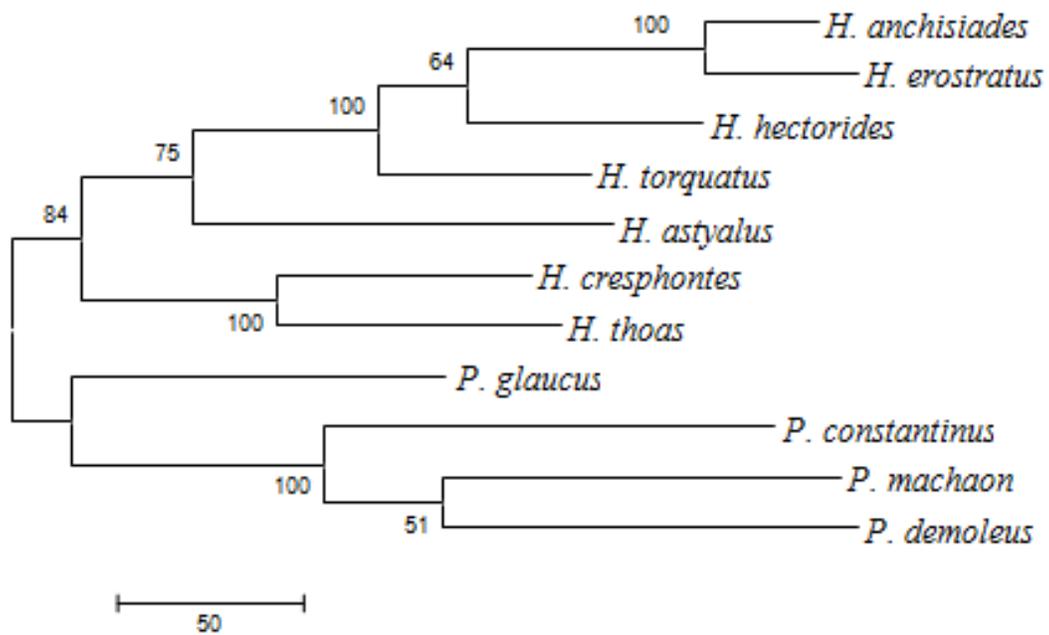


Figure 4-3. The most parsimonious tree for the concatenated molecular data set. Tree rooted at midpoint with bootstrap values above nodes (50% cut-off).

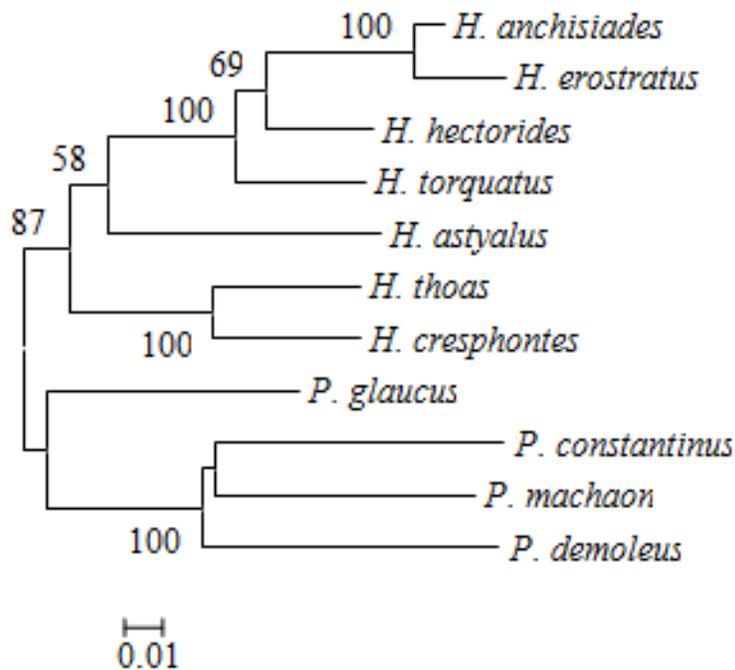


Figure 4-4. Phylogenetic tree inferred from ML analysis of mitochondrial genes. Tree rooted at midpoint with bootstrap values above nodes (50% cut-off).

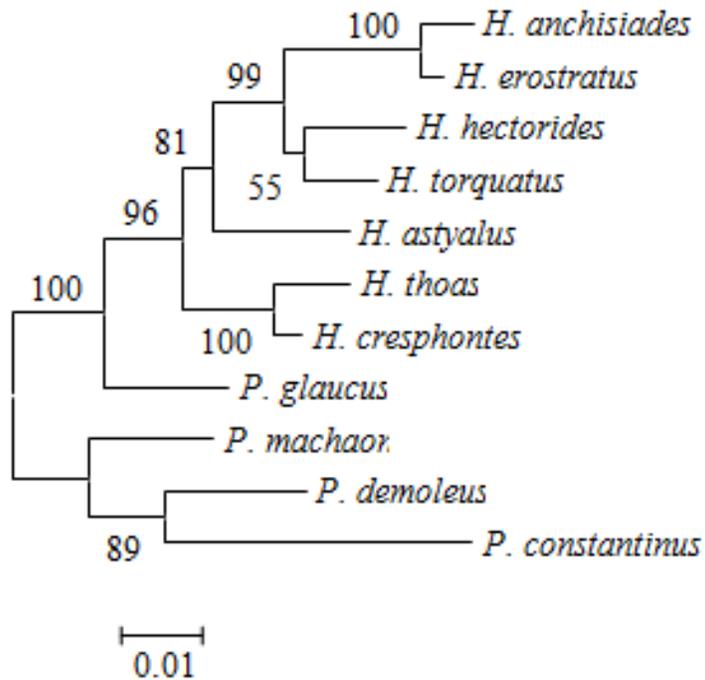


Figure 4-5. Phylogenetic tree inferred from ML analysis of nuclear genes. Tree rooted at midpoint with bootstrap values above nodes (50% cut-off).

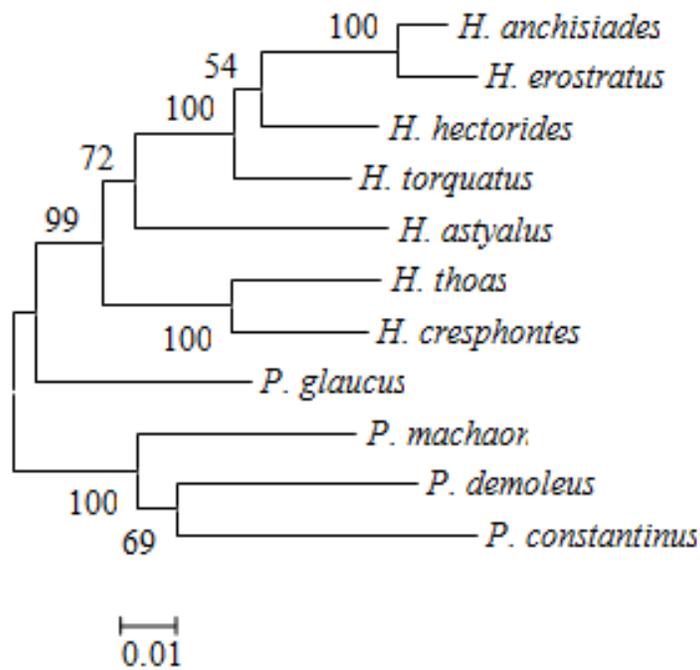


Figure 4-6. Phylogenetic tree inferred from ML analysis of the concatenated data set. Tree rooted at midpoint with bootstrap values above nodes (50% cut-off).

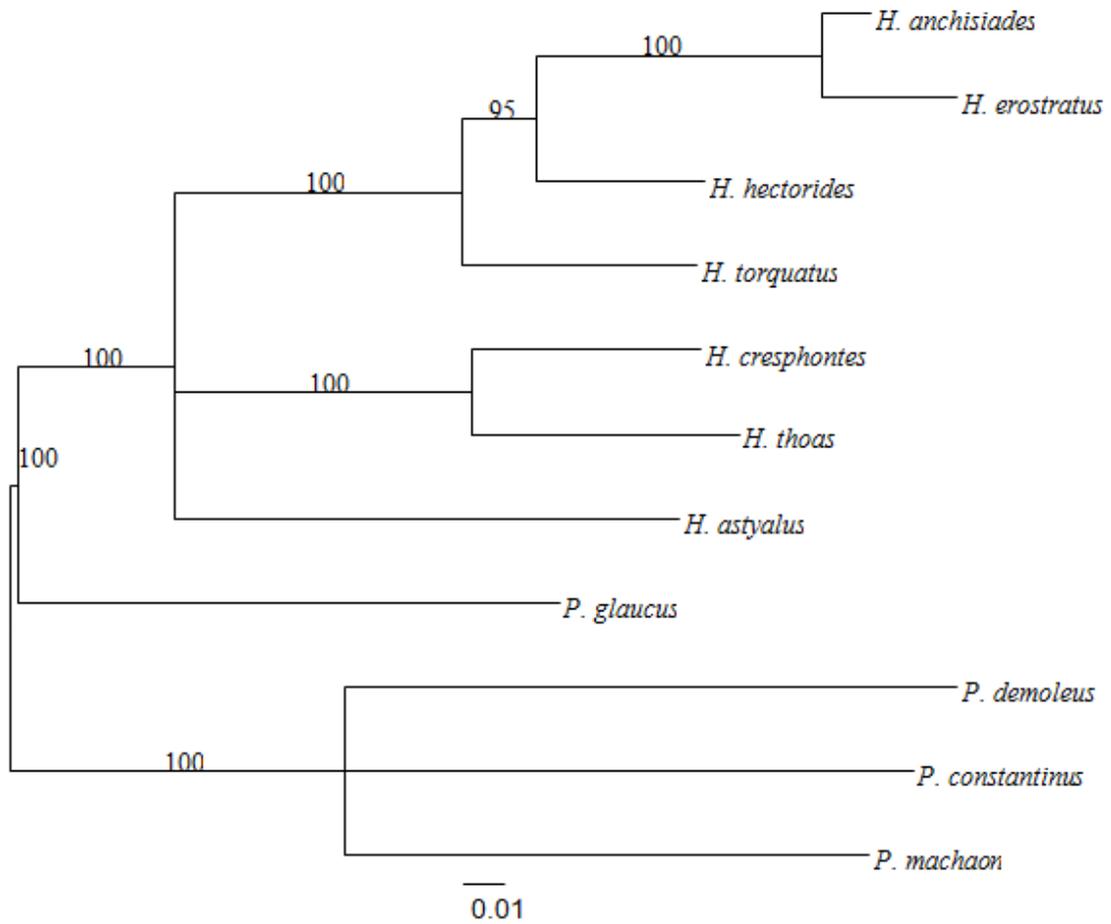


Figure 4-7. Phylogenetic tree inferred from Bayesian analysis of mitochondrial genes. Numbers above the branches indicate Bayesian posterior probabilities with $\geq 95\%$ taken as an indication of significant support. Tree rooted at midpoint.

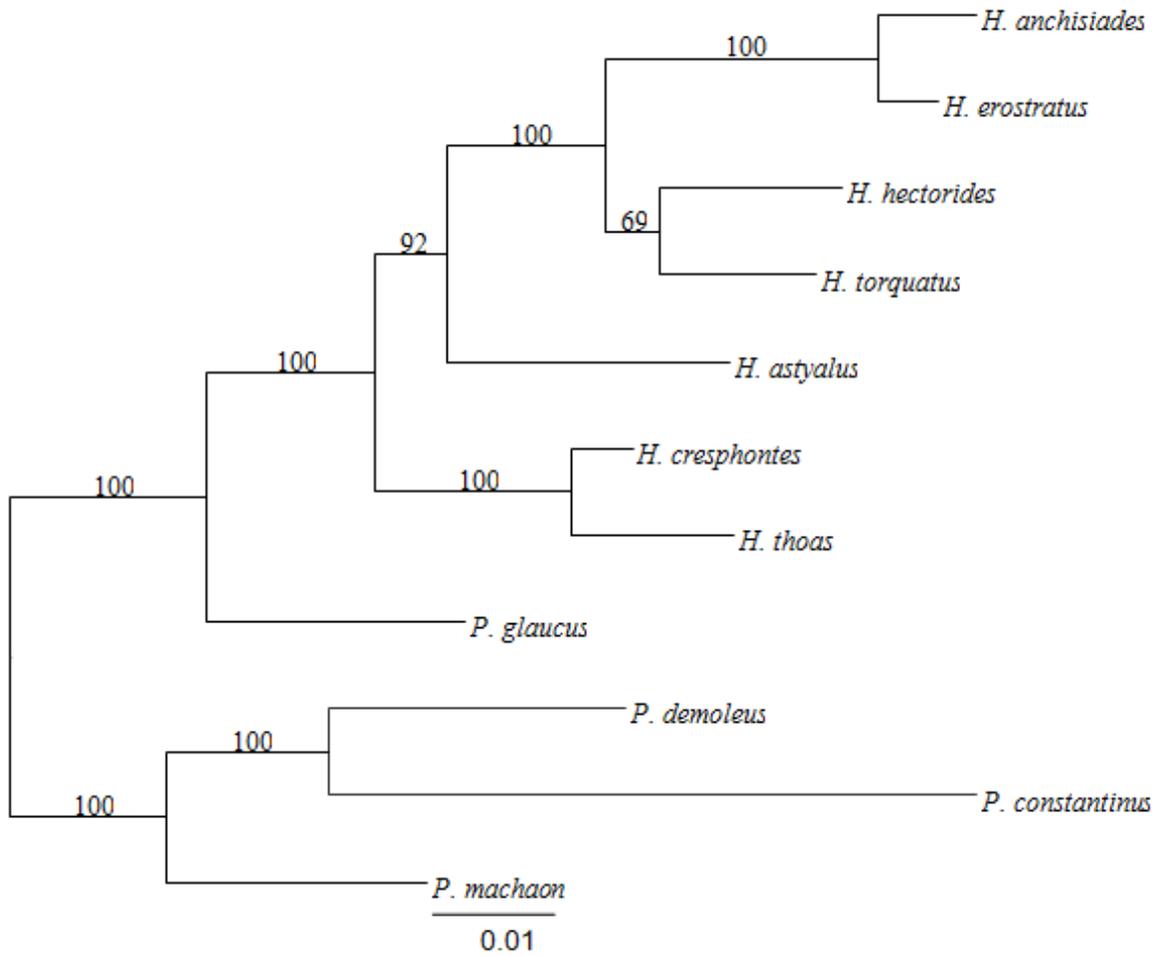


Figure 4-8. Phylogenetic tree inferred from Bayesian analysis of nuclear genes. Numbers above the branches indicate Bayesian posterior probabilities with $\geq 95\%$ taken as an indication of significant support. Tree rooted at midpoint.

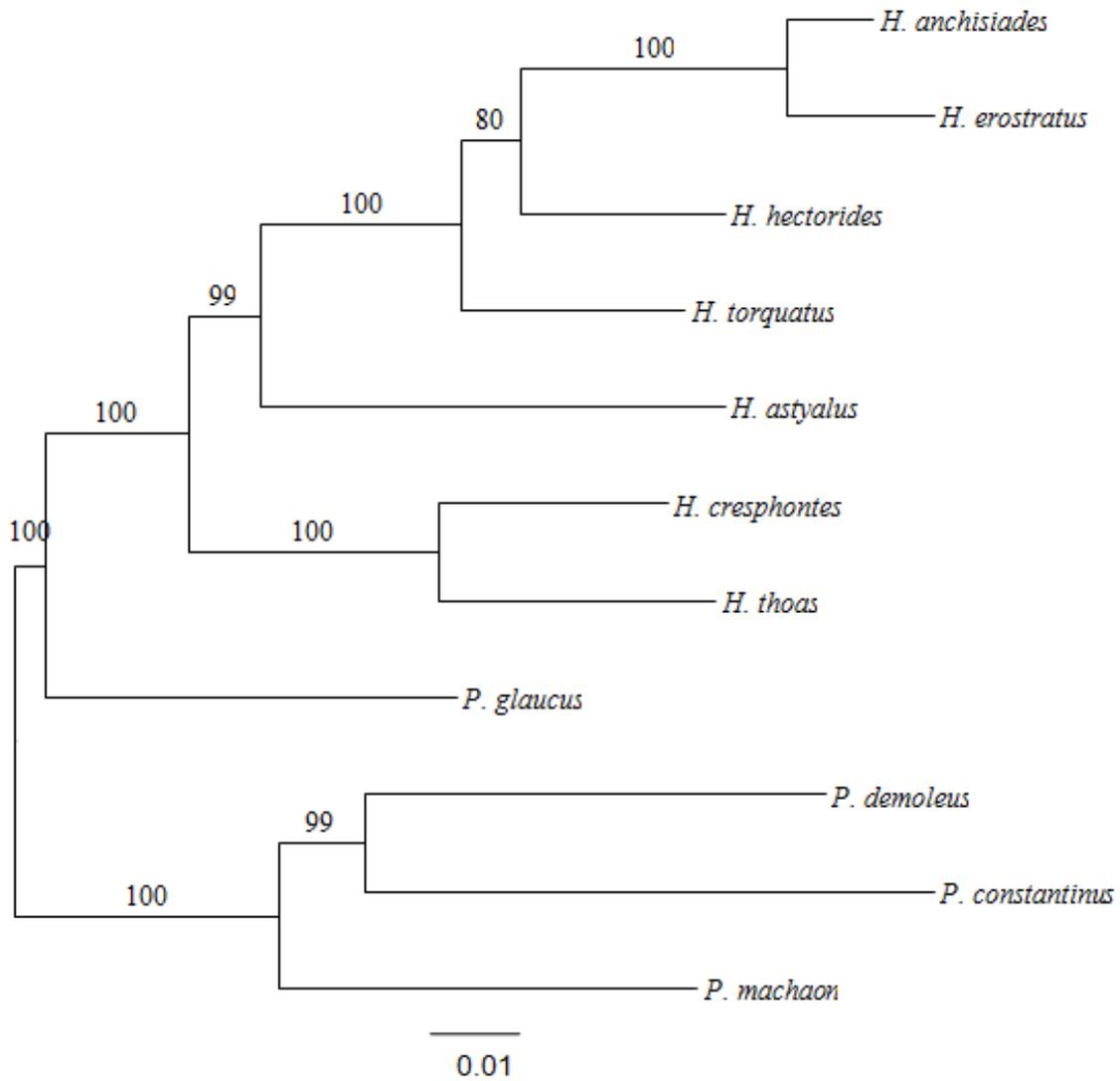


Figure 4-9. Phylogenetic tree inferred from Bayesian analysis of the partitioned concatenated data set. Numbers above the branches indicate Bayesian posterior probabilities with $\geq 95\%$ taken as an indication of significant support. Tree rooted at midpoint. The tree obtained from an analysis of the unpartitioned concatenated data was identical with marginally lower support at the node for *H. torquatus*. The same topology and similar posterior probabilities and branch lengths also resulted from an analysis of the concatenated data without the 68 bp of *tRNA-leucine*.

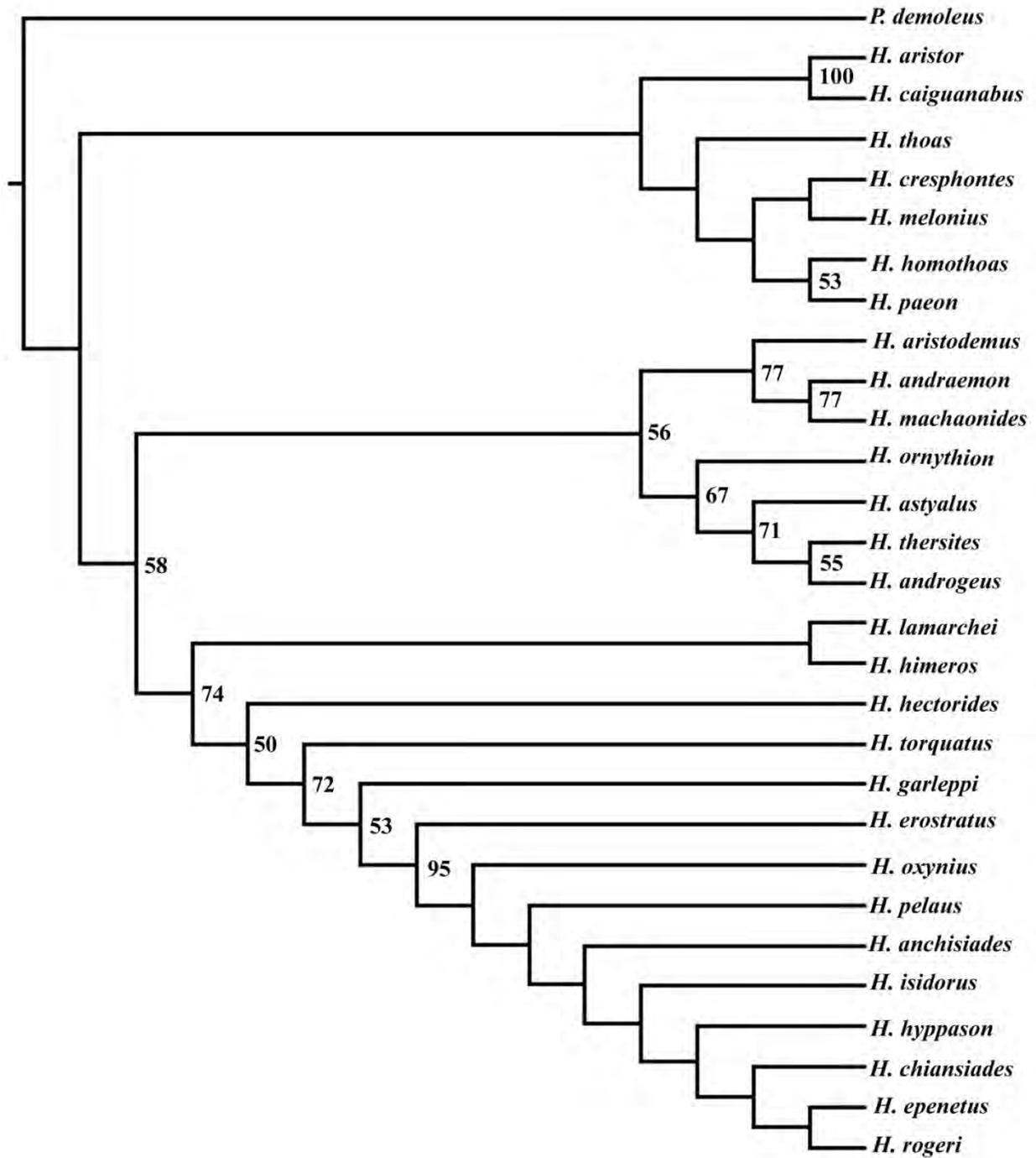


Figure 4-10. Strict consensus tree of the 159 equally parsimonious trees inferred from MP analysis of the unconstrained equally weighted morphological data (MP analysis #1). Tree rooted by the outgroup method. Node labels are bootstrap values $\geq 50\%$.

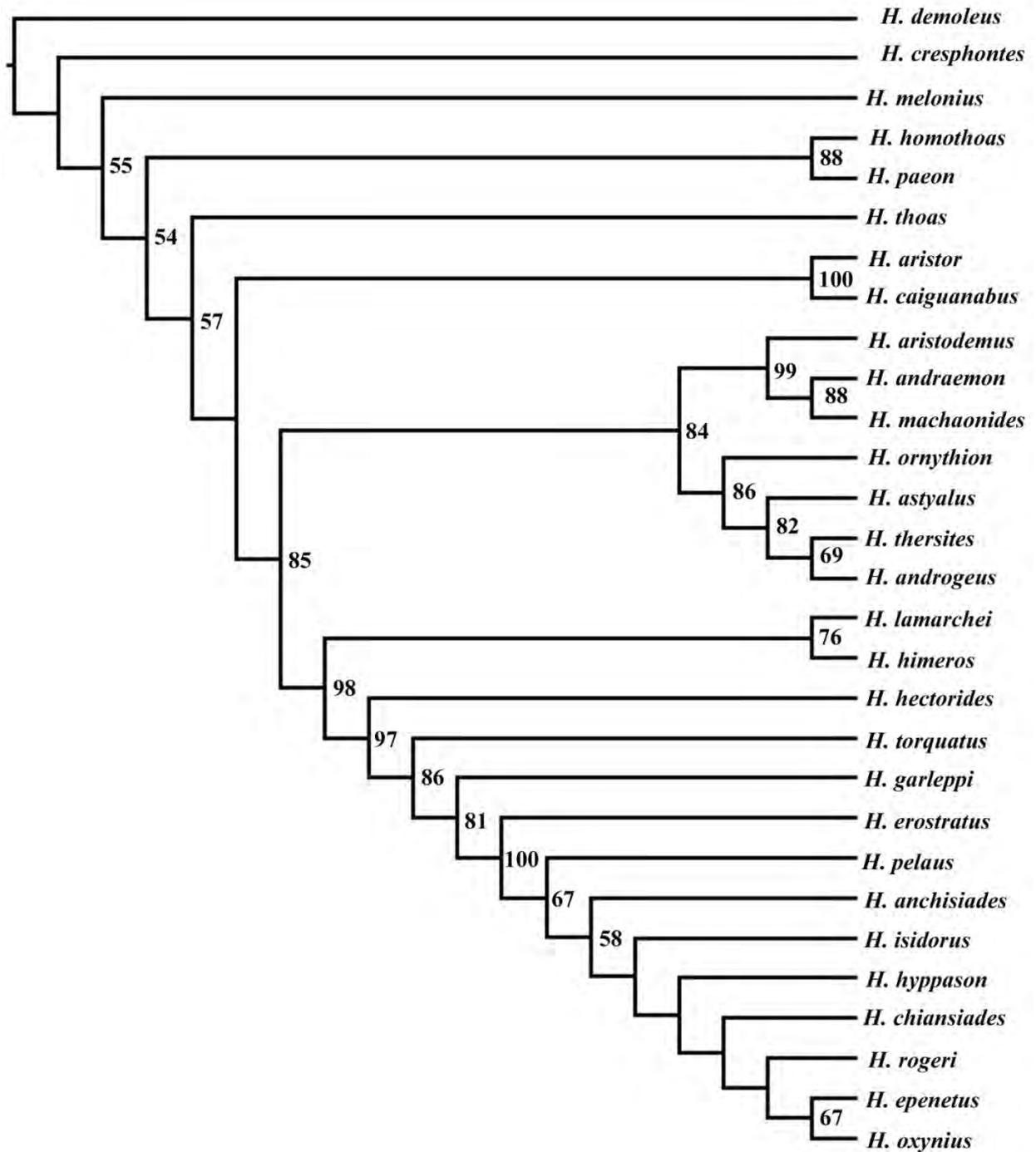


Figure 4-11. Strict consensus tree of the four most parsimonious trees from MP analysis of the unconstrained reweighted morphological data (MP analysis #2). Tree rooted by the outgroup method. Node labels are bootstrap values $\geq 50\%$.

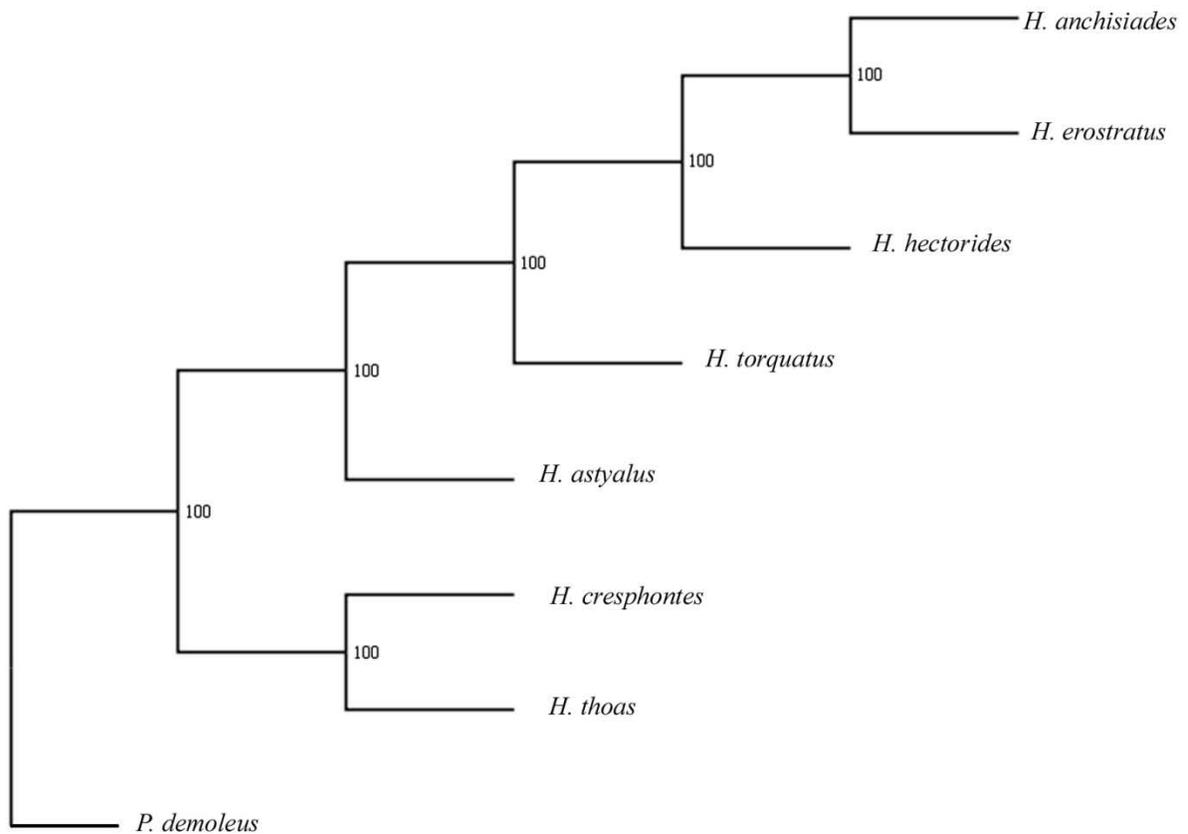


Figure 4-12. Single most parsimonious tree inferred from the MP analysis of the concatenated molecular and morphological data for 8 taxa (MP analysis #3). Tree used as the backbone constraint tree for MP analysis of the constrained reweighted data (Figure 4-13). Tree rooted by the outgroup method. Node labels are bootstrap values $\geq 50\%$.

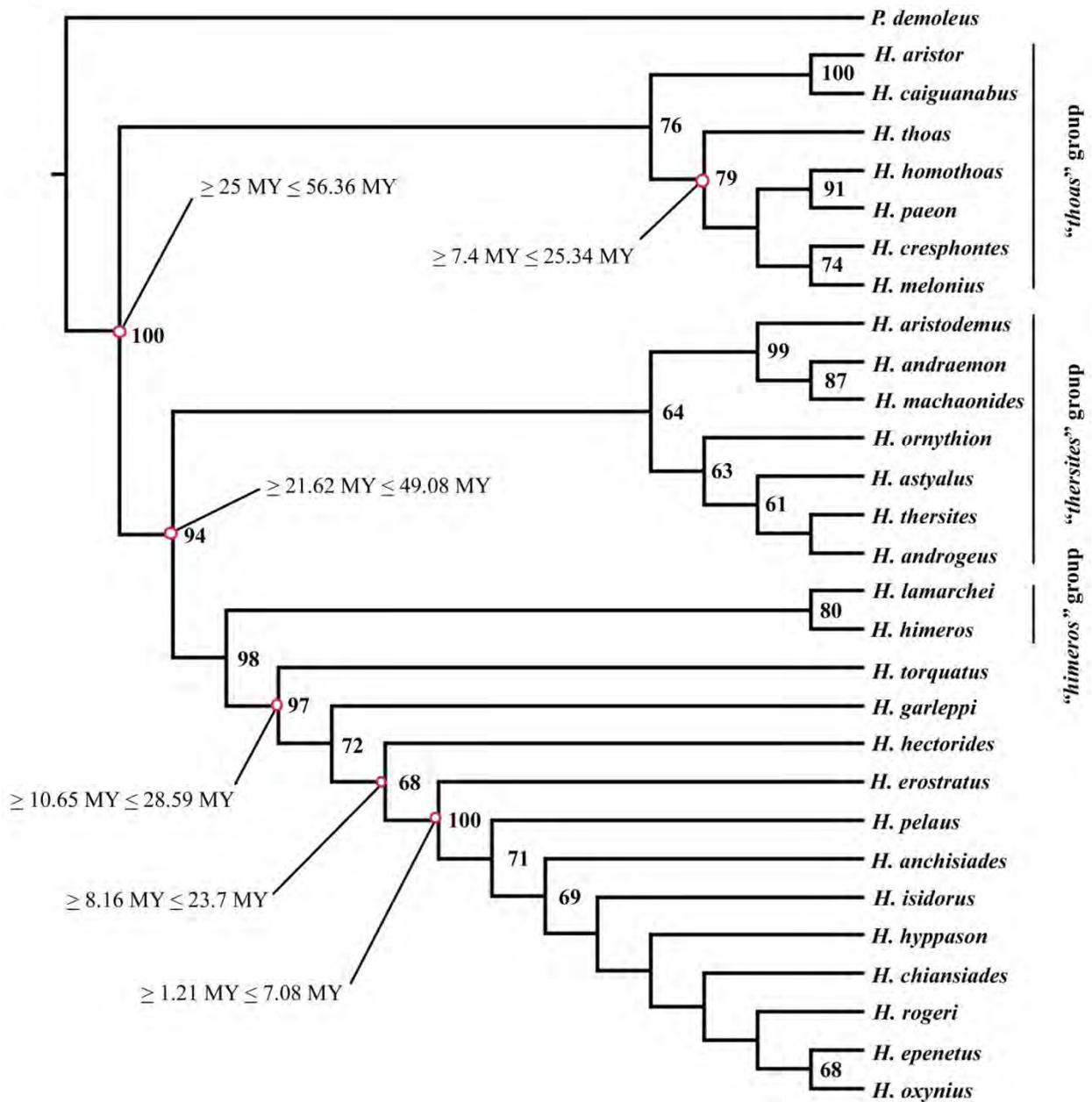


Figure 4-13. Cladogram showing the single most parsimonious tree inferred from the MP analysis of the constrained reweighted morphological data (MP analysis #4). Tree in Figure 4-12 used as the backbone constraint. Tree rooted by the outgroup method. Node labels are bootstrap values $\geq 50\%$. Age estimates in millions of years for specified nodes taken from Zakharov et al. (2004)¹.

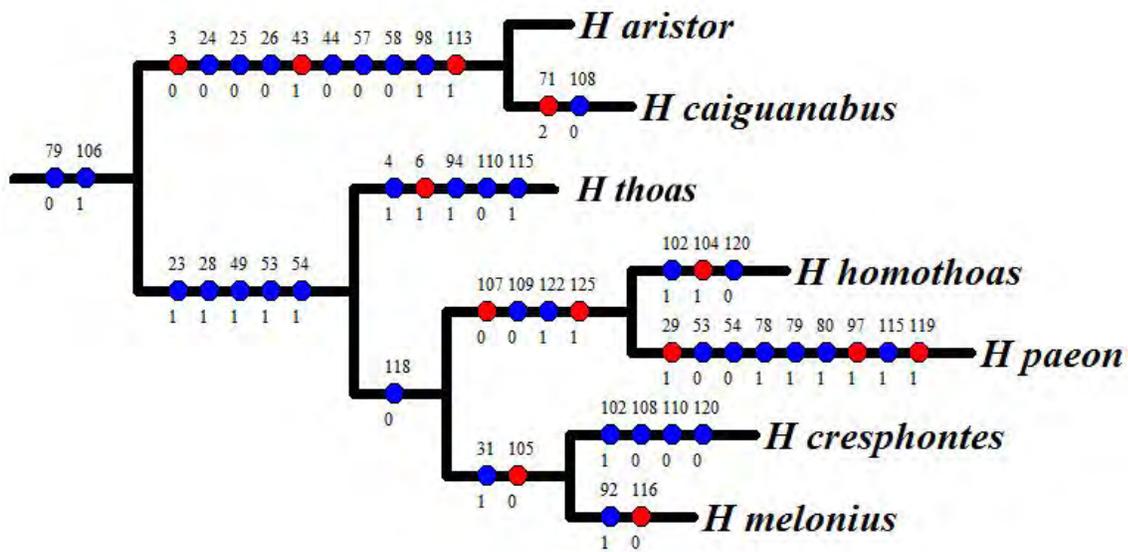


Figure 4-14. Cladogram showing only unambiguous character state changes for the “thoas” subgroup from the MP analysis of the constrained reweighted morphological data (Figure 4-13). Numbers above branches are characters numbers; numbers below the branches are character states. Red circles indicate nonhomoplasious changes (synapomorphies or autapomorphies) whilst blue dots indicate homoplasious changes.

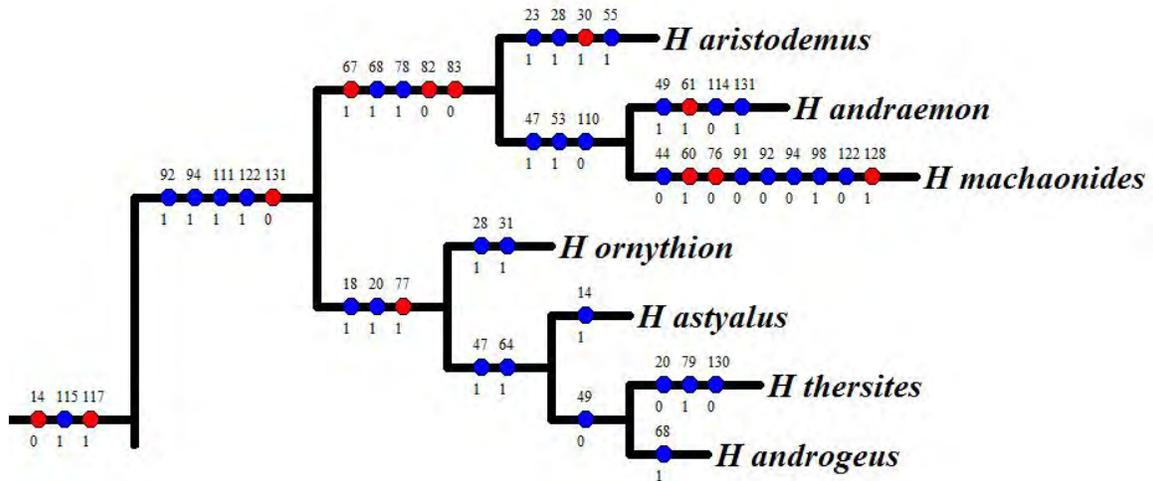


Figure 4-15. Cladogram showing only unambiguous character state changes for the “thersites” subgroup from the MP analysis of the constrained reweighted morphological data (Figure 4-13). Numbers above branches are characters numbers; numbers below the branches are character states. Red circles indicate nonhomoplasious changes (synapomorphies or autapomorphies) whilst blue dots indicate homoplasious changes.

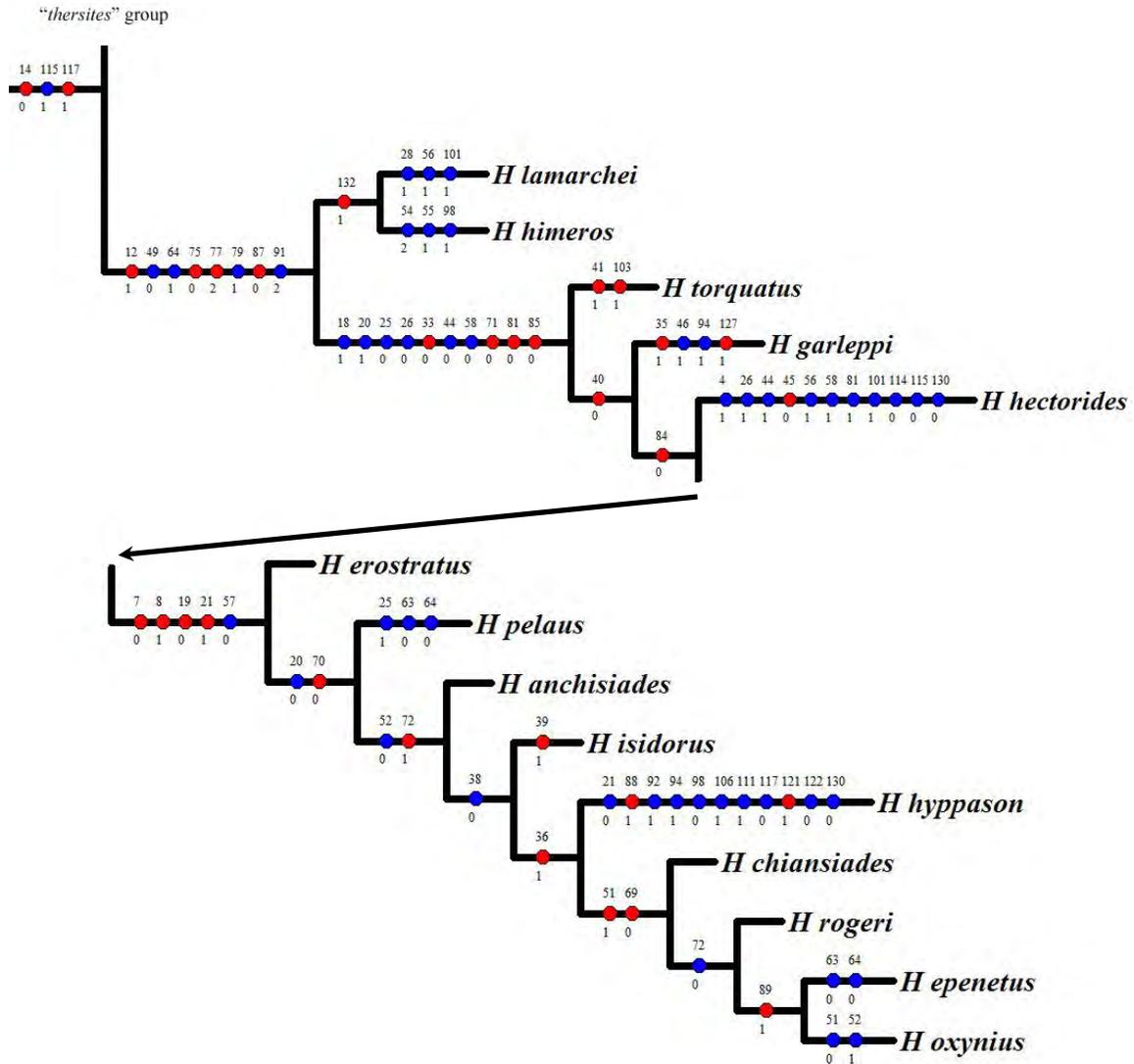


Figure 4-16. Cladogram showing only unambiguous character state changes for the “himeros” subgroup and the remaining taxa from the MP analysis of the constrained reweighted morphological data (Figure 4-13). Numbers above branches are characters numbers; numbers below the branches are character states. Red circles indicate nonhomoplasious changes (synapomorphies or autapomorphies) whilst blue dots indicate homoplasious changes.

CHAPTER 5
HERACLIDES PHYLOGENY

Molecular Phylogeny

The results for the reanalysis of the molecular data mirror work done previously showing that the topology of the group based on seven species of *Heraclides* is relatively stable when a variety of different approaches were implemented. The use of Bayesian analysis on a partitioned concatenated data has not been shown for this group previously. The results from this analysis mirrors the results from the unpartitioned data, but gave stronger support at various nodes. By combining the genes and analyzing them in a partitioned way, stability was achieved in the overall topology with significant increase in support for some poorly supported nodes. However, it should be noted that posterior probabilities are known to be exaggerations of node support when compared to bootstrap values. Bayesian posterior probability is a function of a prior probability and the likelihood of the data under an assumed model. Reasons for this exaggeration in posterior probabilities is not yet fully understood as it is difficult to compare these values with bootstrap values in an objective way (Erixon et al., 2003). With this in mind, posterior probabilities were only considered strong support if they were > 95% (the default for bootstrap is > 50%).

Analysis of the mitochondrial genes (COI, tRNA-leu and COII) revealed a similar topology across the three analyses (MP, ML and Bayesian). Bayesian analysis (Figure 4-7) revealed the same topology for the species as ML (Figure 4-4) but differed from MP (Figure 4-1) in the treatment of *H. astyalus*, *H. hectorides* and *H. torquatus*. In MP (Figure 4-1), *H. hectorides* and *H. torquatus* are shown as sister taxa but the support for this is weak. They do not show up as sister taxa in the trees produced from the Bayesian (Figure 4-7) and ML (Figure 4-4) analyses. The position of *H. astyalus* in relation to the remaining *Heraclides* species included in

the analysis is also unresolved in Bayesian analysis. The out-group topology was also different between analyses. In the Bayesian analysis, the relationship between *P. demoleus*, *P. constantinus* and *P. machaon* is unresolved and shows up as a polytomy (Figure 4-7).

Analysis of the nuclear gene (EF-1 α) revealed a similar topology across the three analyses (MP, ML and Bayesian). Bayesian analysis (Figure 4-8) revealed the same topology for the species as the ML analysis (Figure 4-5). MP analysis (Figure 4-2) differed in the relationship of *H. hectorides* and *H. torquatus*, as the sister relationship seen in the other two analyses breaks down in the MP analysis; also, *P. glaucus* does not show up as sister to the *Heraclides* species. Differences between gene trees from mitochondrial genes and gene trees from nuclear genes are not surprising. Mitochondrial genes are maternally inherited and effectively haploid (1/4th population size of nuclear genes). Mitochondrial genes evolve at a much faster rate than nuclear genes (Moore, 1995) which may cause different topologies based on the type of analysis utilized.

Analysis of the concatenated data (COI, tRNA-leu, COII and EF-1 α) revealed a similar topology across the three analyses (MP, ML and Bayesian; Figure 4-9). Partitioned homogeneity tests revealed incongruence and revealed that tRNA-leucine was responsible for incongruence in the data. Removal of the 68 bp of tRNA-leucine from the concatenated data set, however, had no effect on the topology, but the partitioned homogeneity test suggested that there might be some advantage of treating the genes as partitions. The phylogenetic tree inferred from a Bayesian analysis of the partitioned concatenated data (Figure 4-9) was identical to the inferred relationships from the unpartitioned data but with stronger support. All posterior probabilities were > 95% except for the node corresponding to *H. hectorides* (80%). This suggests that support for this node is not sufficient.

Morphological Phylogeny

The main character previously suggested as synapomorphic of this genus is the shape of the juxta. This character was found to be the most consistent among the *Heraclides* by Munroe (1961) and Hancock (1983). Miller (1987) did not regard this character as evidence for *Heraclides* monophyly, but with additional support from molecular data, the monophyly of this group seems convincing enough to justify its status at the genus level. It should be noted that at least one other species possess similar juxta, *Pterourus [Papilio] victorinus* (Miller, 1987), but the juxta in *Heraclides* is much simpler and always smooth as opposed to being rough in *P. victorinus*. This similarity can also be explained by previous hypotheses that place *Pterourus* as the sister group to the *Heraclides*. Because they are so closely related, it is not surprising that it is difficult to tease out the relationships based solely on genitalia characters. A detailed study of the *Pterourus* is needed to establish characters for this group as well as augment the characters for the *Heraclides*. By doing so, more synapomorphic characters may be discovered for the *Heraclides* as well as for the *Pterourus*.

Maximum parsimony of the 133 morphological characters revealed a tree topology congruent with the topology of the molecular data. This congruence is further evidence that the topology and group structure presented is well supported. It should be noted, however, that the initial analysis of the unconstrained equally weighted characters did not provide strong support for many nodes of the consensus tree for the 159 equally parsimonious trees (Figure 4-10). In this case, strong support is considered as bootstrap values greater than or equal to 70%. In an attempt to get better resolution, the unconstrained data was reweighted by the maximum value of the rescaled consistency indices. This was done until the tree length remained constant. This analysis produced four most parsimonious trees and a strict consensus with increased node support for most nodes not previously strongly supported in the equally weighted analysis.

(Figure 4-11). Even though the support for major nodes had increased, the basal clades were not well resolved.

To better understand if the morphological data was giving different signals from the molecular data, the molecular data available for seven species of the genus *Heraclides* and the outgroup taxon was joined with the morphological data for these species and analyzed under maximum parsimony. The resulting tree revealed very strong support for all the nodes (Figure 4-12) and a topology that reflects the topology produced by the molecular data alone and the morphological data alone. To produce a more stable topology, the tree produced from the concatenation of the molecular and morphological data was used as a backbone constraint on the total morphological data. The resulting single most parsimonious tree (Figure 4-13) revealed strong support for the major nodes and a stable topology; this topology serves as support for hypothesized subgroup structure and species treatments. There was a concern that the trees produced in the different analyses were introducing biases. As such, Templeton (Wilcoxon signed-ranks) tests were conducted. These tests revealed that the length of the trees was not significantly different between analyses, removing any concern that biases introduced created significant change in tree lengths. While no significant changes in tree length occurred, a better resolution of the relationships among the species of *Heraclides* was achieved.

Group Structure and Biogeography

The first clade in the *Heraclides* is the “*thoas*” subgroup. This is supported by the following homoplasious characters: the proximal post-discal spots on the ventral hind wing being in cells m2-m3, m3-cu1 (sometimes present in m1-m2); an uncus as paired horn-like processes (Figure 4-14). While these two characters are homoplasious ones, I believe that they provide good support for this clade. The uncus as a paired structure is seen in only one other species of *Heraclides*, *H. hyppason*. This species may have developed this trait through convergence, as it

appears to have several derived characters not seen in the other similar species. The other supporting character, the location of the proximal post-discal spots on the ventral hindwing appears to be a derived character and not the most basal state of the character. This character can also be seen in only one other member, *H. andraemon*, a member of the sister subgroup, the “*thersites*” subgroup. Seven species comprise this clade, *H. thoas*, *H. cresphontes*, *H. melonius*, *H. homothoas*, *H. paeon*, *H. aristor*, and *H. caiguanabus*. A number of synapomorphies supports relationships among these species and five of the seven species are supported by autapomorphies. The Caribbean endemics, *H. aristor* and *H. caiguanabus*, are supported by three synapomorphies: the absence of the use of Rutaceae as hostplants; the dorsal forewing central band missing elements in cells cu1-cu2, cu2-1a, and 1a-2a, but having the costal branch; and the male genitalia with broad (or wide) juxta arms. Seven other homoplasious characters support the relationship between these two species. These Caribbean endemics perhaps diverged from the common ancestor shared with the rest of the *Heraclides* between 25 and 56.36 Million years ago (around the middle of the Cenozoic era) (Figure 5-1). This potentially means that the other members, being predominantly mainland species, are derived from an ancestor that could possibly be of Caribbean origin or that the Caribbean endemics share a mainland progenitor with the rest of the subgroup. One other Caribbean endemic, the Jamaican *H. melonius*, is nested among the mainland species. Its relationship to *H. cresphontes* is supported by a narrow pseuduncus and the overall structure of the male and female genitalia. Quite possibly, this could be an invasion of Jamaica by an ancestor shared with *H. cresphontes*, a mainland species. The sister relationship between the mainland species *H. homothoas* and *H. paeon* is supported by two synapomorphies, the paired, horn-like uncal processes on the male genitalia are not bifid, and the female genitalia with the paired ventrally extended vestibular processes as raised blunt arms. *H.*

thoas is the only *Heraclides* that utilizes Araceae as host plants. The use of Rutaceae and Apiaceae/Umbelliferae is most likely an ancestral trait for the *Heraclides*.

The second clade is the “*thersites*” subgroup which is supported by the ventrad projection of the female genitalia being knob-like, a synapomorphy. Other homoplasious characters supporting this clade are: a tooth-like projection on the dorsal edge of the harpe on male genitalia; one large spine on the ventral surface of the harpe; the aedeagus strongly curved throughout (appearing arch-like throughout); and the female genitalia with peripheral vestibular plates extended ventrally into processes (Figure 4-15). Seven species comprise this clade, *H. thersites*, *H. androgeus*, *H. astyalus*, *H. ornythion*, *H. aristodemus*, *H. andraemon*, and *H. machaonides*. As with the previous clade, the Caribbean endemics are more closely related to each other than to the rest of the mainland species. This subgroup, along with the remaining species, forms a clade that possibly diverged from the common ancestor shared with the “*thoas*” subgroup around the middle of the Cenozoic era (Figure 5-1). They are supported by two synapomorphies of having a circular cephalic profile in the pupae and the structure dorsad of the ostium on the female genitalia present as a small evagination. The trend of having most of the the Caribbean endemics being more closely related to each other than to the rest of the mainland species, with one Caribbean species, a Jamaican endemic, nested within the mainland species, also observed in the “*thoas*” subgroup, is repeated here (Figure 5-1). This Caribbean clade within the “*thersites*” subgroup is supported by three synapomorphies. These are: the presence of inner post-discal spots on the dorsal hindwing of males; the inner post-discal spots on the ventral hindwing of males diffused; and the inner post-discal spots on the ventral hindwing of females diffused. The relationships within this basal clade (*H. aristodemus*+*H. andraemon*+*H. machaonides*) are strongly supported by bootstrap values but no synapomorphic characters,

although several homoplasious characters are present. The species are however easily separated based on general wing patterns and autapomorphies. The remaining members of this subgroup, (*H. ornythion*+*H. astyalus*+*H. thersites*+*H. androgeus*), are supported by the synapomorphic character - proximal post-discal spots on the ventral hind wing being crescent shaped. The relationships among the members of this clade are not easily ascertained by morphological data, as is evident by the lack of nonhomoplasious characters, and may be best resolved by molecular data. The progenitor of the “*thersites*” subgroup was in all probability a mainland species and there was a possible invasion of the Caribbean in the form of *H. thersites* and one of the three subspecies of *H. androgeus*. The fact that one subspecies of a mainland species can be found throughout the Caribbean, with a sister species being a Caribbean endemic speaks volumes to the constant colonization of the Caribbean by progenitors of the Caribbean members of *Heraclides*. Zakharov et al. (2004^a) theorizes that New World swallowtails were established in South America before the end of the Eocene (~ 35 MYA) and that *Heraclides* evolved during this time.

The progenitor of the remaining taxa is believed to have diverged from the “*thersites*” subgroup (21.62 and 49.08 million years ago) after the “*thersites*” subgroup diverged from the “*thoas*” subgroup (between 25 and 56.36 million year ago). The divergence of these taxa from the “*thersites*” subgroup likely occurred subsequent to an invasion of the Caribbean after the formation of the Greater Antilles; the exact timing of this is not known but based upon the trends seen here this is probable. The loose connection shared between the Caribbean and the mainland around 60 MYA (Zakharov et al., 2004^a) would easily facilitate invasion. After diverging for some time in the Caribbean, additional members of *Heraclides* possibly invaded Jamaica giving rise to *H. melonius* and *H. thersites* possibly through short overwater dispersal or through brief connections with northern Central America around the middle of the Cenozoic (Donnelly, 1988).

I believe that the invasion of Jamaica by the progenitors of *H. melonius* and *H. thersites* is a relatively recent event. Brown and Heinemann (1972), and Smith et al. (1994) treat *H. melonius* as being related to *H. thoas*, possibly a subspecies or being derived from that stock. The results here show that this is not the case. It is more likely that *H. melonius* is more closely related to *H. cresphontes*, being derived from that species or the progenitor of both species. Thus, it is plausible that the Caribbean islands have endured several cycles of invasion events making any attempts at tracing the origin of taxa quite challenging. Brown and Heinemann (1972) suggest that the fauna of the Caribbean can be accounted for by seeing them as an accretion of occasionally acquired species over an extended period.

The relationship among the remaining species is supported by the following synapomorphies: raised bumps on the 5th instar larva; cell cu-1a on the dorsal hindwing without with an eyespot; proximal post-discal spots on the ventral hindwing being oval; and a lack of a well defined eyespot in cell cu-1a on the ventral hind wings. Additionally, the following homoplasious characters can be useful in defining this clade: the absence of sub-marginal spots on the dorsal forewing; the presence of proximal post-discal spots on the dorsal hindwing of females. The spoon shaped harpe on the male genitalia becomes roughly triangular shaped in *H. garleppi*, *H. anchisiades*", and similar taxa (Figure 4-16). The third subgroup, the "himeros" subgroup (*H. himeros*+*H. lamarchei*) branches from the remaining species and is supported by one synapomorphy, the female genitalia has a deep trough between the peripheral vestibular plates and the long ridge-like process parallel to the vestibular plates. The remaining taxa are supported by four synapomorphies with most of the remaining species of separated by strong autapomorphies (Figure 4-16).

H. anchisiades and similar species are believed to have diverged between 1.21 and 7.08 million years ago (Figure 5-1). They are strongly supported by four synapomorphies: females placing eggs on the ventral surfaces of leaves; eggs are laid as tight bunch of many ordered eggs and the larvae are gregarious; mimetic patterns not limited to females; and red spots on the side of the thorax and abdomen. Additionally, the dorsal hindwing of males lack a central band. Of note is *H. hyppason*, which lacks the red spots on the thorax and abdomen but possesses a red spot at the base of the hindwing. Nine species bear striking similarity to each other, *H. anchisiades*, *H. isidorus*, *H. rogeri*, *H. erostratus*, *H. pelaus*, *H. epenetus*, *H. oxynius*, *H. chiansiades*, and *H. hyppason*. These species are not well supported by autapomorphies, in fact, it is extremely difficult to separate these species (with the exception of *H. hyppason*) using genitalia alone. Because of the closeness of these taxa, and their recent divergence time estimation, I suspect that they are still actively involved in the speciation process. In fact, several of these species are known to hybridize (Tyler et al., 1994) and possibly produce viable offspring. This type of species-complex is regarded as a “superspecies” by Tyler et al. (1994) and underscores the complexity of the relationship among these species that makes it difficult to unravel; molecular work may prove helpful in the future. The placement of *H. hyppason* with these remaining species is questionable. The genitalia are quite different, being more similar to the genitalia of the “*thersites*” subgroup, and in the future, this taxon may prove to be quite different genetically. Until such time, its placement with these remaining species will remain questionable. Being predominantly mainland taxa, and having a recent divergence time (between 1.21 and 7.08 million years ago), one would expect to see recent evidence of a re-invasion of the Caribbean from these species, and in fact the Greater Antillean species *H. pelaus* and *H. oxynius* are evidence of this. Based on previous trends in this genus, I theorize that the progenitor of *H.*

pelaus first invaded either Jamaica or Cuba, and later invaded the remaining Greater Antillean islands, giving rise to the four subspecies currently recognized. The progenitor of the Cuban *H. oxynius*, (its mainland sister taxon is *H. epenetus*), is possibly the most recent invader of the Caribbean region, further evidence as to the complexity of faunal sharing between the Caribbean and the mainland.

Smith et al. (1994) and Miller and Miller (2001) accounted for the distribution of West Indian *Heraclides* by applying a modified biogeographic model previously presented. With the additional information provided from the above synthesis of the subgroup structure, I propose that the progenitors of five of the Caribbean species of *Heraclides* (*H. aristor*, *H. caiguanabus*, *H. aristodemus*, *H. andraemon*, and *H. machaonides*) arrived on the proto-Greater Antilles around 60 MYA when these island seeds were loosely connected to the mainland. This loose connection was lost as the proto-Greater Antilles drifted easterly towards their present locations. This allowed for the isolation and subsequent establishment of these Caribbean endemic species. Stock from the mainland *Heraclides* genus continued to invade the Caribbean. This occurred on at least five additional occasions, with the latest Caribbean invasions being that of *H. pelaus* and *H. oxynius*. Jamaica has had the most invasions with three of the five species found on the island (*H. melonius*, *H. thersites*, and *H. pelaus*). This may be due to its historical close ties to Central America by remnants of the Nicaraguan rise. This is by no means a completed story as much work remains in this group. Plans are to first concentrate on the Caribbean *Heraclides* fauna in the hopes that a detailed genetic analysis would be instrumental in deciphering the complex histories and perhaps shed more light on the biogeography of the genus. The genetics of these unresolved taxa need to be investigated in an attempt to unfold the complex relationship among these closely related species.

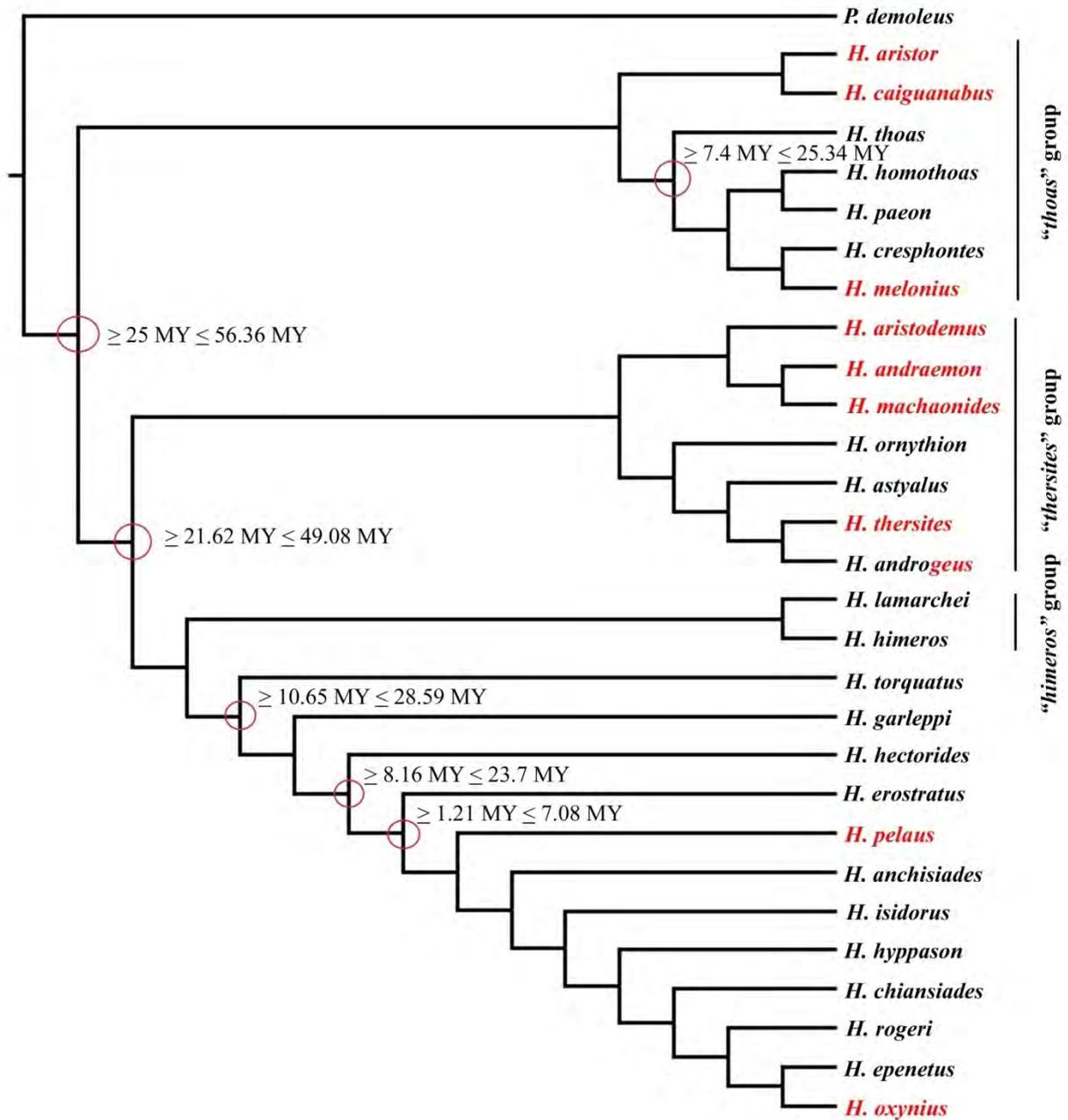


Figure 5-1. Cladogram showing the distribution of Caribbean taxa (in red) and the proposed dates for the divergence of specified nodes. *H. androgeus* is partially red to indicate one subspecies found in the Caribbean. Age estimates in millions of years for specified nodes taken from Zakharov et al. (2004)¹.

CHAPTER 6
SPECIES ACCOUNTS FOR THE GENUS *HERACLIDES*

***Heraclides* Hübner, 1819**

Heraclides Hübner, 1819: 83. Type *Papilio thoas* Linnaeus, 1771.

Calaides Hübner, 1819: 86. Type *Papilio androgeus* Cramer, 1775.

Priamides Hübner, 1819: 87. Type *Priamides hipponous* Hübner, 1819.

Troilides Hübner, 1825: pl. 111, 2f. Type *Troilides tros* Hübner, 1825.

Thoas Swainson, 1833: pl. 121. Type *Papilio thoas* Linnaeus, 1771.

Diagnosis and Variation. Primarily feeders of Rutaceae with some also feeding on Piperaceae; very few feed on other plant families. Eggs are spherical, whitish, pale green or yellowish often turning to brown before hatching and laid singly or in a cluster on the host plant. The larvae are in two main forms: solitary without rows of tubercles; or gregarious and always with a pair of dorsal rows of tubercles. In the adults, the antennal shaft is black with typical swollen terminal segments; palpus very scaly, short, less than ½ length of frons, erect (not porrect). Pectus with long scales; tegula generally black often edged with yellow scales on inner margin; tarsi with spines; epiphysis present on foreleg; tibial spur formula 0-2-2; tarsal claws bifid. Wings are dark with yellow or white bands and/or spots on the forewing and yellow or red and blue spots on the hind wings. Some members of this group mimic the genus *Parides* (Troidini). The genitalia vary greatly but the single most stable character is that found in the juxta. All members of this group have a very simple and deeply emarginated U or V-shaped juxta, a character also corroborated by Munroe (1961) and Hancock (1983). Female genitalia are almost always well sclerotized with elaborate ostial armature.

Host Plant. Table 6-1 gives a list of the host plants of the species for the genus *Heraclides* (Beccaloni et al., 2008).

Distribution. Members of this genus are primarily Neotropical in distribution with some members occurring in sub-tropical and temperate areas. *H. cresphontes* can occur as far north as Ontario, Canada and *H. thoas* can be found as far south as Buenos Aires in Argentina.

Key to *Heraclides* Adults

- 1a. Ventral hindwing proximal postdiscal spots following the shape of the inhabited cell ...2
- 1b. Ventral hindwing proximal postdiscal spots crescent shaped17
- 1c. Ventral hindwing proximal postdiscal oval.....10
- 2a. Forewing and hindwing lacking a narrow but well defined central band.....3
- 2b. Forewing and hindwing with a narrow but well developed central band.....4
- 3a. Forewing upperside with 5 spots of the central band near costal edge; three spots larger than two.....*H. aristor*
- 3b. Forewing upperside with only one or two spots of the costal branch of the central band present; submarginal spots on the hindwing upperside yellow.....*H. caiguanabus*
- 4a. Hindwing underside with proximal postdiscal spots red, rectangular and in cells m1-m2, m2-m3, and m3-cu1; these proximal postdiscal spots extend the length of the cells until abutting against light blue inner postdiscal cells.....*H. melonius*
- 4b. Hindwing upperside with a well developed patch of red proximal postdiscal spots.....*H. aristodemus*
- 4c. Hindwing underside with proximal postdiscal spots small, sometimes absent.....5

- 5a. Hindwing underside with a large red discal spot bordered on the outer edge by blue scales; tail with a yellow border formed from the marginal spot running along the anal edge; the central spot at r5-m1 is triangular, never notched or broken.....*H. paeon*
- 5b. Tail with yellow border formed from the marginal spot running along the outer edge, with a yellow spot at the tip of the tail.....*H. himeros*
- 5c. Hindwing underside without a red discal cell.....6
- 6a. Hindwing deeply fluted, with central spot at r5-m1 on the forewing upperside being the largest.....*H. lamarchei*
- 6b. Hindwing not deeply fluted.....7
- 7a. Upperside with two yellow disjointed bars running across the forewing and hindwing with the edge of the central band parallel to the anal edge of the wing....*H. machaonides*
- 7b. Forewing upperside lacking disjointed bars but possessing well defined central band and submarginal spots.....8
- 8a. Hindwing upperside with distal edge of the central band straight; pseuduncus bifid.....*H. homothoas*
- 8b. Hindwing upperside with the distal edge of the central band bent at vein Sc.....9
- 9a. Visible notch at the base of the clasper.....*H. crespontes*
- 9b. No visible notch at the base of the clasper.....*H. thoas*
- 10a. Hindwing underside with a patch of red scales at the base of the wing.....*H. hyppason*
- 10b. Hindwing underside lacking patch of red scales at the base of the wing.....11
- 11a. Tail long; marginal spots well developed and white.....12
- 11b. Tail medium or absent; marginal spots white or red.....13
- 12a. Forewing upperside mostly black with well developed white marginal spots...*H. oxynius*
- 12b. Forewing upperside with white band running across the wing from about midway the costal edge to the anal angle; forewing marginal spots small.....*H. pelaus*
- 13a. Hindwing marginal spots white and well developed, large; upperside mostly black with the forewing underside having the central band only as a pale arch; hindwing underside with white submarginal spots; proximal postdiscal spots red and not merged with submarginal spots.....*H. epenetus*
- 13b. Hindwing marginal spots small; forewing upperside with large yellow spot touching the inner margin.....*H. chiansiades*
- 13c. Hindwing marginal spots small; when present, spot on forewing upperside never touching the wing inner margin.....14
- 14a. Hindwing upperside with proximal postdiscal and submarginal spots merged.....15
- 14b. Hindwing upperside with proximal postdiscal and submarginal spots separate.....16
- 15a. Hindwing underside with submarginal and proximal postdiscal spots never merged; submarginal spots always larger than proximal postdiscal spots; tail vestigial or absent; when spot present on the forewing upperside it is always in the tornal area.....*H. anchisiades*
- 15b. Hindwing underside with submarginal and proximal postdiscal spots merged; tail very short; when spot present on forewing upperside it is always around where M3 arises from the discal cell.....*H. isidorus*
- 16a. Hindwing upperside with one row of pale yellow spots; tail medium sized; hindwing underside with two full rows of red spots, the submarginal and the proximal postdiscal spots.....*H. erostratus*
- 16b. Hindwing upperside with red spots.....*H. rogeri*

- 17a. Hindwing upperside missing submarginal spots; hindwing upperside with a large patch of metallic green or blue scales; tail short and narrow.....*H. androgeus*
- 17b. Hindwing upperside with submarginal spots; hindwing upperside of female missing large patch of metallic green or blue scales; tail long.....18
- 18a. Forewing and hindwing upperside with a well developed yellow central band 70-80% of the wing, not invading the outer half of the discal cell and missing a discal spot on the forewing20
- 18b. Forewing and hindwing upperside with a well developed yellow central band 70-80% of the wing, invading the outer half of the discal cell and merging with the discal spot on the forewing.....*H. thersites*
- 18b. Forewing and hindwing central band are 30-50% of the wing, invading the discal cell and merging with the discal spot.....*H. astyalus*
- 18c. Forewing central band does not invade the discal cell.....19
- 19a. Forewing central band does not invade discal cell and there is no discal spot; having the costal branch of the central band.....*H. ornythion*
- 19b. Forewing central band does not invade discal cell and there is no discal spot; lacking the costal branch of the central band.....*H. hectorides*
- 20a. Forewing and hindwing upperside with a well developed yellow central band 70-80% of the wing, invading the outer half of the discal cell and merging with the discal spot on the forewing.....*H. thersites*
- 20b. Central band very broad and arching around the edges of the discal cell; there is no apical branch and cell r4-r5 almost always with a yellow spot of the central band; there is almost always a blue inner postdiscal element of the eye spot and almost never a red sub-discal element on underside of the male hind wing.....*H. garleppi*
- 20c. Never with the yellow of the apical branch of the central band in r4-r5; central band does not extend as far to the wing margin.....*H. torquatus*

Females of Sexually Dimorphic Species

- 1a. Female hindwing upperside with a large patch of metallic green or blue scales; tail short and narrow.....*H. androgeus*
- 1b. Hindwing upperside of female missing large patch of metallic green or blue scales; tail long.....2
- 2a. Female forewing has a crescent shaped pale yellow central band.....*H. thersites*
- 2b. Female upperside mostly dark with the hindwing underside having the inner postdiscal spots light blue often reflected on the upperside.....*H. astyalus*
- 2c. Females dark with pale yellow suffusion of central band and other wing elements, or similar to males.....*H. ornythion*
- 2d. Females mostly black with a white central band or suffusion of a white central band on the forewing upperside, submarginal and post discal spots on the hindwing red.....*H. hectorides*
- 2e. Female with the red submarginal and red post-discal spots at m3-cu1 and cu1-cu2 separate.....*H. garleppi*
- 2f. Female with the red submarginal and red post-discal spots at m3-cu1 and cu1-cu2 never separate.....*H. torquatus*

The “*thoas*” Subgroup

This subgroup consists of seven species, *H. thoas*, *H. cresphontes*, *H. melonius*, *H. homothoas*, *H. paeon*, *H. aristor*, and *H. caiguanabus* (Figure 4-14).

Heraclides thoas (Linnaeus, 1771)

Diagnosis. The adults of this species are very similar to *H. cresphontes*, *H. melonius*, *H. homothoas* and *H. paeon*. The subspecies vary so greatly that it becomes very difficult to identify a character that can be found in all subspecies and that will be useful to distinguish it from *H. cresphontes*, which it most closely resembles (Rothschild and Jordan, 1906). A simple way to separate these two species is by the absence of a visible notch at the base of the claspers in *H. thoas* that is present in *H. cresphontes* (DeVries, 1987).

Variation. The size, hue of yellow, number of the spots of the sub-marginal on the dorsal of the forewing, and the intensity of the spots of the proximal post-discal band on the ventral hindwing change throughout the range; typically there are four spots of the sub-marginal on the forewing.

Natural History. The seven subspecies are widespread from Mexico to Argentina and Cuba. In Cuba it is seen often in coastal woodlands and open areas near food plants. Its flight is said to be lazy but can at times be swift and they have been recorded nectaring at *Bougainvillea*, *Poinsettia*, *Bauhinia*, and ornamental shrubs (Smith et al., 1994). They can be found from sea level to 1000 m, especially in areas with high rainfall (DeVries, 1987). Females lay eggs from early morning to late afternoon along forest edges and in secondary growth (DeVries, 1987).

Life History. Smooth spherical whitish eggs are laid singly on the upper surfaces of host plant leaves, turning orange just before hatching. The distinctly humped mature larvae are olive brown and measures over 60 mm in length and bears some resemblance to a small snake’s head and may also resemble bird droppings. Tiny lilac spots are present on the larvae along with a tan saddle and a tan pre-anal patch which is spotted with brown. The ventral surfaces are cream colored, which darkens as you move dorsally. Adult larvae may be seen resting on the branches of host plants or on the leaf’s upper surface (Riley, 1975). Two eye-like marks can be seen on either side of the thoracic segments (Riley, 1975). The pupa has tiny thoracic protuberances with the last abdominal segments ventrally arched. Over-all the color is dark brown shaded with grey and/or olive (Smith et al. 1994).

Distribution (Figure 6-69). Neotropical, from North through to Central and South America.

Remarks. This species is the type for the genus *Heraclides*. It was the first to be described (Linnaeus, 1771) and is today composed of seven subspecies. It is easily confused with *H. cresphontes* and to a lesser extent *H. homothoas* and *H. paeon* with which its range overlaps. *H. melonius* was once considered a subspecies.

Heraclides thoas thoas (Linnaeus, 1771)

Papilio thoas (Linnaeus, 1771): 536.

Papilio archimedes (Fabricius, 1938): 46.

Adult Male (Figure 6-1a) *Body.* Frons yellow, with a well defined central black band of scales continuing from inter-antennal ridge; inter-antennal ridge black with sprinkling of yellow scales in two small patches behind each eye; antennal shaft black with typical swollen terminal

segments; terminal segments show very little yellowing; palpus very scaly, yellow, and short, less than $\frac{1}{2}$ length of frons, erect (not porrect). Pectus with long yellow scales; tegula black with sprinkling of yellow scales, edged with yellow scales on inner margin; legs black with posterior yellow; tarsi with spines; epiphysis present on foreleg; tibial spur formula 0-2-2; tarsal claws bifid. Abdomen yellow with black dorsal medial band generally well developed, sometimes reduced to a thin line.

Forewing. Length 54-60 mm (n=3) Dorsal forewing with a distinctive "X" formed by the central and sub-marginal bands; a well developed narrow yellow central band; central band with an element at r3-r4 towards wing apex and element at r5-m1 the longest; the central band element at r5-m1 can sometimes be notched; the central band has an apical and a costal branch; there is sometimes a central band element in corner where R4 and R5 meet and the discal cell spot is sometimes present as an invasion of cell by the central band; there are 1 to 4 sub-marginal spots at the tornal end, the fourth sometimes reduced in size but rarely absent. The apical spots of the sub-marginal band are typically absent and the outer edges of the central band elements are linear. The spots of the marginal band are reduced to only three at the tornal area between M2 and Cu2 and can be seen on the very edge of the wing. The ventral pattern is more pronounced; the apical and costal branch of the central band are merged to form a swollen upper crescent; sub-marginal spots r3-r4 to cu2-1a are present and almost circular in shape; the discal spot is similar to that above but joined by four yellow discal lines running the length of the discal cell from wing base, getting more diffused and merging towards apex of discal cell. The marginal spots are reduced to only four at the tornal area between M1 and Cu2 and can be seen on the very edge of the wing, more pronounced than the dorsal side.

Hindwing. Hindwing M3 elongate and forms a clubbed tail; tail spot present; the dorsal surface with a narrow central band; yellow sub-marginal spots present; cell cu-1a with an eyespot. The ventral pattern is more pronounced; spots of the inner post-discal band are present at the tornal end from M1 to Cu2, with light blue and yellow scales mixed; the light blue scales are more central. The proximal post-discal spots are often present only as red patches between M1 and Cu1 at the edge of the discal cell; sometimes these are reduced or absent. They follow the shape of the inhabited cell, are arranged as discrete spots, and distributed in cells m2-m3, m3-cu1 (sometimes present in m1-m2). Crescent shaped light blue inner post-discal spots are present as are yellow sub-marginal spots; the cell at cu-1a has an eyespot. The marginal spots are narrow, barely visible at the edge of the wing; these are more pronounced than on the dorsal side.

Genitalia. (Figure 6-36) Male genitalia with valve rim rounded; harpe shape roughly triangular; with one large spine on the ventral surface. The large spine on the ventral surface of the harpe on the male genitalia with the posterior third and tip fused and posterior pointing, and typically serrate (not serrate in *H. thoas autocles*) and never reaching the edge of the valve (reaches the edge of the valve in *H. thoas autocles* and *H. thoas oviedo*). The 8th tergite has the pseuduncus (superuncus) tip straight, tapering broadly; the uncus as paired horn-like bifid processes; with the largest horn ventrad; horns very prominent. Aedeagus on the male genitalia is straight and the U-shaped juxta (furca) has narrow arms.

Adult Female (Figure 6-1b) *Body.* As in the male.

Forewing. As in the male; length 56-67 mm (n-5).

Hindwing. As in the male.

Genitalia. (Figure 6-61) There is significant armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule that opens anteriorly and is supported by a ridge. A broad process dorsad of the ostium with a ventrally indented midline is present. The paired

peripheral vestibular plates are heavily sclerotized present. A trough is present between the peripheral vestibular plates and the structure dorsad of the ostium. A hook-like ventrad projection is also present. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Type(s). Recorded as lost (Honey and Scoble, 2001; Pelham, 2008).

Distribution. Guyana south to lower Amazon, east to Belém, Brazil and south-west to north Mato Grosso, Brazil.

Remarks. Almost always with four sub-marginal spots on the forewing; the sub-marginal spot at m2-m3 is sometimes reduced in size, but rarely absent. Not commonly collected.

Heraclides thoas autocles (Rothschild & Jordan, 1906)

Papilio thoas autocles (Rothschild & Jordan, 1906): 557.

Papilio thoas autocles form *nigro-caudata* (Vázquez, 1949): 234 - Original misspelling.

Papilio thoas autocles aberration *nigrimarginata* (Beutelspacher, 1976): 63.

Papilio thoas autocles form *ochracea* (Beutelspacher, 1976): 65.

Adult Male (Figure 6-1c) *Body*. Similar to the nominate subspecies.

Forewing. Length 42-62 mm (n=170). Similar to the nominate subspecies but sometimes with more than four spots of the sub-marginal spots extending up to the forewing apex. When additional sub-marginal spots are present, they are reduced in size; the central spot at mr5-m1 often has a notch where the costal and apical branches of the central band do not completely merge. Sometimes this notch is absent or replaced by a dot.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-36c2) Similar to the nominate subspecies but with the spine at the end of the harpe not serrate, and passing the edge of the valve.

Adult Female (Figure 6-1d) *Body*. As in the males.

Forewing. Length 50-68 mm (n=59). As in the male.

Hindwing. As in the male.

Genitalia. Similar to the nominate subspecies.

Type(s). “*P. thoas* / *autocles* / Type R.+J./ Nov. Zool. 1906. // Holo- / type // Rothschild / Bequest / B.M.1939-1. // det / L. S. Marks // Guerrero, / Mexico. / (O. T. Baron)”; “*Nigro - / caudata* // T. Escalante / Tierra Blanca / VIII-42, Ver // A. C. Allyn / Acc. 1973-48 // Tipo”; “15-IV-57 / El Tajin / Veracruz / 20 / [label ventral] *thoas* / Ab. [type for *nigrimarginata*]”; “Ex-Coleccion / Salsana // Holotype ♂ / *Papilio thoas autocles* / f. *ochracea* / Beutelspacher, 1976 // CNIN Lep (Mexico) / 11037 // A. Diaz Frances / Yaxchilan, chis. / Oct 1966.”

Distribution. Southern North America (USA-Texas and Mexico) through Central America to Costa Rica and Panama.

Remarks. Tyler et al. (1994) remarks that these are dark with no tail spots but specimens investigated were similar to the typical but with a small eyespot. Very few were dark.

Heraclides thoas brasiliensis (Rothschild & Jordan, 1906)

Papilio thoas brasiliensis (Rothschild & Jordan, 1906): 560.

Papilio thoas impunctata (Boullet & Le Cerf, 1912): 2.

Papilio thoas brasiliensis aberration *completa* (Dufrane, 1946): 114.

Papilio thoas brasiliensis aberration *reducta* (Dufrane, 1946): 115.

Adult Male (Figure 6-1e) *Body*. Similar to the nominate subspecies but typically larger.

Forewing. Length 55-69 (n=25). Similar to the nominate subspecies. Sometimes with more than four spots of the sub-marginal extending up to the forewing apex. When additional sub-marginal spots are present, they are reduced in size. The central spot at mr5-m1 often has a notch where the costal and apical branches of the central band do not completely merge. Sometimes this notch is absent or represented as a spot.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-36c3) Similar to the nominate subspecies but with the spine at the end of the harpe more serrate. Serrations take up the posterior third of the harpe.

Adult Female (Figure 6-1f) *Body*. As in the male.

Forewing. Length 65-75 mm (n=17). As in the male.

Hindwing. As in the male.

Genitalia. Similar to the nominate subspecies.

Type(s). “*Papilio / thoas / brasiliensis / Rothschild & Jordan / det. C.F. Huggins 1974 / ♂ Syntype // Petropolis, / 20.XII.97 / (Foederle). // det / L. S. Marks // Syn- / type // Rothschild / Bequest / B.M.1939-1.*”; “*Coll. Boulet / Museum Paris / Sao Paulo / Bresil / 1909 / C. Ribbe // Syntype ♂ / Papilio thoas / impunctata / Boulet + Le Cerf, 1912*”; “*Bresil / 1900 / Demoulin // ♂ // holotype // ab. completa / Dufrane*”; “*holotype // ab. reducta / Dufrane // Bresil / 1900 / Demoulin // ♂*”.

Distribution. All of Brazil south to Uruguay and Paraguay.

Remarks. Very similar to *H. t. thoantiades* with which it can often be confused, but typically slightly larger.

Heraclides thoas cinyras (Ménétries, 1857)

Papilio cinyras (Ménétriés, 1857): 68.

Papilio lampedon (Gray, 1856): 7-8 - nomen nudum.

Papilio thoas chamadus (Fruhstorfer, 1907)

Papilio cinyras aberration *ridens* (Fassl, 1915): 186-9.

Papilio thoas aberration *flavibrunneus* (Prüffer, 1922): 4.

Adult Male (Figure 6-2a) *Body*. Similar to the nominate subspecies.

Forewing. Length 54-73 mm (n=87). Similar to the nominate subspecies but typically with no sub-marginal spots. Occasionally one sub-marginal spot, much reduced in size, may be present at the tornal area. The central spot at mr5-m1 almost always complete, but occasionally a small notch is present.

Hindwing. Similar to the nominate subspecies but often with a loss of the red sub-marginal element of eye spot. The inner post-discal band element of eye spot is larger and more defined and is often accompanied by a much diffused inner post-discal spot at cu1-cu2.

Genitalia. (Figure 6-36c4) Similar to the nominate subspecies.

Adult Female (Figure 6-2b) *Body*. As in the male.

Forewing. Length 68-74 mm (n=18); as in the male.

Hindwing. As in the male.

Genitalia. Similar to the nominate subspecies.

Type(s). “*Thoas / chamadus / Fruhst. / Pined. // Bolivia / Fruhstorfer // Fruhstorfer Coll. / B.M.1937-285. // Type // Type*”; “*Pap. cinyras ♂, ab. / ridens (Type, Jre’s 1915 / p. 189). Rio songo, 750 m / III. 1943 (III.24 stg.) / Fassl.*”

Distribution. Upper Amazon basin.

Remarks. The adults are typically much larger than all other subspecies and easily spotted by the reduced sub-marginal spots on the forewing.

Heraclides thoas neacles (Rothschild & Jordan, 1906)

Papilio thoas neacles (Rothschild & Jordan, 1906): 558.

Adult Male (Figure 6-2c) *Body.* Similar to the nominate subspecies.

Forewing. Length 46-61 mm (n=89). Similar to the nominate subspecies; the central spot at mr5-m1 almost always notched.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-36c5) Similar to the nominate subspecies but with the spine at the distal end of the harpe more up curved.

Adult Female (Figure 6-2d) *Body.* As in the male.

Forewing. Length 55-66 mm (n=49). As in the male.

Hindwing. As in the male.

Genitalia. Similar to the nominate subspecies.

Type(s). “P. thoas / neacles / Type. R + J. / Nov. Zool. 1906. // Muzo. Col. / XI 96. // det / LS Marks // Holo- / type // Rothschild / Bequest / B.M.1939-1.”

Distribution. Venezuela south-west to Colombia and northern Peru down into southern Amazonas.

Remarks. Very close to the nominate subspecies.

Heraclides thoas oviedo (Gundlach, 1866)

Papilio oviedo (Gundlach, 1866): 279.

Papilio epithoas (Oberthür, 1897): 179.

Adult Male (Figure 6-2e) *Body.* Similar to the nominate subspecies.

Forewing. Length 42-54 (n=11). Typically with seven spots of the sub-marginal band; the three most apical spots being ones smaller, sometimes only two present, sometimes absent; four tornal sub-marginal spots always present.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-36c6) Similar to the nominate subspecies but with the spine at the end of the harpe reaching but not extending beyond the valve edge.

Adult Female (Figure 6-2f) *Body.* As in the male.

Forewing: Length 51-60 mm (n=8). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-61g) Similar to the nominate subspecies, but with a smaller tongue-like process, and with lateral peripheral arms that arise from the inner edges of the peripheral vestibular plates. These arms are roughly square, their outer edges not serrated.

Type(s). “Type / 7242 / Papilio / oviedo / Gundlach ♂”; “vapar / Godman / +Salvin / mass 1890 // Levick / Bequest / 1941-83 // det / L S Marks // Type // Mexico // 5. Papilio Epithoas Ch. Obthr. – Mexico; de la coll. Auguste, / de Bordeaux.”

Distribution. Cuba

Remarks. Slightly smaller than typical *H. thoas*; frequently seen.

Heraclides thoas thoantiades (Burmeister, 1878)

Papilio thoantiades (Burmeister, 1878): 59.

Papilio euclides (Larrañaga, 1923)

Papilio thoas brasiliensis aberration *ochracea* (Giacomelli, 1927).

Adult Male (Figure 6-3a) *Body*. Similar to *H. t. brasiliensis*.

Forewing. Similar to *H. t. brasiliensis*; length 53-67 mm (n=7).

Hindwing. Similar to *H. t. brasiliensis*.

Genitalia. (Figure 6-36c7) Similar to *H. t. cinyras* but with the ventral edge of the harpe more curved.

Adult Female (Figure 6-3b) *Body*. As in the male.

Forewing. Length 52-62 mm (n=5). As in the male.

Hindwing. As in the male.

Genitalia. Similar to the nominate subspecies.

Type(s). “Buen / Ayres // Typus // Col. Antigua // *P. thoantiades* Burm. / Lectotypus ♀ // Typus”; “Holotypus ♀ // ♀ *Papilio Thoas* L / sub. *brasiliensis* / ab. *ochracea* Giac. / La Rioja RA”.

Distribution. Southern Brazil to northern Argentina.

Remarks. It is unclear if this is a valid subspecies. It is very close to *H. thoas brasiliensis* with which it is frequently confused. It is somewhat smaller and is referred to as the spring brood which is found in Argentina by Tyler et al. (1994). They further claim that the summer brood is close in appearance to *H. thoas brasiliensis*. If this is so, I question whether a seasonal brood is enough to warrant subspecies status.

Heraclides cresphontes (Cramer, 1777)

Papilio cresphontes (Cramer, 1777): 106.

Heraclides oxilus (Hübner, [1819]): 83- replacement name.

Papilio cresphontes aberration *lurida* (Schultz, 1908): 92.

Papilio thoas cresphontes aberration *luxuriosa* (Reiff, 1911).

Papilio cresphontes aberration *intacta* (Strand, 1918): 47.

Papilio cresphontes variety *maxwelli* (Franck, 1919): 3.

Papilio cresphontes transition form *forsythae* (Gunder, 1933): 171.

Papilio cresphontes form *melanurus* (Hoffmann, 1940): 633.

Papilio cresphontes pennsylvanicus (Chermock & Chermock, 1945):38.

Diagnosis. Very similar to *H. thoas*, *H. melonius*, *H. homothoas* and *H. paeon*. It can be separated from *H. thoas*, which it most closely resembles, by the presence of a visible notch at the base of the male claspers and a small tubercle on the vaginal orifice of the females (DeVries, 1987). The genitalia are also quite distinct.

Adult Male (Figures 6-3e, 6-4a, and 6-4b) *Body*. Similar to *H. thoas*.

Forewing. Length 40-64 mm (n>300); similar to *H. thoas* but with the central band generally irregularly shaped; central spot at cu1-cu2 almost always cone shaped on the outer edge; discal spot always absent. The sub-marginal spots are lunar shaped, typically three at the tornal end, a fourth smaller sub-marginal spot is sometimes rarely present; the apical sub-marginal spots typically are absent. Marginal spots run length of wing outer margin; there are typically seven present on the very edge of the wing. The ventral pattern is more pronounced; apical and costal branch of the central band merged to form swollen upper crescent of central

band; sub-marginal spots from r3-r4 to cu2-1a are present and almost circular in shape; the four yellow discal lines running the length of the discal cell from wing base are more diffused than in *H. thoas*, merging towards apex of discal cell. Eight marginal spots run the length of the wing outer margin, on the very edge of the wing, and are more pronounced than dorsal side.

Hindwing. Similar to *H. thoas* but with the seven marginal spots more pronounced; the post-discal and inner post-discal bands are absent. The eye spot has the sub-marginal element red and crescent shaped, with a sprinkling of yellow scales at the tips, and the inner post-discal band element as a sprinkling of light blue scales in an arch. A diffused inner post-discal spot is sometimes present at sc-rs cell.

Genitalia. (Figure 6-37) The rim of the valve is rounded. The harpe is roughly cup-shaped, with the distal rounded edge serrated. The 8th tergite has the pseuduncus short and narrow. The uncus terminates in two prominent up curving smooth spines, the dorsal spine being larger than the ventral. There is no sub-terminal swelling. The aedeagus is short and roughly straight with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with narrow arms.

Adult Female (Figures 6-3c, 6-3d, and 6-3f) *Body*. As in the male.

Forewing. Length 50-74 mm (n>200). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-62a and 6-62b) There is little armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule and opens anteriorly, not supported by a ridge. Around the opening of the ostium the plates are not very sclerotized, fused anteriorly. There is no posterior projection. The peripheral vestibular plates are narrow and only slightly sclerotized and fuse anterior to, and below the ostium as a thin line. Short lateral peripheral arms may arise from the inner edges of the peripheral vestibular plates, as in specimen from Costa Rica. A broad, sclerotized tongue-like plate, without a ventrally indented midline, is present above and posterior to the vestibule. It is separated on both sides from the peripheral vestibular plates by a shallow trough. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. A highly variable species that may be best represented as a cline.

Natural History. These butterflies are common and can be frequently seen in the open country, fields, and gardens from sea level to 1000 meters. They are seldom seen in the deep shade of woodland hammocks (DeVries, 1987; Smith et al., 1994). Its flight has been described as somewhat cumbersome yet strong and purposeful, as it moves between nectar sources and may glide for long distances between wing beats (McAuslane, 2009). Males patrol flyways through citrus groves or pine woods in search of females and copulation occurs in the afternoon. They however can be observed flying throughout the day and Smith et al. (1994) mentions observing adults congregating in late afternoon for somewhat communal roosting. Nectar plants include *Schinus terebinthifolius*, *Bougainvillea glabra*, *Bourreria ovate*, *Carica papaya*, *Eupatorium odoratum*, *Lantana involucrate*, *Metopium toxiferum*, *Morinda royoc*, *Pithecellobium keyense*, *Lantana camara*, *Senecio mexicana* and perhaps *Delonix regia* (Minno and Emmel, 1993).

Life History. Cream-colored eggs that are smooth and spherical and between 1 to 1.5 mm are laid on the tip of leaves (Smith et al., 1994), often singly, but where food plant is limited multiple eggs may be seen on a single leaf. Eggs turn reddish before hatching. Larval stages are similar to those of *H. thoas*, often resembling bird or lizard droppings. Mature larvae have a dirty brown color with cream colored lateral lines along the first three segments (Riley, 1975), a median saddle and cream colored posterior patch. Larvae can grow up to 70 mm in length and

have very long deep blood-red osmeterium arms (Smith et al., 1994). Larval abundance can sometimes reach pest status. Pupae are about 45 mm long, are mottled with grey and tan, and appear stick-like; very similar to *H. thoas*.

Type(s). “*Papilio thoas* L. / ab. *luxuriosus* Reiff / Type ♂ // Detroit / Mich. // [label with difficult handwriting]”; “BMNH(E)# 665119 // Possible syntype of / *Papilio crespontes* / Cramer, 1777 / verified by / J. E. Chainey, 2002 // Felder Collⁿ / Rothschild / Bequest / B.M. 1931-1. // *Crespontes.Cram*”; “Holotype ♂ / *Papilio crespontes* / var. *maxwelli* / Franck, 1919 / [label ventral] G. Lamas det. / III. 90 // march 9 / 24 [?]”; “Holotype / ♂ / Collection / of / Jeane D. Gunder / *Papilio* / *crespontes* / Cram. / Tr. F. / *Forsythae* / J. D. Gunder / Type Label // J. D. Gunder / Collection / Ac. 34998 // 21.XI.31 Fla / Florida City / Ex larva”; “C. C. Hoffmann det. / *P. crespontes* / f. *melanurus* Hffn. // C. C. Hoffmann / Chilpancingo / Gro. VII.1910. / 1613. // Tipo”; “Holotype ♂ / *P. crespontes* / r. *pennsylvanica* / JH + RL. Chermock // Carn. Mus. / Acc. 13515 // V-10-1938 / State College / PA”.

Distribution (Figure 6-17). North America (occasionally Canada through to Mexico), Central America to Panama, and Cuba.

Remarks. Sometimes confused with *H. thoas* and reported from areas not recognized as part of its range. It is also often confused with *H. melonius* on Jamaica. This leads often to erroneous sightings for this species. The type for ‘*luxuriosa*’ is labeled ‘*luxuriosus*’ and the type for ‘*pennsylvanicus*’ is labeled ‘*pennsylvannica*’. I propose that only original spellings of names be used for consistency.

Heraclides homothoas (Rothschild & Jordan, 1906)

Papilio homothoas (Rothschild & Jordan, 1906): 561.

Diagnosis. Very similar to *H. crespontes* but with different genitalia, and typically smaller adults.

Adult Male (Figure 6-4e) *Body.* Similar to *H. thoas*.

Forewing. Length 40-54 (n=5). The wing pattern is similar to *H. crespontes*, but almost never with a fourth sub-marginal spot at the tornal area.

Hindwing. Similar to *H. crespontes*.

Genitalia. (Figure 6-38) Similar to *H. crespontes* with the rim of the valve is rounded and the harpe roughly cup-shaped, but with the distal rounded edge with very little serration (much more serrations in *H. crespontes*). The 8th tergite has the pseuduncus short (< 1 mm) and bifurcated. The uncus terminates in a smooth broad blade-like process that terminates as a spine. There is little sub-terminal swelling. The aedeagus is short (≤ 3 mm), roughly straight, with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with narrow arms.

Adult Female (Figure 6-4f) *Body.* As in the male.

Forewing. Length 50 mm (n=2); as in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-62c) Similar to *H. crespontes* but more sclerotized, with longer lateral peripheral arms arising from the much more sclerotized peripheral vestibular plates.

Variation. Variable in size with the Trinidad specimens typically smaller than mainland specimens.

Natural History. Apart from the host plants listed in Table 6-1, nothing more could be gleaned from the literature.

Life History. Not known.

Type(s). “Holo- / type // Nov. Zool. 1906 / Pl. V. Fog. 13 // Rothschild / Bequest / B.M.1939-1 // Papilio / homothoas / Rothschild & Jordan / det. C.F. Huggins 1974 / ♂ Holotype // P. homothoas / type Nov. Zool. / 1906. R. + J. // C. Bolivar / June 1891”.

Distribution (Figure 6-71). The literature lists it as occurring from Panama, through northern Colombia, to northern Venezuela, and Trinidad.

Remarks. This species could be involved in a species complex involving *H. thoas*, *H. cresphontes* and possible *H. paeon*. This species is very close to Costa Rican representatives of *H. cresphontes* but the genitalia suggest that it be treated as a separate species. More work need to be done to understand the relationships among these species.

Heraclides melonius (Rothschild & Jordan, 1906)

Papilio thoas melonius (Rothschild & Jordan, 1906): 556.

Diagnosis. The eye spot is more developed than in any previous species. Spots of the proximal post-discal band at m1-m2, m2-m3, and m3-cu1 the hindwing ventral are well developed and always present extending the length of the cells until abutting against light blue inner spots.

Adult Male (Figure 6-5a) *Body.* Similar to *H. thoas*.

Forewing. Length 46-55 (n=5). Similar to *H. cresphontes*.

Hindwing. Similar to *H. cresphontes* but with well developed eye spot and proximal post-discal band.

Genitalia. (Figure 6-39) The rim of the valve is rounded and the harpe narrows to a distal unserrated tooth which does not go to the edge of the valve. The 8th tergite has the pseuduncus tip straight. The uncus terminates in smooth spines, the dorsal spine shorter than the ventral spine. There is little sub-terminal swelling. The aedeagus is straight, with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with narrow arms.

Adult Female (Figure 6-5b) *Body.* As in the male.

Forewing. Length 57 mm (n=2). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-62d) There is little armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule and opens anteriorly, not supported by a ridge. Around the opening of the ostium the plates are barely sclerotized, not fused anteriorly. There is no posterior projection. The peripheral vestibular plates are broad, sclerotized and fuse anterior to, and below the ostium as a thin line. There are no lateral peripheral arms. There is also no sclerotized tongue-like plate and no shallow trough. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. Size variable; female with more red in the eyespot.

Natural History. It is believed that this species is being out-competed by *H. andraemon andraemon*. A survey of the literature yielded no additional information about this species.

Life History. Not known.

Type(s). “Holo- / type // Jamaica / (Taylor) // Nov. Zool. 1906 / Pl, VII. Fig. 59 // P. thoas / melonius Type. / Nov. Zool. 1906. R+J // Rae Town / 29-7-93 / Bred // det. / LS Marks”.

Distribution (Figure 6-71). Jamaica.

Remarks. Often confused with *H. cresphontes*; this leads to erroneous reports of sightings. It has previously been regarded as a subspecies of *H. thoas* (Brown and Heinemann, 1972; Smith et al. 1994). Its habits and life history information has often been recorded with that of *H. thoas*. No specific literature on its habits or life history not linked to that of *H. thoas* could be found.

Heracles paeon (Boisduval, 1836)

Diagnosis. Similar to *H. cresphontes* and *H. melonius* but with the central band more regular and angled, their outer edges almost forming a straight line. The sub-marginal spot at r5-m1 is triangular in shape and never notched or broken. There are now more proximal post-discal spots on hindwing ventral at m1-m2 to cu1-cu2, sometimes extending to, and joining with eye spot. Also the discal spot in the hindwing ventral can be used to separate this species from the others in this subgroup.

Variation. The spots of the proximal post-discal band are variable in number; adult wing length is not very variable.

Natural History. Apart from the host plants listed in Table 6-1, nothing more could be gleaned from the literature.

Life History. Pale cinnamon-brown eggs are laid singly on the dorsal of leaves, similar to the other members of the *thoas* subgroup. The nearly black newly hatched larva has a pale V mark on the face and a light brown saddle shaped spot on the eighth segment. Tubercles are present on either side of the third segment which is swollen as is typical of *thoas*. *H. paeon* also resembles bird droppings. A fully grown larva is about 50 mm long, with very shiny skin, grey-brown head. The body ground color is a rich amber-brown spotted with paler patches and a broad irregular creamy ochreous stripe running laterally; sometimes this stripe is tinged with pink. There is a pale ochreous stripe above the cool grey prolegs and the osmeterium is described as long slender and orange-yellow. Fully fed larvae tend to retreat to the stems of the plants, sometimes close to the ground. The pupa is about 32 mm long and the adult emerges after about twenty days (Walker, 1882).

Distribution (Figure 6-72). From north-central Mexico through Central America into Colombia and Venezuela in the north to Chile and Bolivia in the south along the western and eastern slopes of the Andes.

Remarks: Easily distinguished from other species in this subgroup by the presence of the red discal spot in the ventral hindwing. There are three recognized subspecies.

Heracles paeon paeon (Boisduval, 1836)

Papilio paeon (Boisduval, 1836): 356.

Papilio paon paon perigino (Bryk, 1953): 6 – original misspelling.

Papilio paeon marxi (Möhn, 2001)

Adult Male (Figure 6-5c) *Body.* Similar to *H. thoas*.

Forewing. Length 46-55 mm (n=9). Similar to *H. cresphontes* or *H. melonius* but wing elements more angular.

Hindwing. Similar to *H. melonius* but with less developed eye spot and a more expanded proximal post-discal band. The discal cell on the ventral side has a red ochreous spot, with blue and black on the distal edge of the spot. This discal spot appears only in this species.

Genitalia. (Figure 6-40) The rim of the valve is rounded and the harpe is cupped shaped with 5 spines along the distal and ventral edge; spines may be long enough to reach the valve edge. The 8th tergite has the pseuduncus tip straight. The uncus terminates in a smooth projection that terminates in a fat upturned spine. There is little sub-terminal swelling. The aedeagus is slightly curved, with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with narrow arms.

Adult Female (Figure 6-5d) *Body*. As in the male.

Forewing. Length 54-56 mm (n = 2). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-62e) There is much armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule and opens anteriorly, not supported by a ridge. Around the opening of the ostium the plates are highly sclerotized and fused anteriorly, below the ostium. These plates merge with highly sclerotized peripheral vestibular plates anteriorly to give rise to a horn-like projection posterior to, and below the ostium. The peripheral vestibular plates are broad and well sclerotized and fuse anterior to, and below the ostium. Very long lateral peripheral spines arise from the inner edges of the peripheral vestibular plates. A highly sclerotized tongue-like plate with several lamellae is present above and posterior to the vestibule and is separated on both sides from the peripheral vestibular plates by a deep trough. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Type(s). “Coll. Lacordaire / Museum de Paris / [ventral with round label affixed] // Type // paeon / Bdv”.

Distribution. Eastern slopes of the Andes from southern Colombia to northern Bolivia.

Remarks. No additional information is available.

Heraclides paeon escomeli (Cockerell, 1927)

Heraclides paeon escomeli (Cockerell, 1927): 48.

Adult Male (Figure 6-5(e) *Body*. Similar to the nominate subspecies.

Forewing. Length 38-55 mm (n = 7). Similar to the nominate subspecies;

Hindwing. Similar to the nominate subspecies.

Genitalia. Similar to the nominate subspecies but with four spines along the distal and ventral edge of the harpe.

Adult Female (Figure 6-5(f) *Body*. As in the male.

Forewing. Length 50 mm (n = 1). As in the male.

Hindwing. As in the male.

Genitalia. Not dissected.

Type(s). “Papilio / escomeli / type Cockerell // Type No. / 33185 / U.S.N.M. // Cotahuasi / 9000ft. / Oct, 1911 / YalePeruvExp”.

Distribution. Southern Peru into central Chile on the western slopes of the Andes.

Remarks. Paler than the other subspecies.

Heraclides paeon thrason (Felder & Felder, 1865)

Heraclides thrason (Felder & Felder, 1864) – nomen nudum.

Heraclides thrason (Felder & Felder, 1865): 74.

Adult Male (Figure 6-6a) *Body*. Similar to the nominate subspecies.

Forewing. Length 47-50 mm (n = 13). Similar to the nominate subspecies.

Hindwing. Similar to the nominate subspecies.

Genitalia. Similar to the nominate subspecies but with three spines along the distal and ventral edge of the harpe. The inner surface of the harpe also appears to have a roughened circular patch.

Adult Female (Figure 6-6b) *Body*. As in the male.

Forewing. Length 52-59 mm (n = 3). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-62f) Similar to the nominate subspecies but with the lamellae on the tongue-like plate more circular.

Type(s). “Felder’s / Type // Bogota / Lindig // Thrason n. // Type // Rothschild / Bequest / B.M.1939-1.”; “Rothschild / Bequest / B.M.1939-1. // Felder / Collⁿ // Bogota / Lindig [type association unsure]”.

Distribution. From north-central Mexico through Central America to western Peru along the western slopes of the Andes, and north to northern Venezuela.

Remarks. Very similar to nominate subspecies.

Heraclides aristor (Godart, 1819)

Papilio aristor (Godart, 1819): 60.

Diagnosis. Distinctive black ground color with five spots of the costal branch of the central band, and the spots of the sub-marginal band, forming a distinctive “Y” on the forewing.

Adult Male (Figure 6-6c) *Body*. Similar to *H. thoas*, except palpus not as densely scaled, yellow, and short, less than ½ length of frons, erect (not porrect). Pectus black with long yellow scales near the neck; legs black with posterior yellow; tarsi with spines; epiphysis present on foreleg; tibial spur formula 0-2-2; tarsal claws bifid; abdomen black with yellow lateral band on each side.

Forewing. Length 47 mm (n = 1); ground color black; dorsal pattern with central band reduced, represented only as the costal branch which meets with the sub-marginal spots at m2-m3 and m3-cu1. The five costal branch spots of central band are small and oval with spots r5-m1 and m3-cu1 smaller than the other three. The ventral surface is the same as dorsal but with a pale discal spot in the discal cell.

Hindwing. Ground color black; lacking a central band; with the sub-marginal complete and crescent shaped. The sub-marginal element of the eye spot is red and bar shaped, with a sprinkling of yellow scales at the outer tip; the inner post-discal band element as a sprinkling of light blue scales in an arch. The well developed tail has no tail spot. The ventral surface reflects the dorsal surface side, but with the spots of the sub-marginal larger; the spots of the inner post-discal band represented as a loose arch-like sprinkling of light blue scales. The eye spot is as the dorsal but with the inner post-discal band element more defined. The proximal post-discal band is represented by two red spots just outside the discal cell at m2-m3 and m3-cu1.

Genitalia. (Figure 6-41) The rim of the valve is narrow with a blunt tip and the harpe narrows to a distal spine which does not go to the edge of the valve; three smaller spines associated with the most distal spine. The 8th tergite has the pseuduncus intermediate ($\geq 1 < 2$ mm) and broad, narrowing to a rounded tip. The uncus terminates in two smooth spines, the dorsal spine longer and up-turned and the ventral spine shorter and down-turned with an inward twist. There is little sub-terminal swelling. The aedeagus is slightly curved, with the vesica simple (no spines or sclerotizations). The juxta is “V” shaped.

Adult Female (Figure 6-6d) *Body*. As in the male.

Forewing. Length 47 mm (n = 1). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-63(a)) There is much armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule and opens anteriorly, not supported by a ridge.

Around the opening of the ostium the plates are very sclerotized, fused anteriorly. There is a small slightly sclerotized bulbous posterior projection. The peripheral vestibular plates are wide and only highly sclerotized and fuse anterior to, and below the ostium as a thin line. A broad, sclerotized tongue-like plate, with a ventrally indented midline, is present above and posterior to the vestibule. It is separated on both sides from the peripheral vestibular plates by a deep sclerotized trough. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. Not very variable.

Natural History. Relatively rare, this species can be found within very dry *Acacia* scrub. Occurrence of this species is closely tied to environmental conditions and some years can be relatively common in very restricted areas; at other times it can be quite rare. They are most common in June and August and it has been suggested that emergence is triggered by rainfall. Adults have been observed nectaring on *Cordia* spp., *Lantana ovatifolia*, and *Antigonon leptopus* (Schwartz, 1989; Smith et al., 1994).

Life history. Unknown.

Type(s). Probably lost or only as published image.

Distribution (Figure 6-73). Hispaniola (Haiti and the Dominican Republic).

Remarks. Possibly closely related to *H. caiguanabus*. IUCN Red list of threatened species lists this species with an indeterminate status.

Heraclides caiguanabus (Poey [1852])

Papilio caiguanabus (Poey [1852]): Plate 15.

Papilio numicus (Hopffer, 1856): 1, plate 1, figure 3 & 4.

Diagnosis. Most wing elements lost except for the sub-marginal on both forewing and hindwing. Remnants of the central band remain as a few spots near wing apex. Females with distinctive white sub-marginal spots instead of yellow; these spots are yellow on the ventral.

Adult Male (Figure 6-6e) *Body.* Frons, labial palp, inter-antennal ridge and antennae similar to *H. aristor*. Pectus black with yellow scales on the anterior surfaces of foreleg only. Tegula similar to *H. aristor* but with yellow reduced to a few scales; tarsi with spines; epiphysis present on foreleg; tibial spur formula 0-2-2; tarsal claws bifid; abdomen black.

Forewing. Length 38-46 mm (n = 4). Ground color black. The pattern is missing the central band, except for two very small spots of the apical branch at r2-r3 and r3-r4. Eight sub-marginal spots are well represented. The marginal spots are well developed. The well developed tails have no tail spot. The ventral surface is similar to the dorsal, with additional spots from the costal branch of the central band showing up at r5-m1 and occasionally at m2-m3, but these tend to be paler. The sub-marginal element of the eye spot is more oval shaped, with yellow at the edges, and with inner post-discal band element as a diffused crescent of light blue scales. The spots of the marginal band are well represented.

Hindwing. Similar to *H. aristor*, but with the sub-marginal spots more robust and of a darker yellow than the rest of the wing spots. The marginal spots are well represented. The tail has no tail spot. The ventral has the inner post-discal band element similar to the dorsal, but more pronounced, with a reduction in the size of the inner post-discal band elements at the wing apex. The two proximal post-discal spots are more developed than in *H. aristor*.

Genitalia. (Figure 6-42) Similar to *H. aristor*, but with more serrations accompanying the distal spine on the harpe. The pseuduncus is a bit shorter and broader than in *H. aristor*.

Adult Female (Figure 6-6f) *Body.* As in the male.

Forewing. Length 46 mm (n = 1). Similar to the male
Hindwing. Similar to the male except the sub-marginal spots are white instead of yellow.
On the ventral, the sub-marginal spots are a very dark hue of yellow.

Genitalia. (Figure 6-63b) Similar to *H. aristor*.

Variation. Sexes dimorphic.

Natural History. Similar to *H. aristor*, this species is somewhat rare. Not much has been recorded on the biology of this species. It is known to frequent open areas around plantations and is rarely found in the mountains.

Life History. Larvae appear to have a similar appearance to those of *H. anchisiades* (Smith et al., 1994) but adults look more closely affiliated with *H. aristor* and the *thoas* subgroup (Rothschild and Jordan, 1906). Mature larvae are black dorsally with dark brown along the sides, bold white lateral markings on the first thoracic segment, and the third to fifth segments. These lateral marks however do not meet to form a saddle (Riley, 1975; Smith et al., 1994).

Type(s). “Type 7240 / Papilio / caiguanabus / Poey // Cuba / Poey Coll.? / No 2 // Papilio / caiguanabus Poey / det. Poey”; “Exch. A.N.S.P. / C. M. Acc. 20359 // Paratype ♀ / Papilio / caiguanabus / Poey // Cuba / Poey Coll.? / No 2 // Papilio / caiguanabus / Poey / det. Poey”; Caiguanabus / Poey / Nomicus Hpfr. / New. Ex. Bull nr 46 f. 17 / Cuba Richt // Holotype ♂ / Papilio nomicus / Hopffer, 1856 // 186”.

Distribution (Figure 6-73). Cuba.

Remarks. IUCN Red list of threatened species lists this species with an indeterminate status.

The “*thersites*” Subgroup

This subgroup consists of seven species, *H. thersites*, *H. androgeus*, *H. astyalus*, *H. ornithion*, *H. aristodemus*, *H. andraemon*, and *H. machaonides* (Figure 4-15).

Heraclides thersites (Fabricius, 1775)

Papilio thersites (Fabricius, 1775): 453.

Papilio palamedes (Fabricius, 1775): 454 – preoccupied name.

Papilio acamas (Fabricius, 1793): 8.

Diagnosis. Well developed central band in the forewing and hindwing of the male. The female forewing has a crescent shaped central band and is missing the SMB.

Adult Male (Figure 6-7a) *Body*. Similar to *H. thoas*.

Forewing. Length 51-59 mm (n = 5). The central band well developed and broad, about 80% of wing; its costal and apical branches generally merged. The discal spot is a diffused spot in the discal cell near the central band. The sub-marginal is lost, and the marginal band is very close to the wing margin and represented by small spots on the wing’s outer edge. The sub-marginal element of the eye spot is small. The ventral looks similar to the dorsal, but with yellow of the central band and the discal spot more diffused. There are about four spots of the sub-marginal near the wing edge. The eye spot has all three elements clearly visible.

Hindwing. The central band is well developed and broad; about 75% of the wing. The spots of the proximal post-discal band are near the wing margin. The spots of the inner post-discal band are seen as sprinklings of light blue scales. No proximal post-discal spots are visible. The eye spot has the proximal post-discal band element red and crescent shaped, with very little yellow scales. The well developed tail has no tail spot. The ventral has the marginal band, sub-

marginal band, inner post-discal band, and proximal post-discal spots visible. The yellow spots of the marginal band are clearly visible, the spots of the sub-marginal are yellow and broad, the spots of the inner post-discal band seen as light blue scales arranged roughly in crescent shapes, and the red spots of the proximal post-discal band are close to the inner post-discal band.

Genitalia. (Figure 6-43) The rim of the valve is rounded and the ventral edge of the harpe is drawn out into a broad heavily sclerotized spine which does not go to the edge of the valve and is free of the valve. There is a vertical serrated tooth-like projection, free of the valve surface, on the dorsal edge of the harpe. The 8th tergite has the pseuduncus intermediate ($\geq 1 < 2$ mm) and broad at the base, narrowing to a rounded tip. The uncus terminates in a small knob. There is little sub-terminal swelling. The aedeagus is long (> 3 mm), strongly curved, with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with narrow arms.

Adult Female (Figure 6-7b) *Body.* Similar to the males but with very little yellowing of the tegula.

Forewing. Length 61-63 mm (n = 2). Ground color is black, with the central band as an arch from the apical branch, curving down to the anal angle. The spots of the sub-marginal are reduced and may be represented by a few at the anal angle, very close to the wing margin, often merging with marginal spots. The ventral surface is similar to dorsal, with the central band ‘arch’ more diffused.

Hindwing. Similar to the male with a loss of the central band. The well developed tail has no tail spot. The eye spot has all three elements clearly visible.

Genitalia. (Figure 6-63c) There is much armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule and opens centrally, supported by a ridge. Around the opening of the ostium the plates are highly sclerotized and fused anteriorly, below the ostium. These plates merge with highly sclerotized peripheral vestibular plates anteriorly to give rise to a knob-like projection posterior to, and below the ostium. The peripheral vestibular plates are broad and highly sclerotized and fuse anterior to, and below the ostium. Very long lateral peripheral arms arise medially from the peripheral vestibular plates. The top of the arms are “antler-like”. There is no sclerotized tongue-like plate, instead there is a slightly sclerotized out-pocketing just above the ostial opening; there is no trough between the peripheral vestibular plates and the out-pocketed ridge on which the ostium opens. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. Sexes dimorphic.

Natural History. This species can frequently be found in dry coastal hills 150 - 600 meters. Adults are most active during the hottest time of the day, and appear to be especially fond of sunshine. Males can be observed flying in lazy circles while females have a more direct and powerful flight. This species can be found flying throughout the year. Nectar sources are varied but I have observed adults males and females having a strong preference for *Lantana* spp., repeatedly visiting patches in an apparent repetitive pattern.

Life History. Eggs are about 1.5 mm, spherical and whitish (pale green according to Brown and Heinemann, 1975). They are laid on the tips of host plant leaves and darken before hatching. Larvae of this species reportedly resemble those of *H. androgeus*. Shortly after hatching the larvae are hairy and black with two grey saddles and a white terminal segment. Larvae then become prickly in appearance with two spots anteriorly, two spots centrally, and two spots posteriorly. They afterwards appear warty in appearance with long pinkish osmeterium. These larvae have the typical bird droppings appearance. They have a shiny head and generally a

dirty brown color. As they mature the osmeterium becomes orange or orange with blue tips. A detailed description of the larvae of this species is provided by Townsend (1893). Pupae are around 38 mm long and 10 mm wide, pale yellow-brown darkening to a mottled grey. Male pupae are light brown with female pupae being black closer to emergence (Brown and Heinemann, 1972; Riley, 1975; Smith et al., 1994).

Type(s). “Pap. Thersites / Fabr. Pag 18 N° 68 [UMG]”; “Co- / type. // Pap. palamedes / Fabr. Pag 18 N° 73 [UMG – two specimens with same label]”.

Distribution (Figure 6-73). Jamaica.

Remarks. The adults are strongly attracted to dense populations of *Lantana* near Guava (*Psidium*) groves.

Heraclides androgeus (Cramer, 1775)

Diagnosis. Similar to *H. thersites* but with reduced pale sub-marginal spots on the male forewing, thin short tails and blue iridescent scales on the wings of the females.

Variation. Very variable with dimorphic sexes.

Natural History. Ranging from lowland to over 1000 m but have been known to occur above 2000 m, adults often frequent open agricultural lands near *Citrus* trees but are primarily a mountain species (Smith et al., 1994). They have a frantic, powerful direct flight several meters in the air. Males are known to puddle. Flight times are throughout the year peaking from June to August. Immature stages have reached minor pest status in the past. Nectar plants include *Citrus* spp., *Zinnia elegans*, *Hibiscus* spp., *Cordia* spp., and *Lantana* spp. (Smith et al., 1994). Typically of this genus, eggs are laid singly on the tip of host plant leaves.

Life History. Eggs are cream-colored although DeVries (1987) described the eggs of *H. androgeus epidaurus* as pale green, turning to deep yellow. Larvae have an orange-brown head with a dark olive body. The anterior portions are expanded into a false head; the prothoracic segments have an orange stripe along each side. These lateral orange stripes become green further along the length and unite with each other dorsally on the 7th segment. A saddle shaped patch is on segment 10 to 12. There are knoblike tubercles on all segments with a blue crescent at each base. There are also rows of blue spots along the length of the body and the prolegs are white; larvae look similar to bird droppings. Pupae are similar to those of *H. thoas* but with cowl being formed from an expansion of the thoracic horn; lichen-like patches may also be present on the body (Riley, 1975; DeVries, 1987; Smith et al., 1994).

Distribution (Figure 6-74). From Florida (US(A) east to Texas and Mexico, south through Central America to South America all the way to northern Argentina. Also found in the Caribbean (not Jamaica).

Remarks. There are three recognized subspecies.

Heraclides androgeus androgeus (Cramer, 1775)

Papilio androgeus (Cramer, 1775): 24, plate 16, figure C & D.

Papilio orestes (Meerburgh, 1777): plate 26, 30.

Papilio polycaon (Cramer, 1779): 17, plate 203, figure A.

Papilio piranthus (Cramer, 1779): 18, plate 204, figure A & B.

Papilio acanthus (Gmelin, 1790): 2231 – misspelling.

Papilio androgeus bagous (Fruhstorfer, 1907): 357

Papilio androgeus form mira (Fassl, 1922).

Papilio androgeos form *feyeri* (Niepelt, 1924): 49 – original misspelling.

Papilio androgeus variety *fassli* (Knop, 1925): 43.

Papilio androgeus androgeus aberration *decellei* (Krüger, 1934): 151.

Papilio hibisci (Fabricius, 1938): 34 – replacement name.

Papilio altheae (Fabricius, 1938): 48 – preoccupied name.

Adult Male (Figure 6-7c) *Body*. Similar to *H. thoas*.

Forewing. Length 52-73mm (n = 43). Similar to *H. thersites*, but with central band narrower, 50% to 60% of the wing. The discal spot is similar to *H. thersites*. The ventral surface is similar to *H. thersites* males, but with sub-marginal spots faint and near the wing margin.

Hindwing. Similar to *H. thersites* males, but with sub-marginal spots very faint, over scaled with black scales, and a very narrow short tail.

Genitalia. (Figure 6-44) Similar to *H. thersites* but with the vertical serrated tooth-like projection shorter and more fan-like.

Adult Female (Figure 6-7d and 6-7e) *Body*. Similar to *H. thersites* females.

Forewing. Length 58-70 mm (n = 15). Blue iridescence can be seen in the scales. It can be seen with or without a large spot between M1, M3, and discal cell; this spot is made up of elements of the central band and the discal spot.

Hindwing. Similar to *H. thersites* females, but with reduced sub-marginal spots and a shorter tail.

Genitalia. (Figure 6-63d) Similar to *H. thersites*.

Type(s). “androgeus / bagous / Fruhst. // Rio Uauppes / Dr. Theod. Koch. / Coll.

Fruhstorfer // Type // Fruhstorfer Coll. / M.M. 1937-286”; “*P. androgeus* ♀ / forma *feyeri* / Niep // 58 26 / Type / Ecuador // Type // Presented by / J. J. Joicey Esq. / Brit. Mus. 1931-291.”; “Holotype // 342 3 // Mus. Rousseau-Decelle // Type *P. androgeus* ♀ / *androgeus* ab. / Y. P. d. [?] *Decellei* Kr. // [?] der / ♀ [?] Paulo de / Oliverza 2/4.32”

Distribution. Guyana to lower Amazon, east to some Andean Valleys and all of Orinoco.

Remarks. From Guyana east to northern Brazil and South through all Amazon area and in some Andean Valleys.

Heraclides androgeus epidaurus (Godman & Salvin, 1890)

Papilio epidaurus (Godman & Salvin, 1890): 224 (also in 3: plate 69, figure 1-3.)

Papilio androgeus epidaurus form *ochracea* (Beutelspacher, 1976): 63.

Adult Male (Figure 6-8a) *Body*. Similar to the nominate subspecies male.

Forewing. Length 50-63 mm (n = 73). Similar to the nominate subspecies male.

Hindwing. Similar to the nominate subspecies male.

Genitalia. (Figure 6-44c2) Similar to the nominate subspecies with slight variations of the vertical serrated tooth-like projection.

Adult Female (Figures 6-7f and 6-8(b) *Body*. Similar to the nominate subspecies female.

Forewing. Length 55-66 mm (n = 37). Similar to the nominate subspecies female but never with large spot; reduced yellow forewing markings. Iridescent scales may be more pronounced.

Hindwing. Similar to the nominate subspecies female.

Genitalia. (Figure 6-63e) Similar to the nominate subspecies.

Type(s). “B. C. A. Lep. Rhop. / *Papilio* / *Epidaurus*, / G. & S. / Godman-Salvin / Coll. 1918.-4. // ♂ // Calobre, / Panama. / Arce. // Type / H. T.”

Distribution. Florida, Caribbean Islands (Trinidad, St Lucia, and St. Vincent; not Jamaica, Texas through Central America to western Ecuador, northern Venezuela.

Remarks. No additional information is available.

Heraclides androgeus laodocus (Fabricius, 1793)

Papilio laodocus (Fabricius, 1793)

Papilio laodocus form *limbatus* (Boullet & Le Cerf, 1912): 24.

Papilio laodocus form *vollmanni* (Lederer, 1961): 45.

Adult Male (Figure 6-8c) *Body.* Similar to the nominate subspecies male.

Forewing. Length 54-60 mm (n = 13). Similar to the nominate subspecies male.

Hindwing. Similar to the nominate subspecies male.

Genitalia. (Figure 6-44c3) Similar to the nominate subspecies with slight variations in the length of the vertical serrated tooth-like projection.

Adult Female (Figure 6-8d) *Body.* Similar to the nominate subspecies female.

Forewing. Length 58-65 (n = 6). Similar to the nominate subspecies female but always with a large bar shaped white spot on the wing at m2-m3, m3-cu1 and into discal cell.

Hindwing. Similar to the nominate subspecies female.

Genitalia. (Figure 6-63f) Similar to the nominate subspecies.

Type(s). “Coll. Boullet / Museum Paris / Paraguay / 1910 / G. A. Baer (Gauzler) // Holotype ♂ / *Papilio androgeus* / *laodocus* f. *limbatus* / Boullet + Le Cerf. 1912 // Type”.

Distribution. Eastern Brazil from Alagoas south to Rio Grande del Sol and west to Paraguay and northern Argentina.

Remarks. No additional information is available.

Heraclides astyalus (Godart, 1819)

Diagnosis. Males always with a discal spot and the females with short tails. Females may be co-mimics with *H. androgeus androgeus* and *H. androgeus epidaurus* females.

Variation. Sexes dimorphic.

Natural History. This butterfly can be found in very humid tropical woodlands and flies from sea level to 1500 meters with *H. androgeus epidaurus* (Le Crom et al., 2002). They are most abundant in June and July, just before or during the rainy season (DeVries, 1987). Adults nectar on *Cordia* sp., *Stachytarpheta* sp., *Lantana* sp., *Ixora* sp., *Inga* sp., and *Senecio* sp and are most active in the morning. Solitary males are often seen puddling alongside pierids and females are rarely collected (DeVries, 1987).

Life History. Eggs are yellow and deposited typically on the leaves of host plants (Scriber and Lederhouse, 1996). Eggs and immature stages resemble those of *H. thoas* except pupae of *H. astyalus* more slender and has a longer thoracic tubercle (DeVries, 1987).

Distribution (Figure 6-75). Widely distributed from Texas through Central America to South America.

Remarks. This species varies across the range. The appearance of the female can be similar to a more melanized male or can be totally different as in the six other subspecies. The males of some subspecies are almost indistinguishable from *H. ornythion* males. There are six recognized subspecies.

Heraclides astyalus astyalus (Godart, 1819)

Papilio astyalus (Godart, 1819): 62.
Heraclides lycophron (Hübner, [1823]): plate 100.
Papilio mentor (Dalman, 1823): 37.
Papilio pirithous (Boisduval, 1836): 358 – preoccupied name.
Papilio oebalus (Boisduval, 1836): 360.
Papilio drepanon (Gray, 1856): 53 – nomen nudum.
Papilio lycophron drepanon (Fruhstorfer, 1907)
Papilio lycophron aberration *delunensis* (Niepelt, 1916): 21, plate 13, figure 10.
Papilio lycophron form *paulina* (Krüger, 1934): 152 – preoccupied name.
Papilio lycophron lycophron form *thersitoides* (Rousseau-Decelle, 1943): 111.
Papilio lycophron pirithous form *suffusa* (Rousseau-Decelle, 1943): 111.

Adult Male (Figure 6-8e) *Body*. Similar to *H. thoas*.

Forewing. Length 34 mm. Similar to *H. androgeus* male, but with the ventral having larger and more pronounced sub-marginal spots.

Hindwing. Similar to *H. androgeus* male but with a longer, wider, and more developed tail and with large yellow spots in the sub-marginal band. The central band also does not go pass the distal edge of the discal cell and the eye spot is much more developed. The ventral also has longer spots of the sub-marginal band.

Genitalia. (Figure 6-45) Similar to *H. androgeus* with slight variations of the vertical serrated tooth-like projection and the shape of the ventral spine on the harpe.

Adult Female (Figures 6-9a and 6-9b) *Body*. Similar to the male, but darker especially on the abdomen. Yellow spots can be seen on the abdomen ventrally on the margins.

Forewing. Length 40-50 mm (n = 6). Similar to the male, but much more melanized, with the spots of the sub-marginal showing, except for the most apical one. The central band is either absent or starts out at the anal edge and fades before reaching the discal cell. A pale arch reminiscent of the central band can be seen around the distal edge of the discal cell. A discal spot is sometimes present. The ventral surface is similar to the dorsal.

Hindwing. Similar to the male, but with shorter sub-marginal spots and now showing the red spots of the proximal post-discal band, except the most apical. The eye spot is more developed and now has the red proximal post-discal band element. The ventral surface is similar to the dorsal, but now showing the most apical post-discal spot.

Genitalia. (Figure 6-64a) Similar to *H. thersites* with slight variations in the raised conjoined sclerotized spikes.

Type(s). “Coll. Dujardin / Museum de Paris // *Astyalus* / God.”; “Naturhistoriska / Riksmuseet / Stockholm / Loan no 83/92 // *Mentor*. / Nov. Sp. Dalm. Anal: / I. p. 37. // Lectotype ♂ / *Papilio mentor* / Dalman, 1823 / G. Lamas det. 1992”; “Coll. Lacordaire / Museum de Paris // Type”; Brezil / Coll. Lacordaire / Museum de Paris / [label ventral] *oebalus* / A // Type”; “*lycophron* / *drepanon* / Fruhst. // Type // Type // Rio Grande / Brasil / ex coll. Fruhstorfer // Fruhstorfer Coll. / M. M. 1937-285”; “342 7 // Theoph Ottn / [?] // Holotype // Theophilo Ottoni / Minas Geracis / Brazil // Type *P. lycophoron* / ♀ f. *paulina* / Kr. // Mus. Rousseau-Decelle”; “Pap. *Lycophron* Hbn. / [?] *lycophron* Hbn / f. *thersitoides* / nova / Holotype ♂ / MMRousseauDecelly[?] // Bella Vista / [?] / Argentina // Mus. Rousseau-Decelle // 342 1 // 31 // Holotype”; “Coll. Boulet / Museum Paris / Paraguay / 1910 / Dancaster // Holotype // Type // Pap. *Lycophron* / ♀ *pirithous* Boisd. / ab. *Suffuse* / Holotype / MrouseauDucelle”.

Distribution. Eastern Brazil and west through Paraguay to Bolivia and Tucuman, and south to Uruguay.

Remarks. The female may at times look similar to a melanized male.

Heraclides astyalus anchicayaensis Constantino, Le Crom & Salazar, 2002

Heraclides astyalus anchicayaensis Constantino, Le Crom & Salazar, 2002: 82.

Adult Male (Figure 6-9c) *Body*. Similar to the nominate subspecies male.

Forewing. Length 55 mm. Similar to nominal subspecies male but lacking the most apical spot of the central band. A well developed eye spot is also present.

Hindwing. Similar to the nominate subspecies male but with the eye spot only showing the sub-marginal element. The ventral has the spots of the inner post-discal band darker blue and the spots of the proximal post-discal band less red, some showing yellow at the edges of the discal cell, merging with the central band and almost being lost near the costal margin.

Genitalia. Not dissected.

Adult Female (Figure 6-9d) *Body*. Similar to the nominate subspecies female.

Forewing. Length 55 mm. Similar to the nominate subspecies female.

Hindwing. Similar to the nominate subspecies female but with the eye spot having a larger sub-marginal element. The inner post-discal band element is also more developed. Here, the proximal post-discal spots are yellow. The ventral surface is similar to the nominate subspecies female but reflecting the eye spot characteristics of the dorsal; the proximal post-discal spots are red.

Genitalia. Not dissected.

Type(s). Original description identifies five types. The following are deposited in the collection of the Constantino family in Cali, Colombia: Holotype - ♂, Department of Valle, río Tatabro, low Anchicayá, 100 m, 1-IV-1978; Allotype - ♀, Department of Valle, Bella Vista, high río Anchicayá, 570 m, 10-VII-1998; Paratype - ♂, Department of Valle, río Aguaclara, bajo Anchicayá, 100 m, 18-V-1986; Paratype – Caimancitom río Cajambre, 75 m, 8-VIII-1983; Paratype – Yatacué, high Anchicayá, 7XI-1998. The following are deposited in the collection of Schmidt-Mumm, Museo del Instituto Von Humboldt, Villa de Leyva, Colombia: ♂, Choco, 200 m, 20-II-1978; ♀, lago Calima, río Bravo, 1200 m, 12-X-1984.

Distribution. West coast of Colombia.

Remarks. No additional information is available.

Heraclides astyalus bajaensis (Brown, Real & Faulkner, 1992)

Papilio astyalus occidentalis (Brown & Faulkner, 1984): 5, figure 3a - 3c - preoccupied name.

Papilio astyalus bajaensis (Brown, Real & Faulkner, 1992) – replacement name.

Adult Male (Figure 6-9e) *Body*. Similar to the nominate subspecies male.

Forewing. Similar to the nominate subspecies male but with the central band narrower and sub-marginal spots near the wing margin.

Hindwing. Similar to the nominate subspecies male but with the central band a little more than ½ the length of the discal cell. The ventral over extends the dorsal central band width just a little and the arrangement of spots are similar to the nominate subspecies male.

Genitalia. (Figure 6-45c2) Similar to the nominate subspecies with slight variations of the vertical serrated tooth-like projection and the shape of the ventral spine on the harpe.

Adult Female (Figure 6-9f) *Body*. Similar to the nominate subspecies female.

Forewing. Length 60 mm (n = 1). Similar to the nominate subspecies female, but darker, with the costal branch of the central band showing as a few spots near the costal margin around the discal cell outer margin.

Hindwing. Similar to *H. astyalus anchicayaensis*, but with wider tails and red post-discal spots. The ventral surface is similar to the dorsal, but with a more defined costal proximal post-discal spot.

Genitalia. (Figure 6-64b) Similar to the nominate subspecies.

Type(s). “*Papilio astyalus / occidentalis / Brown & Faulkner / Paratype // Mexico: Baja Calif. Sur / 49 km.N. Todos Santos / 29 Aug. 1982 / leg: Faulkner, Brown // Allyn Museum / Acc. 1984-3 // MGCL/FLMNH / Specimen no. / 40438 [♂]*”; “*Papilio astyalus / occidentalis / Brown & Faulkner / Paratype // Mexico: Baja Calif. Sur / 49 km.N. Todos Santos / 29 Aug. 1982 / leg: Faulkner, Brown // Allyn Museum / Acc. 1984-3 // MGCL/FLMNH / Specimen no. / 40439 [♀]*”; “*Papilio astyalus / occidentalis / Brown & Faulkner / Paratype // Mex: Baja Calif. Sur / 6 mi. E Todos Santos / X-4-1981 / D. Faulkner & F. Andrews [♀]*”.

Distribution. Southern Baja, California, along the west coast of Mexico to Oaxaca.

Remarks. Adults can sometimes be confused with *H. ornythion* with which it is sympatric. This has interesting biogeographic implications. It may well be that at one point in time these two species shared a common ancestor. They may have initially separated through allopatric speciation and then subsequently became sympatric due to the removal of the original geographic barrier.

Heraclides astyalus hippomedon (Felder & Felder, 1859)

Papilio hippomedon (Felder & Felder, 1859): 393.

Papilio theophron (Felder & Felder, 1864): 311 – nomen nudum

Papilio theophron (Felder & Felder, 1865).

Papilio hippomedon form *iraidari* (Lichy, 1960): 49.

Papilio hippomedon form *taini* (Lichy, 1960).

Adult Male (Figures 6-10 and 6-10c) *Body*. Similar to the nominate subspecies male.

Forewing. Similar to the nominate subspecies male.

Hindwing. Similar to the nominate subspecies male but with yellowing around the edges of the proximal post-discal spots and the central band extending outside of the discal cell.

Genitalia. (Figure 6-45c3) Similar to the nominate subspecies with slight variations of the vertical serrated tooth-like projection and the shape of the ventral spine on the harpe.

Adult Female (Figures 6-10b and 6-10(d) *Body*.

Forewing. Length 45 mm (n = 2). Similar to the nominate subspecies.

Hindwing. Similar to the *H. androgeus epidaurus* female, but with the iridescent scales limited to the area outside the discal cell in place of the post-discal spots; also with the short thin tail. The dorsal of the wing can also resemble the ventral of the *H. androgeus epidaurus* female. The ventral surface reflects the dorsal surface of the *H. androgeus epidaurus* female, but the spots more defined.

Genitalia. (Figure 6-64c) Similar to the nominate subspecies.

Type(s). “*Hippomedon n. // Rothschild / Bequest / B. M. 1939-1. // Type // Felder / Collⁿ // Type*”; “*Nova / Grande / Lindig // Theophron n. // Felder / Collⁿ // Rothschild / Bequest / B. M. 1939.1.*”; *Tipo / Papilio astyalus / hippomedon Fld / f. indiv. ♀ / iraidari Ly // col. / J. Requena // Fotografia / N^o 5 del / studio de / R. Lichy (1960) // Rancho Grande / A. R. Venezuela / 1100 m*

12.vi.58 // R. Lichy det. 1959”; “Tipo Papilio astyalus / hippomedon Fld. / f. inviv ♀ / taini Ly // Fotografia / N° 7 del / studio de / R. Lichy (1960) // R. Lichy det. 1959 // Rancho Grande // 1200 m R. [?] / Venezuela 19.vi.53 / C. J. [?]”; “Rothschild / Bequest / B. M. 1939-1. // Felder / Collⁿ // Lecto / Type // Nova / Grande / Lindig”.

Distribution. Panama to northern Colombia, east through Venezuela to lower and middle Amazon.

Remarks. No additional information is available.

Heraclides astyalus pallas (Gray [1853])

Papilio pallas (Doubleday [1845]) nomen nudum.

Papilio pallas (Gray [1853]): 39, plate 6, figure 1.

Papilio hozaus (Ehemann, 1921)

Adult Male (Figure 6-10e) *Body*. Similar to the nominate subspecies.

Forewing. Similar to *H. astyalus bajaensis* males in the south of Mexico, but with the central band broader in other parts of the range.

Hindwing. Similar to *H. astyalus bajaensis* males in the south of Mexico, but with the central band broader in other parts of the range.

Genitalia. (Figure 6-45c4) Similar to the nominate subspecies with slight variations of the vertical serrated tooth-like projection and the shape of the ventral spine on the harpe.

Adult Female (Figure 6-10(f) *Body*. Similar to the nominate subspecies female.

Forewing. Length 55-58 mm (n = 2). Similar to that of *H. astyalus hippomedon*.

Hindwing. Similar to that of the *H. androgeus androgeus* female and the *H. astyalus hippomedon* female variant, with the dorsal and ventral resembling the ventral of the *H. androgeus androgeus* and *H. androgeus epidaurus* female; the tail is short and thicker.

Genitalia. (Figure 6-64d) Similar to the nominate subspecies.

Type(s). “Pallas // Oajaca / Mexico. / Purch. From / Hanweg / 44 – 13 // Mexico // Type”; “P. hozaus Ehem. ♂. / Type / Underwood col. ¾. / San Jose Costa Rica // Ehrman Coll. / Car. Mus. / Acc. 7815. // Oberthür / Collection / Acc. 12720 // Type”

Distribution. Southern Texas to northern Costa Rica.

Remarks. This subspecies is sympatric with *H. astyalus bajaensis* in the southern part of Mexico around Oaxaca. They can also be confused with males of *H. ornythion*. The similarity of this subspecies with *H. astyalus bajaensis* makes it difficult to separate the subspecies in the Oaxaca region. This suggests that these two subspecies may be closest to each other and to *H. ornythion*.

Heraclides astyalus phanias (Rothschild & Jordan, 1906)

Papilio lycophron phanias (Rothschild & Jordan, 1906): 575.

Papilio lycophron brunneus (Prüffer, 1922): 2.

Adult Male (Figure 6-11a) *Body*. Similar to the nominate subspecies male.

Forewing. Similar to *H. astyalus hippomedon* male; tail slightly longer and wing overall darker.

Hindwing. Similar to *H. astyalus hippomedon* male; tail slightly longer and wing overall darker.

Genitalia. (Figure 6-45c5) Similar to the nominate subspecies with slight variations of the vertical serrated tooth-like projection and the shape of the ventral spine on the harpe.

Adult Female (Not figured) *Body.* Similar to the nominate subspecies female.

Forewing. Length 43-58 mm (n = 12). Similar to a very dark form of *H. astyalus bajaensis*, with or without a spot near the costal margin.

Hindwing. Similar to a very dark form of *H. astyalus bajaensis*, but without all other spots except for the sub-marginal ones.

Genitalia. Not dissected.

Type(s). “Lectotype / phanias / foto KB 9/88 // Rothschild / Bequest B. M. 1939-1. // Zamora, / Ecuador, / 3-4000ft. / (O. T. Baron). // Lecto / Type”

Distribution. Western and southern Venezuela to the Andes in Colombia and south to Bolivia across the entire western Amazon.

Remarks. A dark form in both the males and females (Tyler et al., 1994).

Heraclides ornythion (Boisduval, 1836)

Papilio ornythion (Boisduval, 1936): 354.

Diagnosis. Almost never with a discal spot.

Adult Male (Figures 6-11b, 6-11d, and 6-12a) *Body.* Similar to *H. astyalus bajaensis* male.

Forewing. Length 43-57 (n = 170). Similar to the *H. astyalus bajaensis* and some *H. astyalus pallas* males but without the discal spot.

Hindwing. Similar to the *H. astyalus bajaensis* and some *H. astyalus pallas* males but with the yellow sub-marginal spots being more extensive and confluent.

Genitalia. (Figure 6-46) Similar to *H. astyalus* but with slight variations of the vertical serrated tooth-like projection and the shape of the ventral spine on the harpe.

Adult Female (Figures 6-11c, 6-11e, and 6-12b) *Body.* Similar to the *H. astyalus* female.

Forewing. Length 45-61 mm (n = 27). Similar to the male or darker, gradually losing the central band, becoming darker from the inner margin up to the costal margin.

Hindwing. Similar to the male or with the loss of the central band.

Genitalia. (Figure 6-64e) Similar to *H. thersites*.

Variation. Females may resemble males or may appear as a darker form.

Natural History. A survey of the literature provided no additional information.

Life History. Not much is known of this butterfly's life history except that the larvae, which are similar to that of *H. astyalus* but more orange in color.

Type(s). Probably in Museum National d'Histoire Naturelle, Paris, France (MNHP). A request for information sent and the type was not found. The original description did not provide adequate information about the type. Type presumed lost.

Distribution (Figure 6-76). Southern Texas and Arizona and most of Mexico.

Remarks. This species is closely associated with *H. astyalus*. It is often indistinguishable from the sympatric *H. astyalus* in parts of the range. Additional investigations are needed into the relationship between these two species. The male and female genitalia are also similar and cannot be used to easily separate the species lending further evidence to the theory that these two species are closely related. This is also supported by the phylogeny of the group.

Heraclides andraemon Hübner, [1823]

Diagnosis. Central band with most of the spots rectangular, almost parallel to the outer margin of the wing, and generally of equal size, except for the most apical in the. The forewing also has a discal spot and is missing the sub-marginal spots. The hindwing has the central band decreasing in diameter from the costal margin to a point at the inner margin. There is also a spot of black scales within the yellow central band, at the apex of the discal cell on the hindwing.

Variation. Three subspecies are described. Within a given subspecies there may be differences in the brilliance of the yellow coloration and size of wing pattern elements.

Natural History. Common in Cuba, throughout the Bahamas, Turks and Caicos, and Cayman Islands. The Cuban subspecies first appeared in Jamaica in 1945 and has since been well established, often becoming a pest on *Citrus*, and thought to be outcompeting native swallowtails because of its abundance. It has also been sporadically reported from the Florida Keys. It frequents hardwood hammocks and marginal areas around them and will also visit gardens. A very fast and active flier it has a very direct flight and is most active at noon (Smith et al., 1994). Open field communal roosting has been recorded for this species. Adults visit a variety of nectar sources including cultivated garden plant, *Citrus*, *Bourreria ovata*, *Dalbergia brownei*, *Lantana involucrata*, *Stachytarpheta jamaicensis*, *Bidens*, *Heliotropium angiospermum*, *Metopium toxiferum*, *Morinda royoc*, *Zanthoxylum fagara*, *Melanthera aspera*, and *Melanthera nivea*. Males generally fly along trails and the edges of hammocks while females search in hammocks for adequate host plants to lay eggs (Mino & Emmel, 1993). It appears to fly throughout the year from late March to November, peaking in July and August. Yellowish-green eggs are laid on the leaf tips and dorsal of young leaves of food plants.

Life History. Females lay whitish eggs that turn brown before hatching. Eggs hatch after five days to give a warty looking first instar with the first segment white. After molting the first time the larvae are mainly black with the first and last segments white (Brown and Heinemann, 1972). Larvae have been reportedly reared on *Citrus*, *Zanthoxylum fagara*, *Ruta*, *Amyris elemifera*, *Fagara*, and *Piper*. The larvae are similar to that of *H. cresphontes*, but smaller, with the head of mature larva dark brown, and the body being a mottled reddish-brown and gray. There is a creamy saddle with a few bluish and white spots and a whitish lateral line along the sides. The ventral side and prolegs are lilac. There are two small forward-pointing lobes on the prothorax and the anterior portion of the caterpillar's body is strongly curved away from the substrate (Smith et al., 1994; Mino and Emmel, 1993). Pupae are pinkish brown with green spotted brown wing cases and abdomen and appear twig like. Mino and Emmel (1993) records adults being eaten by dragonflies.

Distribution (Figure 6-77). Florida Keys, the Bahamas, Cayman Islands, Cuba and Jamaica.

Remarks. Quite abundant, often can be regarded as a pest. There are three recognized subspecies.

Heraclides andraemon andraemon Hübner, [1823]

Heraclides andraemon Hübner, [1823]: plate 98 & 99.

Papilio (Heraclides) andraemon hernandezii Torre, 1936: 333.

Adult Male (Figures 6-12c and 6-12e) *Body*. Similar to *H. thoas* but with the club of the antenna yellow almost to the last segment.

Forewing. Length 38-46 mm (n = 20). The central band has rectangular spots which are almost parallel to the outer margin; most of these spots are equal in size except for the spots of the apical and costal branches. The costal and apical branches meet at the junction where the R4 joins the R5 vein. The discal spot is bar-like, in the upper section of the discal cell perpendicular to the axis of the discal cell. The long tail has a prominent tail spot. The ventral reflects the dorsal, but with the yellow of the spots and bands more extensive and confluent. The sub-marginal spots are present on the ventral except for the most apical.

Hindwing. The central band decreases in diameter from the costal margin to a point at the inner margin. The eye spot is well developed but is missing the proximal post-discal element. The inner post-discal element of the eye spot is a crescent shape of blue light blue scales. The spots of the inner post-discal band are present as diffused aggregations of light blue scales reduced in size as they arch up to the costal margin. There is a spot of black scales within the yellow central band, at the apex of the discal cell. The ventral surface reflects the dorsal surface but with the inner post-discal spots more pronounced and the red proximal post-discal spot at m3-cu1 very large, almost triangular sandwiched between two smaller more diffused proximal post-discal spots.

Genitalia. (Figure 6-48) The rim of the valve is rounded and the harpe is angular, almost box shaped, with a downward pointing spine at the end of the ventral rim and with the distal surfaces covered with serrations and elevated from the valve and reaching the valve edge. The valve encircles the harpe dorsally. The 8th tergite has the pseuduncus short (<1 mm) and broad at the base, narrowing to a rounded tip. The uncus terminates in a small knob. There is little sub-terminal swelling. The aedeagus is short (≤ 3 mm), straight, with the vesica simple (no spines or sclerotizations). The juxta is "U" shaped with narrow arms.

Adult Female (Figures 6-12d and 6-12f) *Body.* Similar to the male except the club of the antenna is significantly less yellow.

Forewing. Length 45-50 mm (n = 10). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-65a) The ostium lies in a shallow wrinkled vestibule and opens centrally, supported by a ridge. Around the opening of the ostium the plates are sclerotized and fused anteriorly, below the ostium. These plates merge with the highly sclerotized peripheral vestibular plates anteriorly to give rise to a horn-like projection posterior to, and below the ostium. The peripheral vestibular plates are broad, short, and highly sclerotized and fuse anterior to, and below the ostium. Thick, circular lateral peripheral arms arise from the inner edge of the peripheral vestibular plates. The top of the arms are smooth and oval. There is no sclerotized tongue-like plate, instead there is a slightly sclerotized out-pocketing just above the ostial opening; there is no trough between the peripheral vestibular plates and the out-pocketed ridge on which the ostium opens. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Type(s). Probably lost or exists only as published image. The original description was lacking in adequate information and no image was seen.

Distribution. - Cuba, Jamaica, Little Cayman, and Cayman Brac.

Remarks. The population in Jamaica is thought to have been introduced.

Heraclides andraemon bonhotei (Sharpe, 1900)

Papilio bonhotei (Sharpe, 1900): 201.

Adult Male (Figure 6-13a) *Body*. Similar to the nominate subspecies.

Forewing. Length 36-46 mm (n = 90). Similar to the nominate subspecies.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-48c2) Similar to the nominate subspecies.

Adult Female (Figure 6-13b) *Body*. Similar to the nominate subspecies.

Forewing. Length 47-49 mm (n = 3). Similar to the nominate subspecies.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-65b) Similar to the nominate subspecies.

Type(s). “Nassau / (J. L. Bonhote.) / 13.6.98. / Bahamas / 1900 7 / [label ventral] Papilio / bonhotei, / E.M.Sharpe / ♂ Type // Type / [label ventral] Papilio / bonhotei / EM.Sharpe / ♂”.

Distribution. Florida Keys and Bahamas.

Remarks. Listed as endangered by the Florida Committee on Rare and Endangered Plants and Animals (FCREPA) and has a Florida Natural Areas Inventory (FNAI) status of S1 however, the State Wildlife Grants - Species of Greatest Conservation Need program gives it a low status.

Heraclides andraemon tailori (Rothschild & Jordan, 1906)

Papilio andraemon tailori (Rothschild & Jordan, 1906): 571.

Adult Male (Figure 6-13c) *Body*. Similar to the nominate subspecies.

Forewing. Length 42 mm (n = 1). Similar to the nominate subspecies.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-48c3) Similar to the nominate subspecies.

Adult Female (Figure 6-13d) *Body*. Similar to the nominate subspecies.

Forewing. Length 45-50 mm (n = 2). Similar to the nominate subspecies.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-65c) Similar to the nominate subspecies but with a larger horn-like projection below the ostium.

Type(s). “P. andraemon / tailori Type. / Nov. Zool. 1906. / R. & J. // Nov. Zool. 1906 / Pl. VIII. Fig. 51 // Rothschild / Bequest / B.M.1939.1. // G. Cayman / iv '06 / Taylor // Holo- / type”.

Distribution. Grand Cayman.

Remarks. Not considered endangered but can be quite rare in the dry season.

Heraclides aristodemus (Esper, 1794)

Diagnosis. With a distinctive “X” or “Y” on the forewing formed by the central band and the sub-marginal band; well developed post discal spots on the hindwing ventral.

Variation. The male has more visible yellow on the club of the antenna.

Natural History. Generally a dry lowland scrub and tropical hardwood hammock species, it can at times be found above 1000 m or straying into gardens and open areas (Smith et al., 1994). It also likes arid areas such as *Acacia* woods (Schwartz, 1989.) Adults fly rapidly near the ground (2 meters) but may sometime hover or fly leisurely in circular a pattern. This butterfly is not easily approached. Adults have been observed puddling and are most active in late morning with a second less active period before dusk. Flight period is between March and October but they are most abundant during the months of May, July, August, and October. Emergence is thought to be linked to rainfall and is thought to be a univoltine species, although a second brood occasionally occurs (Minno and Emmel, 1993). Nectar plants include *Lantana*

spp., *Bidens* spp., *Bauhinia divaricata*, *Alternanthera ramosissima*, *Borrchia arborescens*, *Canella winterana*, *Capraria biflora*, *Coccoloba diversifolia*, *Coccoloba uvifera*, *Dalbergia brownie*, *Heliotropium angiospermum*, *Melanthera aspera*, *Morinda royoc*, *Psidium guajava*, *Psychotria nervosa*, *Rania aculeate*, *Stachytarpheta jamaicensis*, *Cordia sebestena*, *Cordia exarata*, and *Tournefortia hirsutissima* (Minno and Emmel, 1993; Smith et al., 1994). Typical of most *Heraclides*, eggs are laid on the tips of leaves of host plants.

Life History. The small spherical cream-colored eggs darken before hatching and the larvae can grow up to 45 mm in length. Mature larvae are dark brown and have irregular blotches, cream in color, on their sides and back. There are several rows of blue dots along the body and the prolegs are cream in color. When disturbed, larvae tend to thrash their heads from side to side. Larvae are similar to those of *H. thoas*, being dark brown and twig like, possess a few dorsal protuberances and may grow up to 35 mm in length (Minno and Emmel, 1993; Smith et al., 1994).

Distribution (Figure 6-78). Florida Keys, the Bahamas, Cayman Islands, Cuba, Hispaniola, Puerto Rico, and the Turks and Caicos.

Remarks. This species can easily be considered more closely aligned with the “*thoas*” subgroup due to the general pattern of the wing and its natural and life history. The phylogeny supports its inclusion in the “*thersites*” subgroup and the most recent date it could have shared a common ancestor with the “*thoas*” subgroup may have been as far back as 21.62 MYA. Any resemblance to the “*thoas*” subgroup may be a result of convergent evolution. It may also be that this species is the oldest in this subgroup and thus the closest to the common ancestor shared with the “*thoas*” subgroup. There are five recognized subspecies.

Heraclides aristodemus aristodemus (Esper, 1794)

Papilio aristodemus (Esper, 1794): 8, plate 2.

Papilio cresphontinus (Martyn, 1797): plate 3, figure 4; plate 4, figure 10.

Papilio daphnis (Gray [1853]): 39 – preoccupied name.

Adult Male (Figure 6-13e) *Body.* Similar to *H. thoas* but with a broader black band on the dorsal abdomen.

Forewing. Length 47-56 mm (n = 2). Similar to *H. cresphontes*, but with the central band narrower and running the length of the wing. There is always a notch in the central band at r5-m1 where the apical and costal branches meet. There are usually only four sub-marginal spots, angles in towards the central band; together they form a rough “X” on the wing. The ventral reflect the dorsal but with the yellow being more confluent and runs almost to the wing margin in the sub-marginal spots.

Hindwing. With a well developed marginal band that flows around the edge of the long tail. There is no tail spot. The sub-marginal has the three apical spots circular and the more anal spots crescent shaped. The eye spot has the red sub-marginal element and a more diffused light blue inner post-discal element but lacks the post-discal element. The central band is much wider than on the forewing and gets paler as you move from the costal edge to the inner margin. The ventral has the yellowing more confluent and extending into the tail. The inner post-discal spots are well represented and the proximal post-discal spots are diffused and pale.

Genitalia. (Figure 6-47) Similar to the previous species (*H. thersites*, *H. androgeus*, *H. astyalus* and *H. ornythion*). Differs in that the ventral spine on the harp arises earlier. The

vertical serrated tooth-like projection is larger, flatter, and more triangular shaped, with more serrations on the outer edges.

Adult Female (Figure 6-13f) *Body*. As in the male.

Forewing. Length 45-58 mm (n = 3). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-64f) Similar to *H. thersites*.

Type(s). “Originalexemplar. // Esper. Ausl. Schm p. 240. / T. LIX. Equ. Archiv 19. / Fg 2. // Papilio / ♂ aristodemus Esp / Nov. Z. XIII p. 569. 72. // Collection / [?]”

Distribution. Hispaniola, Mona Island, and Puerto Rico.

Remarks. The palest of the subspecies.

Heraclides aristodemus bjordalae (Clench, 1979)

Papilio bjordale (Clench, 1979): 275.

Adult Male (Figure 6-14a) *Body*. Similar to the nominate subspecies.

Forewing. Length 37-42 mm (n = 35). Similar to the nominate subspecies but with the submarginal running the length of the wing and not forming an “X” with the spots of the central band. Central spots smaller and more angular.

Hindwing. Similar to the nominate subspecies but with a weaker eye spot and more developed inner post-discal spots which appear as diffused patches along the wing. Red proximal post-discal spots are in cells m1-m2 to cu1-cu2. The ventral has the yellow more confluent and the red proximal post-discal spots well developed; a small discal spot can also be seen at the apex of the discal cell but this is much smaller than in *H. paeon*.

Genitalia. (Figure 6-47c2) Similar to the nominate subspecies.

Adult Female (Figure 6-14b) *Body*. As in the male.

Forewing. Length 47-50 mm (n = 2). As in the male.

Hindwing. Similar to the male but with more developed band of red proximal post-discal spots.

Genitalia. (Figure 6-64g) Similar to the nominate subspecies.

Type(s). “Holotype ♀ / Papilio aristodemus / bjordale / H. Clench // Holotype No. / 690 / Carn. Mus. Ent. // Bahamas: Great / Inagua: Man of / War Bay, 4.X.1975 / Karen Bjorndal / CM Acc 29104”.

Distribution. Mayaguana, Turks and Caicos Islands, Great Inagua island and central Bahamas.

Remarks. Close to *H. aristodemus majasi*.

Heraclides aristodemus majasi L. Miller, 1987

Heraclides aristodemus majasi Miller, 1987: 2, figures 1-6.

Adult Male (Figure 6-14c) *Body*. Similar to *H. aristodemus bjordalae*.

Forewing. Length 36-45 mm (n = 2). Similar to *H. aristodemus bjordalae* but with a slightly wider central band.

Hindwing. Similar to *H. aristodemus bjordalae* but with the proximal post-discal band of spots paler.

Genitalia. (Figure 6-47c3) Similar to the nominate subspecies.

Adult Female (Figure 6-14d) *Body*. As in the male.

Forewing. Length 46-50 mm (n = 2). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-64h) Similar to the nominate subspecies.

Type(s). “Allyn Museum Photo / No. 87040819 / 7/8 // Allyn Museum / Acc. 1986-19 // Holotype ♂ / *Heraclides / aristodemus / majasi* / Lee D. Miller // Bahamas: Crooked I. / vic. Pitts Town / 27.ix.1986 / M. Simon & L. Miller / Sta. 1986-17”; “Bahamas: Crooked I. / 2-4 mi. E Pitts Town / 23.ix.1986 / M. Simon & L. Miller / Sta. 1986-3 // Allyn Museum / Acc. 1986-19 // Allyn Museum Photo / No. 870408A / 5/6 // Paratype ♂ / *Heraclides / aristodemus / majasi* / Lee D. Miller”.

Distribution. Crooked and Acklin Islands, central Bahamas.

Remarks. Close to *H. aristodemus bonhottei*.

Heraclides aristodemus ponceana (Schaus, 1911)

Papilio ponceana (Schaus, 1911): 438.

Papilio aristodemus driophilus (Clench, 1979): 273.

Adult Male (Figure 6-14e) *Body*. Similar to the two previous subspecies.

Forewing. Length 42-52 mm (n = 5). Similar to the two previous subspecies.

Hindwing. Similar to the two previous subspecies.

Genitalia. (Figure 6-47c4) Similar to the nominate subspecies.

Adult Female (Figure 6-14f) *Body*. Similar to the two previous subspecies.

Forewing. Length 50-55 mm (n = 3). Similar to the two previous subspecies.

Hindwing. Similar to the two previous subspecies.

Genitalia. (Figure 6-64i) Similar to the nominate subspecies.

Type(s). “*Papilio / ponceana / type Sch. // Type / No. 16774 / U.S.N.M. // Collection / W. Schaus // Miami / Fla.*”; “*Bahama Ids. / H. K. Clench, 1975 / C. M. Acc. 27783 // Cat Id.: vic. / Cutlass Bay / (nr Dolphin Head) / 6.vi.1975. Sta. 259b // Holotype No. / 680 / Carn. Mus. Ent. // Holotype ♀ / Pap. aristodemus / driophilus / H. Clench*”.

Distribution. Florida Keys and northern Bahamas.

Remarks. The original description names the type as *Papilio ponceana*. The type specimen is also labeled *Papilio ponceana*. Protected under the US Endangered Species Act, listed as endangered by the Florida Committee on Rare and Endangered Plants and Animals (FCREP(A) and has a Florida Natural Areas Inventory (FNAI) status of S1. Recently it is only known from Islands of Biscayne NP, northern Key Largo, and one recent sighting (2006) from Deering Estate. This subspecies is considered one of the rarest resident butterflies of North America (Emmel, 1994; Daniels and Emmel, 2004). This species has been subject of a highly successful recovery plan and its biology has been published in a multispecies recovery plan for South Florida (U.S. Fish and Wildlife Service, 1999). Major threats to this butterfly’s survival include pesticide use, extreme climatic events and collecting. Between 1996 and 1997, after three years of reintroductions, a high point of between 1,200 and 1,400 butterflies were recorded in the population. A survey in 2002 records between 190 and 230 adults butterflies in the population (Black and Vaughan, 2005).

Heraclides aristodemus temenes (Godart, 1819)

Papilio temenes (Godart, 1819): 63.

Adult Male (Figure 6-15a) *Body*. Similar to the nominate subspecies but some individuals may have a slightly broader central band.

Forewing. Length 45-46 mm (n = 2). Similar to the nominate subspecies.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-47c5) Similar to the nominate subspecies.

Adult Female (Figure 6-15b) *Body*. Similar to the nominate subspecies.

Forewing. Length 46-51 mm (n = 2). Similar to the nominate subspecies.

Hindwing. Similar to the nominate subspecies.

Genitalia. (Figure 6-64j) Similar to the nominate subspecies.

Type(s). “Anc. Collection / Museum de Paris / [label ventral] temenes / God. // Type”; “temene / temenes. // Type // Papilio temenes / Godart / ? Co-type // Papilio / temenes / 58”.

Distribution. Cuba.

Remarks. No additional information is available.

Heraclides machaonides (Esper, 1796)

Papilio machaonides (Esper, 1796): 191.

Papilio lycoraeus (Godart, 1819): 63.

Diagnosis. Two distinctive and disjointed bars across the forewing.

Adult Male (Figure 6-15c) *Body*. Similar to *H. andraemon*.

Forewing. Length 54-60 mm (n = 32). The central band is disjointed. The costal branch is present as a short bar across the apex of the wing beginning at the costal margin and stopping halfway to the outer margin at m1-m2. The apical branch of the central band is missing; the rest of the central band angles in from the anal angle and abuts the discal cell at m3-cu1 where it joins with the discal spot. The discal spot is bar shaped, along the upper 1/3 of the discal cell, perpendicular to the axis of the discal cell. The sub-marginal spots are small and bar shaped. The ventral surface reflects the dorsal surface with the yellow more confluent.

Hindwing. Similar to *H. andraemon* but with the central band much broader. The inner margin of the central band runs almost parallel with the wing inner margin until cell cu1-cu2 where it meets with the two crescent shaped remnants of the yellow post-discal spots. The eye spot is well developed, having the three components. The inner post-discal spots are as loose crescent-like shapes of light yellow scales, reduced in size they arch up to the wing apex. The sub-marginal spots are well represented and the tail spot is very marginal on the long tail. The ventral has the yellow of the central band merged with the post discal spots, almost covering the wing, but stops just in front of the inner post-discal spots. The inner post-discal spots are more defined and span the extent of the wing.

Genitalia. (Figure 6-49) The rim of the valve is rounded and somewhat broad, the harpe is small, tapering distally to a dull point with serrations on the dorsal edge of the point. The 8th tergite has the pseuduncus short (<1 mm) and broad at the base, narrowing to a rounded tip. The uncus terminates in a small knob. There is little sub-terminal swelling. The aedeagus is short (≤ 3 mm), straight, with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with narrow arms.

Adult Female (Figure 6-15d) *Body*. As in the male.

Forewing. Length 55-63 mm (n = 3). As in the male.

Hindwing. As in the male.

Genitalia. (Figure 6-65d) The ostium lies in a shallow wrinkled vestibule and opens centrally, supported by a ridge. Around the opening of the ostium the plates are sclerotized and

fused anteriorly, below the ostium. These plates merge with the highly sclerotized peripheral vestibular plates anteriorly to give rise to a large knob-like projection posterior to, and below the ostium. The peripheral vestibular plates are narrow, highly sclerotized and fuse below the ostium. Thin, long, lateral, symmetrical, horn-like peripheral arms arise from the inner edge of the peripheral vestibular plates near the ostial opening. The top of both arms taper posteriorly into spines. There is no sclerotized tongue-like plate, instead there is a slightly sclerotized out-pocketing just above the ostial opening; there is no trough between the peripheral vestibular plates and the out-pocketed ridge on which the ostium opens. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. The male has a distinctive yellowing at the tip of the antenna club.

Natural History. Endemic to the island of Hispaniola (Schwartz, 1989) and recorded as abundant in both Haiti and the Dominican Republic (Collins & Morris, 1985, Smith et al. 1994) flying along paths in lowland forests and at the margins of forests, sometimes entering gardens, fields, and plantations. There are unsubstantiated reports of the butterfly in Puerto Rico and Cayman Islands. It is primarily a forest butterfly found up to about 1000 ft (Schwartz, 1989) above sea level and capable of rapid highly agile flight if startled. It prefers mesic wooded habitats, often flying near the top of large trees (five meters) but frequently dipping lower (two meters above ground). It commonly flies along with *H. androgeus epidaurus*, a much higher flyer (Schwartz, 1989). Peak flight months are July and August with lesser numbers being seen March, April, May, November December & January. Adults have been recorded nectaring on *Citrus*, *Ixora* sp., *Bauhinia divaricata*, *Asclepias curassavica*, *Cordia haitensis*, *Psychotria brachiata*, *Ponsiella*, and *Lantana ovatifolia*. Adults are not known to puddle but individuals may visit a puddle or moist mud (Schwartz, 1989).

Life History. Larvae are similar to *H. crespontes* (Coustis, 1983; Smith et al., 1994) and known to feed on *Citrus*.

Type(s). “Original exemplar. // Esper. Ausl Schm. P. 191-192 / T.XLVI Equ. Archiv 6. / Fg 2. // Collection / Berlag // Papilio ♀ machaonides Esp. / Nov. Z. XIII p.591. 74.”; “Type // Anc. Collection. / Museum de Paris / [label ventral] lycoraeus / God.”; “Papilio machaonides / Esper / ? Co-Type of / lycoraeus Godart // Lycoraeus // Papilio / lycoraeus / Esp // Type”.

Distribution (Figure 6-79). Hispaniola

Remarks. May be more closely associated with *H. andraemon*.

The “*himeros*” Subgroup

This subgroup consists of two species *H. lamarchei*, and *H. himeros* (Figure 4-16).

Heraclides lamarchei (Staudinger, 1892)

Papilio lamarchei (Staudinger, 1892): 428.

Diagnosis. The forewing dorsal has almost lost the costal branch of the central band and the hindwing margin is more fluted than in any of the other species of this genus; the tail is very long and is without a tail spot.

Adult Male (Figure 6-15e) *Body.* Similar to *H. thoas* except with the frons, interantennal ridge, and legs darker, and with a broader black dorsal medial band on the dorsal abdomen. Also the ventral of the abdomen is darker.

Forewing. Length 43-53 mm (n = 6). Similar to the *H. androgeus* male but with the central band thinner and more uniform in width along the wing. The costal branch of the central band is almost lost, its elements appearing as pale sprinkling of yellow scales near the costal margin. The central spot at r5-m1 is elongated and has no notches. There is no discal spot. The ventral surface is also similar to *H. androgeus* with the presence of the sub-marginal spots, except for the most apical. The yellowing on the ventral surface is not very confluent and is almost identical to the dorsal.

Hindwing. The central band is similar to that of *H. thoas* but with the sub-marginal spots much more marginal; the two most anal spots are crescent shaped and the other four are circular. The hindwing margin is much more fluted, and the tail longer than any of the other members of this group; there is no tail spot. The eye spot is represented by the sub-marginal element and a very scarce sprinkling of the light yellow scales of the inner element. The inner post-discal spots are represented by only loose sprinklings of yellow scales and are not well represented. The post-discal spot is represented by one red spot at m3-cu1. The ventral surface reflects the dorsal surface with the addition of the proximal post-discal element of the eye spot and three more red proximal post-discal spots at m1-m2, m2-m3, and cu1-cu2. The six inner post-discal spots are also more defined, having more yellow scales.

Genitalia. (Figure 6-50) The rim of the valve is rounded, the harpe tapering broadly distally to 6 spines of varying lengths. The 8th tergite has the pseuduncus intermediate ($\geq 1 < 2$ mm) and broad at the base, narrowing to a rounded tip. The uncus terminates in a small knob. There is little sub-terminal swelling. The aedeagus is slightly curved, with the vesica simple (no spines or sclerotizations). The juxta is "U" shaped with a broad base.

Adult Female (Figure 6-15f) *Body.* As in the male.

Forewing. Length 54 mm (n = 1). Similar to the male but with the costal branch of the central band more evident.

Hindwing. Similar to the male but with fewer inner post-discal spots and only two proximal post-discal spots at m3-cu1 and a smaller at cu1-cu2.

Genitalia. (Figure 6-65e) Similar to *H. andraemon*. The ostium lies in a shallow wrinkled vestibule and opens centrally, supported by a ridge. Around the opening of the ostium the plates are sclerotized and fused anteriorly, below the ostium. These plates merge with the highly sclerotized peripheral vestibular plates anteriorly to give rise to a small knob-like projection posterior to, and below the ostium. The peripheral vestibular plates are narrow, highly sclerotized and fuse below the ostium. Thick, circular lateral peripheral arms arise from the inner edge of the peripheral vestibular plates. The top of the arms are smooth and oval. There is no sclerotized tongue-like plate, instead there is a slight out-pocketing just above the ostial opening; there is no trough between the peripheral vestibular plates and the out-pocketed ridge on which the ostium opens. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. Not much variation except in the number of proximal post-discal spots of the hindwing of males and females.

Natural History. A survey of the literature yielded no additional information.

Life History: Unknown.

Type(s). "Lamarchei / Stgr. // Origin. // Foto / KB IX/88 // Lysithous God. // Bolivia".

Distribution (Figure 6-79). Northern Bolivia to Tucuman and the slopes of the Andes.

Remarks. Nearest to *H. himeros* (Rothschild and Jordan, 1906).

Heraclides himeros (Hopffer, 1865)

Diagnosis. Having a long tail but reduced fluting of the hindwing. The tail also has a very small and marginal tail spot and a distinctive yellow stripe along the outer margin.

Variation. The yellow of the wing elements in the females appear more confluent than that on the males. I however do not treat the sexes as being dimorphic.

Natural History. Tyler et al. (1994) listed the only host plant as *Esenbeckia leiocarpa* (Rutaceae).

Life History. A survey of the literature yielded no additional information.

Distribution (Figure 6-79). Espírito Santo, Rio de Janeiro, Bahia, Goias and Toucantis in Brazil.

Remarks. IUCN Red list of threatened species lists this species with an indeterminate status. Very rare, may be extinct or near extinction. There are two recognized subspecies.

Heraclides himeros himeros (Hopffer, 1865)

Papilio mentor (Boisduval, 1836) – preoccupied name.

Papilio himeros (Hopffer, 1865): 26.

Papilio herodotus (Capronnier, 1874): 10 – nomen nudum.

Papilio lycophron variety *minor* (Burmeister, 1878) - replacement name

Papilio herodotus (Oberthür, 1879)

Adult Male (Figure 6-16a) *Body.* Similar to *H. thoas*.

Forewing. Similar to *H. lamarchei* but with the costal branch of the central band as a well developed spot at r3-r4. The central band is also broader and more angled, tapering almost to a point from the inner margin up to the wing apex. The ventral surface generally reflects the dorsal except that the yellowing extends over all the discal cell area.

Hindwing. Similar to *H. lamarchei* but with much reduced fluting, a very small marginal tail spot, and a yellow stripe along the outer margin of the tail. The sub-marginal spots are also much larger and wedge shaped. The eye spot only has the sub-marginal element and the inner post-discal spots are missing except for a very few light blue scales at cu1-cu2. Also, similar to *H. lamarchei*, there is only one post-discal spot at m3-cu1. The ventral surface generally reflects the dorsal with the inner post-discal spots much more represented. The eye spot lacks the red proximal post-discal element and has a light sprinkling of the inner element. There are only two proximal post-discal spots at m2-m3 and m3-cu1.

Genitalia. Similar to that of *H. anchisiades* and similar taxa, but with the single median spine on the harpe much longer, but not as large as the ventral spine of the “*thersites*” subgroup.

Adult Female (Figure 6-16b) *Body.* As in the male.

Forewing. Similar to the male but has lost the costal branch of the central band. The central band is more angled away from the apex of the wing.

Hindwing. More fluted than in the males with the marginal spots much larger. The sub-marginal spots have been lost, except for the two most apical. The eye spot has the sub-marginal element and a much diffused inner element. The ventral has the sub-marginal spots red, except for the two most apical which are yellow and the inner post-discal spots much diffused.

Genitalia. Similar to *H. lamarchei*.

Type(s). “Mentor ♀ / nach Hon- / rath. // 98 // Holotype ♀ / *Papilio himeros* / Hopffer, 1865 // 192 // *Himeros* / Hpfr. *[?] / 1865 / Brasilia Bescke”; “Brezil / Coll. Lacordaire / Museum de Paris // Syntype ♂ / *Papilio mentor* / Boisduval, 1836”; “*Herodotus* Bo / Brasil. //

Levick Bequest / B.M. 1941-83 // Type // Bresil; 1 ♀ . Specimen typicum. // Ex Museu D^[?]Boisduval // Herodotus, Oberthür.”

Distribution. Few locations near Espírito Santo, Rio de Janeiro in Brazil.

Remarks. Very rare, probably near extinction.

Heraclides himeros baia (Rothschild & Jordan, 1906)

Papilio himeros baia (Rothschild & Jordan, 1906): 614.

Adult Male (Figure 6-34a and 6-34b) *Body.* Similar to the nominate subspecies.

Forewing. Similar to the nominate subspecies.

Hindwing. Similar to the nominate subspecies but lacking the red post-discal spot at m3-cu1 on the dorsal and the red post-discal spot at m2-m3 on the ventral.

Genitalia. Unknown.

Adult Female *Body.* Unknown.

Forewing. Unknown.

Hindwing. Unknown.

Genitalia. Unknown.

Type(s). “Lectotype / baia / KB Foto 9/88 // Rothschild / Bequest / B.M. 1939-1. // Bahia / Brasilia / Fruhstorfer. // Lecto- / type”.

Distribution. Bahia, Goias and Tocantins in Brazil.

Remarks. Represented by type photographs, probably very rare or extinct.

The Unresolved Subgroup

The following species are not well resolved in the phylogeny and have not been placed in any specific subgroups.

Heraclides hectorides (Esper, 1794)

Papilio hectorides (Esper, 1794): 5, plate 1, figure 1.

Papilio argentus (Martyn, 1797): plate 14, figure 3 & 4.

Papilio torquatinus (Esper, 1799): 206, plate 51, figure 2.

Papilio pandrosus (Godart, 1819): 62 – preoccupied name.

Papilio lysithous (Godart, 1819): 73.

Menelaides chirodamas (Hübner, [1825]): plate 103.

Papilio mezentius (Doubleday, 1844): 417.

Papilio torquatinus aberration *melania* (Oberthür, 1879).

Papilio hectorides form *catamelas* (Rothschild & Jordan, 1906): 616.

Papilio hectorides agordus (Fruhstorfer, 1915): 70.

Papilio hectorides lysirte (Fruhstorfer, 1915): 70.

Diagnosis. Males with the central band is narrow, tapered towards the wing apex, lacks a costal branch, with apical branch slightly curved towards the wing apex. Females may have a white, very narrow central band in the forewing, and a short central band in the hindwing that does not go to the inner margin or be almost completely dark except for the red spots on the hindwing. Sexes dimorphic.

Adult Male (Figure 6-16c) *Body.* Similar to *H. lamarchei*.

Forewing. Length 40-48 mm (n = 44). The central band is narrow and tapered towards the wing apex. There is no costal branch, and the apical branch is slightly curved towards the wing apex. There are no sub-marginal or marginal spots visible above, but sub-marginal spots are present below, and there is no discal cell spot. Ventral surface reflects the dorsal but with more confluence.

Hindwing. Very similar to *H. lamarchei* but with smaller sub-marginal spots and two additional red proximal post-discal spots at m1-m2 and m3-cu1. The ventral surface is similar to *H. lamarchei* but with the spots smaller.

Genitalia. (Figure 6-50) Similar to *H. lamarchei*, but with 7 distal spines, decreasing in size from the ventral to the dorsal edge of the harpe.

Adult Female (Figures 6-16d and 6-16(e)) *Body*. As in the male.

Forewing. Length 40-51 (n = 21). May have a white, very narrow central band that lacks the costal branch and angles away from the wing apex as you move from the inner margin up to the wing apex; the central band fades out before reaching the costal margin. Alternatively females may be dark, with a faint hint of the central band. The ventral surface reflects the dorsal surface with the addition of some white sub-marginal spots.

Hindwing. Short central band in the hindwing that does not extend to the inner margin, or be almost completely dark except for the red sub-marginal spots and the red post-discal spots. When present, the central band extends from the costal margin to m3-cu1 where it coalesces with the first of the last two red post-discal spots. The eye spot has the elements spaced, the proximal post-discal element in line with the proximal post-discal spots. The sub-marginal spots are all red and sickle shaped (two most anal) or s-shaped (the remaining four). The inner post-discal spots are present as loose gatherings of light blue scales. The ventral surface reflects the dorsal surface almost identically but with more scales in the inner post-discal spots and the three most anal of the sub-marginal spots.

Genitalia. (Figure 6-65f) There is moderate armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule and opens anteriorly, not supported by a ridge. Around the opening of the ostium the plates are sclerotized and fused anteriorly. There is no posterior projection. The peripheral vestibular plates are narrow and only slightly sclerotized and fuse anterior to, and below the ostium as a thin line. Short lateral peripheral arms arise from the inner edges of the peripheral vestibular plates. The outer edges of the arms are irregular. A broad, sclerotized tongue-like plate, with a ventrally indented midline, is present above and posterior to the vestibule. It is merged on both sides to the peripheral vestibular plates. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. Sexes dimorphic. Females also come in two forms; one form is more melanic with a very faint white central band in the forewing and hindwing.

Natural History. A survey of the literature yielded no additional information.

Life History. Clusters of one to eight orange colored eggs are deposited by the females on the ventral of host plant leaves in shady areas (Penz, 1991). Aubert et al. (1999) gives larval host plant as Piperaceae. Additionally, Penz (1991) reported that *H. hectorides* were oligophagous on Piperaceae and Rutaceae and found eggs and larvae on *Piper* sp. and *Zanthoxylum* sp; he reported one larva on *Citrus limon* but did not observe larval utilization of the plant. Larvae spent three to six days at each instars for the first four instars with instar number five being five to twelve days. Occasionally a sixth instar can be observed (Penz, 1991).

Type(s). “Original exemplar // Esper. Ausl. Schm. [image of remaining labels difficult to decipher]”; “Original exemplar // Esper. Ausl. Schm. P 206. 207. / T.LI. Fg 2. // Papilio / hectorides Esp. / Br Z. XIII. P. 615. 110 [?] // [label unclear]”; “Brezil / ? / Museum de Paris / Jordan det. // Syntype ♂ / Papilio lysithous / Godart, 1819”; “mezentius / 22-220. Dbl. // W. Coast / 1706 // Type”; “aberration / melania, Obr. // Type // Typicum / Specimen // Ex Museo / D^[?]Boisduval // Levick Bequest / B.B. 1941-83.”; “lectotype / catamelas / Foto KB 9/88 // Lecto- / type // Rothschild / Bequest / B. M. 1939-1. // S. Catarina / Brazil”; “Type // agordus / 7-115 Fruh. // Fruhstorfer Coll. / B.M. 1937-285. // Paraguay / ex coll Fruhstorfer”; “Rio grande / Brazil. / Fruhstorfer // Fruhstorfer Coll. / B.M. 1937-285. // Type // lysirte. / 22-220 Fruh”.

Distribution (Figure 6-79). South-eastern Brazil from Bahia west to Brasilia, Mato Grosso and Paraguay and south to Argentina.

Remarks. Most closely associated to *H. lamarchei* and *H. himeros*; more information is needed about the life histories and habits of these three species.

Heraclides garleppi (Staudinger, 1892)

Diagnosis. The males have the central band very broad and arching around the edges of the discal cell; there is no apical branch and cell r4-r5 almost always with a yellow spot of the central band. There is almost always a blue inner post-discal element of the eye spot and almost never a red proximal post-discal element on ventral of the male hind wing. The females have the red sub-marginal and red proximal post-discal spots at m3-cu1 and cu1-cu2 separate.

Variation. Sexes dimorphic. The nominate subspecies does not have the central band in the male forewing interrupted by a bar. This is seen only in the other two subspecies.

Natural History. A survey of the literature yielded no additional information.

Life History. Unknown

Distribution (Figure 6-80). Guyana across to middle Amazon, west to Rio Tapajós, and Manaus, to eastern Peru and eastern Colombia; south to Bolivia.

Remarks. This species is very close to *H. torquatus* with which it is frequently confused. Tyler et al. (1994) lists various characters for separating this species from *H. torquatus*. None of those characters were verifiable and new ones are proposed here. There are three recognized subspecies.

Heraclides garleppi garleppi (Staudinger, 1892)

Papilio garleppi (Staudinger, 1892): 427.

Adult Male (Figures 6-16f and 6-17a) *Body.* Head similar to *H. thoas* but darker. The pectus is darker, with a suffusion of yellow scales on the anterior portions of the legs. The abdomen is similar to *H. thoas* but with black stripes laterally.

Forewing. Length 54-56 mm (n = 2). A broad central band, lacking in the apical branch is present. There is no discal spot and no sub-marginal or marginal spots. The central band is almost always represented by a spot at r4-r5. The ventral surface reflects the dorsal surface with the addition of a few pale yellow sub-marginal spots.

Hindwing. The central band is very broad, more than ½ the width of the wing. There are pale yellow sub-marginal spots and even paler less organized yellow inner spots. The eye spot is faint but represented by a red sub-marginal element and a pale yellow sprinkling of the inner element. The tail is long and slender. The ventral surface is similar to the dorsal but with the sub-marginal spots half-moon shaped and the inner post-discal spots more developed. There are also

four red proximal post-discal spots from m1-m2 to cu1-cu2. The eye spot almost always has the inner post-discal element blue and almost never with a red post-discal element.

Genitalia. (Figure 6-51) The rim of the valve is rounded, the harpe tapering broadly distally to 2 large spines. The ventral spine is larger than the dorsal more distal spine. The 8th tergite has the pseuduncus intermediate ($\geq 1 < 2$ mm) and broad at the base, narrowing to a rounded tip. The uncus terminates into a curved rod. There is little sub-terminal swelling. The aedeagus is slightly curved, with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with narrow arms.

Adult Female (Not figured) *Body.* No representatives were seen.

Forewing. No representatives were seen.

Hindwing. No representatives were seen.

Genitalia. No representatives were seen.

Type(s). “Garleppi / Stgr. // Foto / KB IX/88 // Bolivia 300 m. / Rio Juntas / 1891. Garlepp. // Origin”.

Distribution. Northern Bolivia.

Remarks. IUCN Red list of threatened species lists this species with an indeterminate status.

Heraclides garleppi interruptus (Staudinger, 1892)

Papilio garleppi variety *interruptus* (Staudinger, 1892): 427.

Adult Male (Figures 6-17c, and 6-18e) *Body.* Similar to the nominate subspecies male.

Forewing. Length 43-50 mm (n = 8). Similar to the nominate subspecies male but with the central band interrupted or broken in two at m2-m3 by the black of the grown color.

Hindwing. Similar to the nominate subspecies male.

Genitalia. Not dissected.

Adult Female (Figure 6-17(d)) *Body.* Similar to male but black, with white spots behind the eyes and anterior portions of the thorax.

Forewing. Length 45 mm (n = 1). Central band represented as a large white spot at cells m3-cu1 and cu1-cu2. No other spots are on the wing.

Hindwing. There is no central band and all the spots are red. The sub-marginal and proximal post-discal spots at m3-cu1 and cu1-cu2 are merged forming two larger spots. The other sub-marginal spots are all represented. No inner post-discal spots are visible and there are usually two other tornal proximal post-discal spots, aside from the two merged ones. The eye spot is poorly developed and is represented by the red sub-marginal and the red post-discal elements being almost in line with, and forming the most terminal spots of the post-discal and sub-marginal bands. The ventral surface generally reflects the dorsal except that the sub-marginal and post discal spots at m3-cu1 and cu1-cu2 are never merged and there is no m1-m2 post-discal spot. The tail is small and slender and often not much longer than the other fluted areas of the wing.

Genitalia. (Figure 6-66b) There is moderate armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule and opens anteriorly, not supported by a ridge. Around the opening of the ostium the plates are highly sclerotized and fused anteriorly. There is a small horn-like posterior projection resulting from a fusion of the peripheral vestibular plates and the plates around the ostial opening. The peripheral vestibular plates are broad and highly sclerotized and fuse anterior to, and below the ostium. Short lateral peripheral arms arise from

the inner edges of the peripheral vestibular plates. The arms are anchored in three places. The outer edges of the arms are irregular. Above the ostium are two additional projections. There is a broad, sclerotized tongue-like plate, with two smaller arms arising above the ostial opening. This plate fuses on both sides to the peripheral vestibular plates. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Type(s). “Garleppi var. / Interruptus / Stgr. // Foto / KB IX/88 // S. P. de Olivenca / Amazon. Sup. / 1891. Michael. // Origin”.

Distribution. Rio Tapajós, and Manaus, to eastern Peru and eastern Colombia.

Remarks. No additional information is available.

Heraclides garleppi lecerfi Brown & Lamas, 1994

Papilio garleppi variety *insidiosus* (Le Cerf, 1923): 360 – preoccupied name.

Heraclides garleppi lecerfi Brown & Lamas, 1994: plate 83 – replacement name.

Adult Male (Figure 6-17(e)) *Body*. Similar to *H. garleppi interruptus* male.

Forewing. Length 39-41 mm (n = 3). Similar to *H. garleppi interruptus* male.

Hindwing. Similar to *H. garleppi interruptus* male. The blue cells of the inner post-discal element of the eye spot may be absent.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figure 6-17f, 6-18a, and 6-18b) *Body*. Similar to *H. garleppi interruptus* female.

Forewing. Length 41-47 mm (n = 12). Similar to *H. garleppi interruptus* female but with the forewing spot lower, at cu1-cu2 and cu2-1a, or absent.

Hindwing. Similar to *H. garleppi interruptus* female but with less, smaller spots.

Genitalia. (Figure 6-66c) Similar to *H. garleppi interruptus*.

Type(s). “Guyane francaise / St Laurent Maroni / 1919[?] / L. Seraphin / Museum de Paris // Holotype ♂ / *Papilio garleppi* var. / *insidiosus* Le Cerf, / 1923 // Type”; “*P. garleppi* Stg. / ssp. *Insidiosus* / ♂ Cotype Le Cf. / F. Le Cerf det. 1923 // Don du / Museum / de Paris / par Mr. Le Cerf. // Guyane Franc / [? de ?] / Collection Le [?]”.

Distribution. Guyana west to lower Amazon.

Remarks. No additional information is available.

Heraclides torquatus (Cramer, 1777)

Diagnosis. Similar to *H. garleppi* but with the blue inner post-discal element of the male hindwing absent but the red proximal post-discal element well represented.

Variation. Sexes dimorphic. Hind wing spots variable.

Natural History. This butterfly can be found between 400 and 800 meters above sea level (DeVries, 1987) in humid tropical woodland forests (Le Crom et al., 2002); flight period is reported to be May to July. Adult males are fast fliers with a swooping circling flight and are often seen along the edges of forests and in semi-open areas. Females are confined mainly to the shade of the forest and closely resemble female *Parides* which they are thought to mimic. *Stachytarpheta* sp. is recorded as a nectar plant. Adults have been seen visiting wet sand in the afternoons (DeVries, 1987)..

Life History. The greenish-yellow colored eggs are laid singly. Larvae resemble those of *H. thoas* but bear prominent dorsal tubercles. Pupa resembles those of *H. anchisiades* but more slender (DeVries, 1987). A survey of the literature yielded no additional information.

Distribution (Figure 6-81). Eastern and western coasts of Mexico through Central America into South America all the way to Paraguay and Bolivia.

Remarks. Staudinger (1884) described a male specimen as ‘*tasso*’ (Figures 6-34c and 6-34d) but this has since been treated as an aberration of this species (Tyler et al., 1994; Lamas, 2004). I am inclined to agree with previous authors and treat ‘*tasso*’ as a mere aberration. It is also possible that this could be a valid species or a hybrid of some kind (Johnson and Matusik, 1987).

Johnson and Matusik (1987) on *Heraclides tasso* (Staudinger, [1884]): “Traditional taxonomic criteria strongly suggest the lectotype of *H. tasso* represents a valid species. If so, it is possibly extinct or perhaps has not been collected since its original description. A number of “rare” papilionid taxa are known from only a few specimens...; others have been collected only in disparate time periods... Field and biological work must determine if extant natural populations exhibit the phenotypes of *Papilio tasso* syntypes and whether their unique characters are attributable to hybridization or aberration.”

Rozycki (2004) identified another male specimen similar to the type but with narrower tails and more color on the hind-wing ventral. Similarly, a female *tasso*-like aberration is in the collection of the McGuire Center for Lepidoptera and Biodiversity, FLMNH – Wilson collection (Figure 6-19f). This is a far ranging species and the limited numbers of aberrations that have been found are not consistent enough to warrant being described as a new species or subspecies at this point. These specimens were also from very different locations across the range of this species. If a population displaying similar but stable characteristics can be found, this would warrant further study and possibly elevation to species or subspecies level.

Heraclides torquatus torquatus (Cramer, 1777)

Papilio torquatus (Cramer, 1777): 123, plate 177, figure A & B.

Princeps caudius (Hübner, [1809]): plate 117.

Papilio patros (Gray, [1853]): 43, plate 7, figure 7.

Papilio torquatus variety *flavida* (Oberthür, 1879): 115.

Papilio tasso (Staudinger [1884]) - regarded as an aberration.

Papilio torquatus form *theras* (Rothschild & Jordan, 1906): 621.

Papilio torquatus form *cleolas* (Rothschild & Jordan, 1906): 621.

Papilio torquatus variety *dubia* (Boullet & Le Cerf, 1912): 31 – preoccupied name.

Papilio torquatus aberration *modestus* (Röber, 1927): 401.

Papilio garleppi interruptus form *xanthica* (Rousseau-Decelle, 1943): 111.

Papilio torquatus aberration *leo* (Okano, 1985): 1-17.

Adult Male (Figure 6-18c) *Body.* Similar to *H. garleppi* male.

Forewing. Length 36-48 mm (n = 110). Similar to *H. garleppi interruptus* male but almost never with the yellow of the apical branch of the central band in r4-r5. Also the central band is narrower and does not extend as far to the wing margin.

Hindwing. Similar to *H. garleppi* male but with the eye spot missing the blue inner post-discal element and with the red proximal post-discal element present. The tails are typically much wider and longer.

Genitalia. (Figure 6-52) The rim of the valve is rounded; the harpe is spoon-shaped with the distal edge highly serrated. The 8th tergite has the pseuduncus short (< 1 mm) and broad at the base, narrowing to a rounded tip. The uncus terminates into a knob-like structure. There is little sub-terminal swelling. The aedeagus is slightly curved, with the vesica simple (no spines or sclerotizations). The juxta is “u” shaped with a broad base.

Adult Female (Figures 6-17b, 6-18d, and 6-18f) *Body.* Similar to *H. garleppi interruptus* female.

Forewing. Length 42-50 mm (n = 35). Similar to *H. garleppi interruptus* female but with the white spot on the forewing slightly smaller.

Hindwing. Similar to *H. garleppi interruptus* female but always with the sub-marginal and proximal post-discal spots at m3-cu1 and cu1-cu2 merged. The tail is more defined and typically longer.

Genitalia. (Figure 6-66a and 6-66d) There is moderate armature around the ostium of the bursa. The ostium lies in a shallow wrinkled vestibule and opens centrally, supported by a ridge. Around the opening of the ostium the plates are sclerotized and fused anteriorly. There is a large horn-like posterior projection resulting from a fusion of the peripheral vestibular plates and the plates around the ostial opening. The peripheral vestibular plates are narrow and highly sclerotized and fuse above and below the ostium. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Type(s). “BMNHE # 665118 // Syntype of / *Papilio torquatus* / Cramer, 1777 / verified by / J.E.Chainey,2002 // Rothschild / Bequest / B.M.1939-1. // Surinam / Coll Lenep // Syn- / type”; “Ega / Bras // Type // patros / 22-222 Gray. // Ega, / Amazons. / Coll. By / Bates. / 51 43.”; “♀ f. *Flavida* / Obth. // Teffe (Ega) / Amazonas / Mds Mathan / 7^{bre}8^{bre}1879 // Levick / Bequest / 1941-83 // Lecto- / type”; Lectotype / theras / KB foto 9/88 // Lecto- / type // Rothschild / Bequest / B.M.1939-1. // Surinam / V. – IX. // Fruhstorfer”; “cleolas / lectotype / KB foto 9/88 // Rothschild / Bequest / B.M.1939-1. // Salinas / Beni R. vii.95 / M. Stuart // Lecto- / type”; Coll. Boulet / Museum Paris / 1909 / Doncaster // Holotype ♂ / *Papilio torquatus* / var. *dubia* / Boulet + Le Cerf, 1912”; “Schupp // *Papilio torquatus* / f. *modestus* Röb. / Type // Staatsamml. / München / Brasilien / Manicore / VIII // Holotype ♀ / *Papilio torquatus* / ab. *modestus* / Röber, 1927”; “Pap ♀ 2a / 19. ix. 32 // Holotype // 343 7 // Iquitos / Amazon // Mus. Rousseau-Decelle // *Papilio garleppi* / spp. *interruptus* Stgr. / ♀ f. *xantica nova* / Holotype MRousseauDecelly”.

Distribution. Guyana to Orinoco and upper Amazon.

Remarks. There are eight recognized subspecies.

Heraclides torquatus atsukoae (Okano, 1985)

Papilio torquatus atsukoae Okano, 1985: 2, figures 7, 8, and 17-28.

Adult Male (Figure 6-19a) *Body.* Similar to the nominate subspecies male.

Forewing. Length 40-43 mm (n = 3). Similar to the nominate subspecies male but with the apical portions of the central band bar shaped, extending almost to the wing margin.

Hindwing. Similar to the nominate subspecies male.

Genitalia. Similar to the nominate subspecies but with the distal serrated edge of the harp almost bifurcate.

Adult Female (Figure 6-19b) *Body.* Similar to the nominate subspecies female.

Forewing. Length 43-47 mm (n = 4). With the spot high on the wing; made up of a central spot at m3-cu1 merged with a discal spot.

Hindwing. Similar to the nominate subspecies female but with the sub-marginal and post discal spots almost all merged. The ventral with the sub-marginal and proximal post-discal spots at m2-m3, m3-cu1, and cu1-cu2 merged. The spot formed by this merger is very confluent, often going into the discal cell.

Genitalia. (Figure 6-66e) Similar to the nominate subspecies.

Type(s). Holotype, allotype, and 6 paratypes in the collection of K. Okano. Two syntypes deposited at the Natural History Museum, London, England (BMNH). Author states “Holotype: Male, San Salvador, El Salvador, Central America, Sept.10, 1984. Allotype: Female, Same above, Aug.20, 1984”.

Distribution. El Salvador.

Remarks. No additional information is available.

Heraclides torquatus jeani Brown & Lamas, 1994

Papilio orchamus (Boisduval, 1836): 300 – preoccupied name.

Papilio torquatus jeani Brown & Lamas, 1994: plate 84 – replacement name.

Adult Male (Figure 6-19c) *Body*. Similar to the nominate subspecies male.

Forewing. Length 36-42 mm (n = 10). Similar to the nominate subspecies but with apical portions of the central band more elliptical and extending near the margin.

Hindwing. Similar to the nominate subspecies male.

Genitalia. Similar to the nominate subspecies but with a wider distal end.

Adult Female (Not figured) *Body*. Not examined.

Forewing. Not examined.

Hindwing. Not examined.

Genitalia. Not dissected.

Type(s). “*Papilio Orchamus* ♀ / Gray (Catal. Lepid. Insects / in the coll. British museum / pl. vii, fig. 6) Colombia. // Ex Museo / D^m Boisduval // Levick / Bequest / 1941-83 // Colombia”.

Distribution. Central and western Colombia to northern Venezuela.

Remarks. Very scarce subspecies.

Heraclides torquatus leptalea (Rothschild & Jordan, 1906)

Papilio torquatus leptalea (Rothschild & Jordan, 1906): 620, plate 5, figure 18.

Adult Male (Figure 6-19e) *Body*. Similar to the *H. torquatus atsukoe* male.

Forewing. Length 38-48 mm (n = 17). Similar to the *H. torquatus atsukoe* male but with the apical upper spot of the central band more elliptical than bar shaped.

Hindwing. Similar to the *H. torquatus atsukoe* male.

Genitalia. Similar to *H. torquatus jeani*.

Adult Female (Figure 6-19d) *Body*. Similar to the nominate subspecies female.

Forewing. Length 38-40 mm (n = 2). Similar to the nominate subspecies female but with a smaller white spot on the wing.

Hindwing. Similar to the nominate subspecies female but with a shorter tail.

Genitalia. (Figure 6-66f) Similar to the nominate subspecies.

Type(s). “Type // *P. torquatus / leptalea* Type . / Nov. Zool. 1906. R&J. // Equateur / Balzapamba / Prov. de Bolivar / M de Mathan / 9^{bre}1893 a Fev 1894 // Nov. Zool. 1906 / Pl.V. Fig. 18 // Levick Bequest / B.M.1941-83.”.

Distribution. Western Ecuador.

Remarks. Females thought to mimic *Parides*.

Heraclides torquatus mazai (Beutelspacher, 1977)

Papilio torquatus tolus form *semimaculata* (Vázquez, 1949): 237.

Papilio tolus mazai (Beutelspacher, 1977): 150.

Papilio torquatus atsukoae (Okano, 1985): 1-17.

Adult Male (Figures 6-35a and 6-35b) *Body*. Similar to the *H. torquatus atsukoae* male.

Forewing. Similar to the *H. torquatus atsukoae* male.

Hindwing. Similar to the *H. torquatus atsukoae* male.

Genitalia. Not dissected.

Adult Female (Figure 6-20b) *Body*.

Forewing. Similar to the nominate subspecies with no central band. White marginal spots may be present.

Hindwing. Having all the sub-marginal and all but the two most apical proximal post-discal spots all separated. The tail is well developed.

Genitalia. Not dissected.

Type(s). “Holotipo // C. Beutelspacher B. det / *Papilio Tolus mazai* ♂ / Beutelspacher // Roberto de la Maza / Mismaloya, Pto. Vallarta, / Jol. / 2-IX-1974”.

Distribution. Western Mexico to El Salvador along the coast.

Remarks. The females are very different from the females of the other subspecies in the pattern of the proximal post-discal and sub-marginal spots. I have no representatives to dissect.

Heraclides torquatus polybius (Swainson, 1823)

Papilio polybius (Swainson, 1823): plate 92.

Papilio trojanus (Boisduval, 1836): 301.

Papilio polybius form *albosignata* (Rousseau-Decelle, 1943): 112.

Adult Male (Figure 6-20c) *Body*. Similar to the *H. torquatus jeani* male.

Forewing. Length 37-42 mm (n = 16). Similar to the *H. torquatus jeani* male

Hindwing. Similar to the *H. torquatus jeani* male.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figure 6-20d) *Body*. Similar to the nominate subspecies female.

Forewing. Length 48 mm (n = 1). Similar to the nominate subspecies female but with the white spot on the wing primarily at cu1-cu2, merging with a small discal spot.

Hindwing. Similar to the nominate subspecies female but with the spots on the hindwing suffused with white scales.

Genitalia. (Figure 6-66(g)) Similar to the nominate subspecies.

Type(s). “Bresil // Holotype // 344 5 // Mus Rousseau-Decelle // *Pap. torquatus* Cr / spp. *polybius* Swains. / ♀ f. *albosignata* nov. / Holotype MRousseauDecelly”.

Distribution. From Bahia in eastern Brazil to Santa Catarina and into forests of Paraguay and Bolivia.

Remarks. No additional information is available.

Heraclides torquatus tolmides (Godman & Salvin, 1890)

Papilio tolmidès (Goodman & Salvin, 1890): 229.

Adult Male (Figure 6-20e) *Body*. Similar to the *H. torquatus jeani* male.

Forewing. Length 38 mm (n = 1). Similar to the *H. torquatus jeani* male.

Hindwing. Similar to the *H. torquatus jeani* male but may have the light blue inner post-discal element of the eye spot as well as the red post-discal element.

Genitalia. Similar to *H. torquatus atsukoae* but with the distal edge of the harpe a bit wider and with less serrations.

Adult Female (Figure 6-20f) *Body*. Similar to *H. torquatus atsukoae* female.

Forewing. Length 39-42 (n = 8). Similar to *H. torquatus atsukoae* female but with a slightly larger white spot.

Hindwing. Similar to *H. torquatus atsukoae* female but with a shorter tail. The specimen figured had lost its tails.

Genitalia. (Figure 6-66h) Similar to the nominate subspecies.

Type(s). “Chiriqui / 95 Jr. // Tolmidès / Godm.+Salv.”.

Distribution. Guatemala to Panama.

Remarks. No additional information is available.

Heraclides torquatus tolus (Godman & Salvin, 1890)

Papilio tolus (Godman & Salvin, 1890): 228, plate 70, figure 1-4.

Papilio tolus form *prorsus maculata* (Vázquez, 1949): 235 – original misspelling.

Papilio torquatus tolus form *semipunctata* (Vázquez, 1949): 235.

Adult Male (Figures 6-20a and 6-21a) *Body*. Similar to *H. torquatus atsukoae* male

Forewing. Length 42-44 mm (n = 4). Similar to *H. torquatus atsukoae* male but with the central band wider.

Hindwing. Similar to *H. torquatus atsukoae* male but with the central band wider.

Genitalia. Similar to *H. torquatus atsukoae* but with the distal end of the harp bifurcate.

Adult Female (Figure 6-21b) *Body*. Similar to *H. torquatus mazai* female.

Forewing. Length 45-53 (n = 11). Similar to *H. torquatus mazai* female.

Hindwing. Similar to *H. torquatus mazai* female but with the tornal sub-marginal and proximal post-discal spots merged. The ventral surface has the spots beginning to show separation.

Genitalia. Not dissected.

Type(s). “[Balsas] Bralsas, Gro. / 1-1932 // Tipo // A. C. Allyn / Acc. 1973-48 // Semi - / maculata”; “B.C.A.Lep.Rhop. / Papilio / tolus, / G. & S. / Godmann-Salvin / Coll. 1918.-4. // ♂ // Tampico, / Tamaulipas. / Richardson. // Type / H.T. // Sp. figured.”; “A. C. Allyn / Acc. 1973-48 // Prorsus - / maculata // T. Escalante / Tierra / Blanca. / VII-40 // Tipo”; “L. Vázquez det. / P. torquatus tolus / f. ♀ semipunctata Vázq // Tipo // CNIN Lep (Mexico) / 10786 // Iguala Gro. / VIII – 33”; “A. C. Allyn / Acc. 1973-48 // Semi- / punctata // T. Escalante / Tierra / Blanca / VIII-40 // Tipo”.

Distribution. North eastern Mexico to Yucatan and south to Honduras and El Salvador.

Remarks. No additional information is available.

Heraclides hyppason (Cramer, 1775)

Papilio hyppason (Cramer, 1775): 46, plate 29, figure E.

Papilio amosis (Cramer, 1780): 139, plate 269, figure A & B preoccupied name.

Papilio hippason variety *paraensis* (Bates, 1861): 225 – original misspelling.

Papilio hippasonides (Grose-Smith, 1902): plate 22, figure 3 & 4.

Papilio hyppason form *ptilion* (Rothschild & Jordan, 1906): 602.

Papilio hyppason rousseau-decellei (Le Moulton, 1933): 16 – original misspelling.

Papilio hyppason form *unimaculata* (Rousseau-Decelle, 1943): 111 – preoccupied name.

Papilio hyppason form *modestior* (Varea, 1975).

Diagnosis. A patch of red scales at the base of the hind wing. Absence of the central band on the hindwing and only a partial white spot on the forewing touching the inner edge.

Adult Male (Figures 6-21c and 6-21e) *Body.* Similar to *H. thoas* but black all over, with red spots on the cervical collar posterior to the head.

Forewing. Length 42-52 mm (n = 16). With a very pale yellow spot, the only representative of the central band, from the anal margin up to about halfway c1-c2. The ventral has the spot even smaller, as a sprinkling of pale yellow scales.

Hindwing. The eye spot is absent; instead the sub-marginal and post-discal red spots seem to have merged to produce long red spots in cells cu2-a1, cu1-ci2, and sometimes m3-cu1. The other smaller spots of the sub-marginal are near the margin. The two most apical may be white or missing. The ventral has smaller spots. The hindwing also has red spots at the base of the wing near to the body. There is no tail.

Genitalia. (Figure 6-53) The rim of the valve is rounded. Similar to *H. thersites*, *H. androgeus*, *H. astyalus*, *H. ornythion*, and *H. aristodemus* in having the ventral edge of the harpe is drawn out into a broad heavily sclerotized spine which does not go to the edge of the valve and is free of the valve. There is a vertical serrated tooth-like projection, free of the valve surface, on the dorsal edge of the harpe. It differs from the aforementioned species in having the spine very close to, and almost touching, the serrated tooth-like projection. This projection is also much broader than seen before. The 8th tergite has the pseuduncus intermediate ($\geq 1 < 2$ mm) and broad at the base, narrowing to a rounded tip. The uncus terminates in a small upturned point. There is some sub-terminal swelling. The aedeagus is long (> 3 mm), strongly curved, with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with narrow arms.

Adult Female (Figures 6-21d and 6-21f) *Body.* As in the male.

Forewing. Length 49-54 mm (n = 9). Similar to the male but with the spot larger and higher, with its center at around the middle of m3-cu1.

Hindwing. Similar to the male but with the red spots larger, the ventral with spots smaller than the dorsal.

Genitalia. (Figure 6-67a) There is much armature around the ostium of the bursa. The ostium lies in an out pocketed vestibule and opens centrally, supported by a ridge. Around the opening of the ostium the plates are highly sclerotized and fused below the ostium. There is no posterior projection. The peripheral vestibular plates are very broad and highly sclerotized and fuse below the ostium. Very long lateral peripheral spines arise from the top edge of the peripheral vestibular plates. There is a small sclerotized tongue-like plate, indented ventrally. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. Sexes slightly dimorphic; the position of the white spot on the forewing of the female.

Natural History. Males and females of this butterfly are thought to be co-mimics with *Mimoides ariarathes gayi* and can be seen flying along rivers and streams; they are also known to siphon water from damp sandy sites.

Life History. A survey of the literature yielded no additional information apart from the osmeterium being well developed (Goose, 1891).

Type(s). “Lectotype / (possibly) / *Papilio* / *hyppason* / Cramer / 1775”; “BMNH(E)# 665036 // Felder / Collⁿ // Surinam / Coll / [?] // Syntype of / *Papilio amosis* / Cramer, 1780 / verified by / J.E. Chainey, 2002 // N^o 42 / *Amosis* / Cr. III. 26g.C.D. // Rothschild / Bequest / B.M.1939-1.”; “Lecto / type // *Papilio* / *hyppason*, / Cram. / Godman-Salvin / Coll. 1917.-2. // *hyppason* // ♀ // Para. / I. Amazons / H. W. Bates.”; “Rio Songo (1200 m) / Bolivia (Yungas) / 1895-6. Garlepp // Syntype ♂ / *Papilio hippasonides* / Gross-Smith, 1902”; “Lectotype / *ptilion* / KB foto 9/88 // Rothschild / Bequest / B.M.1939-1. // type // Lecto- /type // 700 // Iquitos”; “loc; cm / Orenoque / Venezuela / col. le Moults // Holotype // 343 5 // Mus. Rousseau-Decelle // decrit [?] *Novitates . Entomologicae* 1933 / [?] 4 cr 6 / [?] 4 / mt matala Rio Aguero / Venezuela”; “Pap. *Hyppason* / Ig, 3 VI 12 // Pap. *hyppason* / ♂ Cr. / ab. *unimaculata* / Holotype / MRousseauDecelly // 343.1 // Holotype // Mus. Rousseau-Decelle // Iquitos / Amazon”.

Distribution (Figure 6-82) Amazon region.

Remarks. This species is different in appearance to all the other members of this genus. The male genitalia is similar to the “*thersites* subgroup” of species, a possible result of convergent evolution.

Heraclides epenetus (Hewitson, 1861)

Papilio epenetus (Hewitson, 1861): plate 5, figure 13 & 14.

Diagnosis. The dorsal surface is almost completely black, without any spots except for the marginal spots of the forewing and even larger marginal spots of the hindwing.

Adult Male (Figure 6-22a) *Body.* Similar to *H. thoas* but dark all over with red spots laterally and red spots behind the eyes and head.

Forewing. Length 37-47 mm (n = 8). Completely dark with only the marginal spots showing. The marginal spots are small. The central band from the ventral shows up as a pale arch. Ventral with the central band running up from the anal angle fading out as it arches around the end of the discal cell; there is no costal or apical branch.

Hindwing. Completely dark with the exception of well represented marginal spots running the length of the outer edge. There is no tail or eyespot. The ventral surface is also missing the central band but has all the sub-marginal and post discal spots with white and red scales respectively. No inner post-discal spots are seen.

Genitalia. (Figure 6-54) The rim of the valve is rounded and the harpe tapers to a rounded edge with a median spine-like point, not reaching the edge of the valve, and is free of the valve surface. There are no serrations on the rounded distal edge of the harpe. The 8th tergite has the pseuduncus intermediate ($\geq 1 < 2$ mm) and broad at the base, narrowing to a rounded tip. The uncus terminates in a small knob-like process. There is little sub-terminal swelling. The aedeagus is slightly curved, with the vesica simple (no spines or sclerotizations). The juxta is “U” shaped with a wide base.

Adult Female (Figure 6-22b) *Body.* As in the male.

Forewing. Length 47 mm (n = 1). As in the male.

Hindwing. As in the male but with the ventral markings slightly larger and more diffused.

Genitalia. (Figure 6-67b) Similar to *H. thersites* but with fewer armature (less sclerotized). The ostium lies in a shallow wrinkled vestibule and opens centrally, supported by a ridge. Around the opening of the ostium the plates are highly sclerotized and fused anteriorly, below the ostium. These plates merge with highly sclerotized peripheral vestibular plates anteriorly to

give rise to a knob-like projection posterior to, and below the ostium. The peripheral vestibular plates are broad and highly sclerotized and fuse anterior to, and below the ostium. Long lateral peripheral arms arise medially from the peripheral vestibular plates. The top of the arms are almost square. There is no sclerotized tongue-like plate, instead there is a slightly sclerotized out-pocketing just above the ostial opening; there is no trough between the peripheral vestibular plates and the out-pocketed ridge on which the ostium opens. The corpus bursa has a long strap-like or zipper-like signum that is medially seamed and oriented longitudinally on the corpus bursa.

Variation. None. Males and females are alike.

Natural History. Adults of this species are rare. A survey of the literature yielded no additional information.

Life History. Larvae resemble those of *H. anchisiades* (Rothschild and Jordan, 1906) and are gregarious feeders on *Citrus* sp. (Tyler et al., 1994). A survey of the literature yielded no additional information.

Type(s). "Forest of Cinchona / Peru // Type // 108. *Papilio epenetus* ♂ / W. Ecuador Hew. // Type / H.T. // Presented by J. J. Joicey Esq. / Brit. Mus. 1931-291. // *Epenetus*, Hew. / Ecuador. Type."

Distribution (Figure 6-82). Western Ecuador.

Remarks. No additional information is available.

Heraclides oxynius (Geyer, [1827])

Papilio oxynius (Geyer, [1827]): plate 21.

Papilio oxynius form *niveomarginatus* (Rousseau-Decelle, 1933): 306.

Papilio oxynius form *ochracea* (Rousseau-Decelle, 1933): 272.

Papilio augustus (Boisduval, 1836): 358.

Diagnosis. Dark with large marginal spots and a long tail.

Adult Male (Figures 6-22c) *Body.* Similar to *H. epenetus*.

Forewing. Length 39-42 mm (n = 3). Similar to *H. epenetus* but with enlarged marginal spots. The ventral surface is the same as the dorsal.

Hindwing. With a long tail and large marginal spots. Two faint red sub-marginal spots may be present at m2-m3 and a brighter one at m3-cu1. The ventral has all the spots of the sub-marginal and the sub-marginal element of the eye spot. There is a faint scattering of white scales of the proximal post-discal band but no inner post-discal element of the eye spot.

Genitalia. (Figure 6-54) Similar to *H. epenetus* but with a few serrations on the distal edge of the harpe near the spine-like point.

Adult Female (Figure 6-22d) *Body.* As in the male.

Forewing. Length 42 mm (n = 1). Similar to the male but with a faint representation of the central band running from the upper third of the costa, arching down to the tornal area of the wing.

Hindwing. Similar to the male but with the scales of the proximal post-discal spots brighter and the eye spot with both the proximal post-discal and sub-marginal elements.

Genitalia. (Figure 6-67c) Similar to *H. epenetus*.

Variation. Females have brighter coloring of the proximal post-discal band on the ventral of the hindwing.

Natural History. This butterfly frequents sunny areas in forest clearings. It is a mountain species generally staying away from coastal areas. Flight period is recorded as May to September

but, similar to its island companion *H. caiguanabus*, little is known of this butterfly's habits and more study is needed. Nectar plants include *Eupatorium odoratum*.

Life History. Mature larvae can get up to 50 mm in length with a reddish orange head capsule, reddish orange osmeterium, yellow at the edges of the head capsule, and a pair of whitish spots dorso-laterally located on the rust-colored first segment. There is a fine dorsal line of white spots on the anterior and posterior of each segment, with variously colored white, orange, and pinkish short lines and spots on the dorsal and lateral surfaces. Ground color of the larvae is dusky olive (olive –brown) and the spiracle openings are white with the prolegs olive green and the thoracic legs rust colored (reddish orange). Larvae are gregarious, resting in the day on the trunk of host plants and dispersing to feed at night (Riley, 1975; Smith et al., 1994). Information on larval behavior suggests a close affinity to *H. anchisiades* and similar taxa. Gundlach (1891) was one of the first to describe the immature stages of this insect.

Type(s). “Holotype // Cuba / Guantanamo / Collection Le Moulton // *Papilio oxynius* Hbn. / f. ♀ ochracea f. nova / Holotype MRousseauDecelly // 343 2 // Mus. Rousseau-Decelle”; “*Papilio / oxynius* Hbn. / f. ♀ niveomarginatus / MRousseauDecelly / Holotype // Holotype // Cuba / Guantanamo / Collection Le Moulton // 343 3 // Mus. Rousseau-Decelle”.

Distribution (Figure 6-82). Cuba.

Remarks. No additional information is available.

Heraclides pelaus (Fabricius, 1775)

Diagnosis. With long tails and a distinctive white band across the forewing dorsal starting at the costal margin and extending to the anal angle.

Variation. Almost none. Females look similar to the males but with larger spots.

Natural History. Primarily a woodland species, it is known from sea level to 1220 meters (Schwartz, 1987); it is reported to fly with *H. oxynius*, *Anetia cubana*, and *Greta cubana* by Smith et al. (1994), and *Pterourus homerus* by Brown and Heinemann (1972), but these butterflies, primarily the males, may sometimes visit fields, plantations or grassy riverbanks. Brown and Heinemann (1972) records the typical elevation of this species as 300 to 900 meters. Females confine themselves more to the forests. Males may exhibit territorial behavior such as hill-topping or circling each other. Most common in June and July, they are thought to be a univoltine species (Schwartz, 1987). They are rapid fliers and flutter their wings while nectaring on a number of plant which include *Bidens alba*, *Bauhinia divaricata*, *Lantana camara*, *Lantana ovatifolia*, *Ageratum conyzoides*, *Tournefortia hirsutissima*, and *Eupatorium* spp (Smith et al., 1994).

Life History. Similarly to *H. oxynius*, larvae aggregate when resting but feed solitarily. Gregarious larvae feed solitarily during the day. First instar larvae are olive colored with a white posterior saddle with the third instar larvae remaining olive with an additional saddle appearing in the midsection with the first thoracic segment also turning white (Sourakov, 2009). Mature larvae on Puerto Rico are described as having an olive-brown body intricately marked with dark brown anteriorly; two dull yellow saddles and a dull yellow head marked with brown with a creamy inverted “Y”. The body also possesses numerous filmy white markings with lateral creamy patches. There are small warts with lavender spots on most segments with the prolegs being pale and delimited dorsally by a narrow white line and the thoracic legs being yellowish and brown tipped (Walcott, 1923; Smith et al., 1994). Brown and Heinemann (1972) recounted Cockerell's (1893) description of mature larvae in Jamaica as being 40 mm long with a shiny brown head with white spots laterally, a dark brown body with tubercles on the first four

segments. The most anterior of these tubercles are ochreous. The sides of the body have creamy grey-marbled dashes from segment five to seven. The pro-legs are grey blotched with a darker color and the thoracic legs are brown (Cockerell, 1893; Brown and Heinemann, 1972; Riley, 1975; Smith et al., 1994).

Distribution (Figure 6-83). Cuba, Jamaica, Hispaniola and Puerto Rico.

Remarks. The gregarious nature of larvae has been used previously to place this species as closely associated with *H. anchisiades* and similar taxa (Rothschild and Jordan, 1906; Brown and Heinemann, 1972; Hancock, 1983). There are four recognized subspecies.

Heraclides pelaus pelaus (Fabricius, 1775)

Papilio pelaus (Fabricius, 1775): 444.

Papilio ornofagus (Weidemeyer, 1863): 147 – nomen nudum.

Adult Male (Figure 6-22e) *Body.* Similar to *H. epenetus*.

Forewing. Length 47-50 mm (n = 8). The central band as a white band across the wing, from about midway the costal margin to the anal angle. The ventral surface reflects the dorsal.

Hindwing. Similar to *H. oxynius* male but with three sub-marginal spots brighter at m2-m3, m3-cu1, and cu1-cu2. The ventral surface is missing the inner post-discal element of the eyespot and the sub-marginal element is white. There are at least five of the white proximal post-discal spots present. The tail is long and well developed.

Genitalia. (Figure 6-55) Similar to *H. epenetus*.

Adult Female (Figure 2-22f) *Body.* As in the male.

Forewing. Length 50 mm (n = 1). As in the male.

Hindwing. Similar to the male but may have up to four red sub-marginal spots.

Genitalia. (Figure 6-67d) Similar to *H. epenetus*.

Type(s). “Pap. pelaus / Fabf. Pag 4 No 12 [UMG -2 specimens with same label]”.

Distribution. Jamaica.

Remarks. No additional information is available.

Heraclides pelaus atkinsi (Bates, 1935)

Papilio pelaus atkinsi (Bates, 1935): 113.

Adult Male (Figure 6-23a) *Body.* Similar to the nominate subspecies.

Forewing. Length 49-53 mm (n = 6). Similar to the nominate subspecies but darker.

Hindwing. Similar to the nominate subspecies but darker, without the proximal post-discal spots but with three large red sub-marginal spots at m2-m3, m3-cu1, and cu1-cu2. The ventral has all the sub-marginal spots larger than the dorsal, and extending up the wing.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figure 6-23(b)) *Body.* As in the male.

Forewing. Length 53 mm (n = 2). As in the male.

Hindwing. Similar to the male but with all the red sub-marginal spots on the dorsal. The ventral has larger spots.

Genitalia. Not dissected.

Type(s). “M.C.Z. / Type / 16689 // *Papilio pelaus* / *atkinsi* Bates / Holotype // Name P. *pelaus* ♂ / Date Apr 17, 1910 / R. Seco[?] / Guantanamo, Cuba”.

Distribution. Cuba.

Remarks. Females may be a little paler than the males and this subspecies has the largest spots. It is markedly different from all the other subspecies.

Heraclides pelaus imerius (Godart, 1819)

Papilio imerius (Godart, 1819): 69.

Papilio augias (Ménétries, 1832): 293 – preoccupied name.

Adult Male (Figure 6-23c) *Body*. Similar to the nominate subspecies.

Forewing. Length 44-48 mm (n = 3). Similar to the nominate subspecies but at times the markings can appear reduced.

Hindwing. Similar to the nominate subspecies.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figure 6-23d) *Body*. As in the male.

Forewing. Length 47-50 mm (n = 2). Similar to the nominate subspecies female.

Hindwing. Similar to the nominate subspecies female.

Genitalia. (Figure 6-67e) Similar to the nominate subspecies.

Type(s). “*Papilio pelaus* Fab. / form *imerius* / Godart / ? Type // *imerius* // Type // *Papilio* / *imerius* / 46”; “Type // *imerius* / Godt. // Jude Orientale (Fauy) / [?] d’Haiti / ? / Museum de Paris / [label ventral] Type de / Godart / ind. Orient”.

Distribution. Hispaniola.

Remarks. Almost identical to the nominate subspecies, just a little darker.

Heraclides pelaus puertoricensis Möhn, 1999

Heraclides pelaus puertoricensis Möhn, 1999: 2.

Adult Male (Figure 6-23e) *Body*. Similar to the nominate subspecies

Forewing. Length 39-48 mm (n = 5). Similar to the nominate subspecies

Hindwing. Similar to the nominate subspecies

Genitalia. Similar to the nominate subspecies.

Adult Female (Figure 6-23f) *Body*. As in the male.

Forewing. Length 40-49 mm (n = 3). Similar to the nominate subspecies female.

Hindwing. Similar to the nominate subspecies female.

Genitalia. (Figure 6-67f) Similar to the nominate subspecies.

Type(s). Original description states “Holotypus: ♂ Puerto Rico (ex pupa, 12.6.1984), leg. Garrison.” No information is given as to deposition or location of type(s).

Distribution. Puerto Rico.

Remarks. No additional information is available.

Heraclides anchisiades (Esper, 1788)

Diagnosis. White spot in the tornal area of the forewing dorsal with center near vein Cu₂, never touching wing margin, yellow below in females; where tornal spot is missing, there is a white suffusion of scales on the upper half of the wing always into the discal cell; red spots on the body laterally.

Variation. Extremely variable over the entire range.

Natural History. This butterfly is very common and can be found between sea level and 1,400 meters. It frequents disturbed areas and can be seen visiting flowers at the edge of forests,

in pastures or gardens. Nectar plants used include *Lantana camara*, *Ixora coccinea*, *Senecio confusus*, *Hamelia patens*, and *igna* sp. (DeVries, 1987; Le Crom et al., 2002). Adults appear to mimic *Parides* females (Tyler et al., 1994).

Life History. Yellow, spherically shaped, 1.35 mm diameter eggs (van Dinter, 1957) are laid in clusters of up to seventy on the ventral surface of leaves of the host plants. Females will spend up to one hour depositing eggs if not disturbed. Young larvae have a mottled shiny green and white pattern (DeVries, 1987) and hatch synchronously and immediately consume the egg cases (Young et al., 1986). All larval stages are gregarious; fourth and fifth instar larvae aggregate in groups of up to 104 individuals on the trunk of the host tree during the day and feed at night (van Dinter, 1957; Young et al., 1986; DeVries, 1987; Tyler et al., 1994; Le Crom et al., 2002). The mature larva has an eyespot each side of thorax (Rothschild and Jordan, 1906) and are dull brown with white areas dorsally and anally. The osmeterium is orange in color and the dull brown pupa is twig-like with green areas that bear the appearance of lichen (DeVries, 1987). The cryptic larva can be brown or olive green depending on the type of substrate they pupate over be it a coarse live or dry tree trunk (brown) or a flat surface with green foliage (green) (Le Crom, et al., 2002). The life history and parasitoids that affect this butterfly are well studied, and multiple works can be found such as van Dinter (1957), Young et al. (1986), and Chumpitasi (2003) among others.

Distribution (Figure 6-84). Southern USA through Mexico and Central America to South America.

Remarks. There are five recognized subspecies. There is an unidentified specimen from José María Caro, Calera, Chile (Figure 6-29(f) that is believed to belong to this species. If other similar specimen can be located from the same area and a stable population can be discovered further study and possibly the designation of a new subspecies of *H. anchisiades* would be warranted. The description of a new species or subspecies from single specimens should be discouraged as this could merely be an aberration as in the case of *tasso*.

Heraclides anchisiades anchisiades (Esper, 1788)

Papilio anchises (Stoll, 1780)

Papilio anchisiades (Esper, 1788): 53, plate 13, figure 1 & 2.

Priamides hipponous (Hübner, [1819]): 87.

Papilio archelaus (Godart, 1819): 32.

Papilio theramenes (Felder & Felder, 1861): 74.

Heraclides matusiki Johnson & Rozycki, 1986: 383.

Adult Male (Figures 6-24a, 6-24c, 6-24e, and 6-30e) *Body.* Similar to *H. epenetus*.

Forewing. Length 40-58 mm (n = 104). May or may not possess a white tornal spot, the remnant of the central band in the tornal area of the wing. Spot of variable size or may be absent. Ventral reflects the dorsal.

Hindwing. Very short or no tail. Eye spot not developed. Sub-marginal and proximal post-discal spots merge and often present as three large red spots. The two spots at m3-cu1 and cu1-cu2 almost always complete. The eye spot appears as another incomplete spot and a fourth spot that is incomplete may be present at m2-m3, sometimes absent. Ventral with all spots separate; the sub-marginal spots not merged with the post-discal spots. Additional sub-marginal spots go up the edge of the wing to the apex. The size of the spots is highly variable. The most posterior marginal spot is red.

Genitalia. (Figure 6-56) Similar to *H. epenetus* but with a several serrations on the distal edge of the harpe near the spine-like point. Serrations are larger than in *H. oxynius*.

Adult Female (Figures 6-24b, 6-24d, 6-24f, and 6-30f) *Body.* As in the male.

Forewing. Length 45-61 mm (n = 47). Similar to the male but with the white tornal spot larger and yellow on the ventral.

Hindwing. Similar to the male but with larger spots. The most posterior marginal spot is red.

Genitalia. (Figure 6-68a) Similar to *H. epenetus* but with spines at the end of the peripheral arms.

Type(s). “♀ horcan // Coll^{on} / E. Moreau // Type // Guyana / Maroni // Bull. Soc. Ent. France, / 1923, p. 144. Exemplaire / Figure Planche 1. // Museum Paris / Ex-Coll. / E. Moreau / R. Borelly / 1956 // Type”; “*Papilio anchisiades* / Esp. / Godman & Salvin / Coll. 1918 4 // ♀ // Venezuela / Druce Coll // Coll. / Kaden. // Type // Syntype / *Papilio theramenes* / Felder & Felder / det. P. Ackery 1994 // *Theramenes* / Ven // Syn- / type”; “Photographed / specimen (39a/15P / Tyler; Brown; & Wilson; / 1992. Swallowtail / Butterflies of the / Americas /pl/fig 81/11 // Gift of New York / Zoo. Soc., Dept. / Tropical Research / William Beebe, Dir // Type // Holotype / *Heraclides* / matusiki / K. Johnson / + Rozycki // Caritipo, / Venezuela / I-VII 1912 // South / America. // *Genitalia* dissected / by Johnson, Rozycki / and Matuski, 1985-- / No. 13 alcohol AMNH // Loaned VIII-89 / Source AMNH”; “[Specimen figured by Stoll (1780) plate 318, figure A previously selected as lectotype for *Priamides hipponous* Hübner and *Papilio anchisiades* Esper].

Distribution. Western Colombia through Guyana to French Guiana, all of Amazon to Bolivia and central Brazil.

Remarks. No additional remarks.

Heraclides anchisiades capys (Hübner, [1809])

Princeps capys (Hübner, [1809]): 120, figure 3 & 4.

Papilio evander (Godart, 1819): 32 – preoccupied name.

Adult Male (Figures 6-25a and 6-25c) *Body.* Similar to the nominate subspecies.

Forewing. Length 40-55 mm (n = 23). Similar to the nominate subspecies male but without the white tornal spot. There anterior half of the wing is paler where the ventral pattern of a white suffusion of scales shows above. The ventral with a white suffusion of scales on the anterior half of the wing, remnants of the central bend; this whiter area always includes portions of the discal cell.

Hindwing. Similar to males of the nominate subspecies.

Genitalia. Similar to the nominate subspecies but without serrations.

Adult Female (Figure 6-25b) *Body.* As in the male.

Forewing. Length 48-60 mm (n = 21). Similar to the males.

Hindwing. Similar to females of the nominate subspecies.

Genitalia. (Figure 6-68b) Similar to the nominate subspecies.

Type(s). Probably lost or only known as a published image. The original description was lacking in additional useful information.

Distribution. North-eastern, eastern and southern Brazil to Bolivia, south to Tucuman and Buenos Aires in Argentina.

Remarks. No additional information is available.

Heraclides anchisiades idaeus (Fabricius, 1793)

Papilio idaeus (Fabricius, 1793): 16.

Papilio pandion (Bates, 1861) - nomen nudum.

Papilio anchisiades variety *pandion* (Bates, 1863).

Papilio pandion (Felder & Felder, [1865]): 79 – name erroneously thought preoccupied.

Papilio pandonius (Staudinger, 1894) – replacement name.

Adult Male (Figures 6-25e, 6-26a, 6-26c, and 6-25e) *Body*. Similar to the nominate subspecies.

Forewing. Length 40-54 mm (n = 179). Similar to the male of *H. anchisiades capys*, sometimes with a completely dark wing.

Hindwing. Similar to the male of *H. anchisiades capys*.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figures 6-25d, 6-25f, 6-26b, and 6-26d) *Body*.

Forewing. Length 38-60 mm (n = 93). Similar to the female of *H. anchisiades capys* but with less white suffusion on the ventral.

Hindwing. Similar to the females of the nominate subspecies but with additional red submarginal spots, the most apical sometimes mixed with white. The ventral with more red post-discal spots.

Genitalia. (Figure 6-68c) Similar to the nominate subspecies.

Type(s). “♀ // Lion Hill, / Panama. / McLeannan. // B.C.A.Lep.Rhop. / *Papilio* / *pandion*, / Feld. // Holotype ♀ / *Papilio anchisiades* / var. *pandion* Bates, 1863 // *Papilio* / *anchisiades*, Esp. / subsp. *idaeus*, Fabr. / Godman-Salvin / Coll. 1918.-4.”; “Lectotype ♂ / *Papilio pandion* / C. Felder + R. Felder / by G. Lamas '91 // Hellg / Mexico”; “[unsure of type association] *Papilio* / *anchisiades* ♂ / *anchisiades* Esp. / det.W.Forster 1955. // La Florida Peru / henda Taulis / ca. 1000m – I.IV.1952 / leg. H. –W. Koapcke”.

Distribution. Southern USA to Colombia and North-western Venezuela.

Remarks. No additional information is available.

Heraclides anchisiades lamasi Brown, 1994

Papilio anchisiades lamasi Brown, 1994: plate 81.

Adult Male (Not figure(d) *Body*. Not examined.

Forewing. Not examined.

Hindwing. Not examined.

Genitalia. Not dissected.

Adult Female (Figure 6-26f) *Body*. Similar to the nominate subspecies.

Forewing. Length 60 mm (n = 1). Similar to the female of *H. anchisiades capys*.

Hindwing. Similar to the female of *H. anchisiades capys*.

Genitalia. Not dissected.

Type(s). “-Palmar- / (Ecuad) / R.Haertsch S. // ex coll. / Erhardt // Holotype ♂ / *Heraclides anchisiades* / *lamasi* K. Brown, / 1994 // Foto / KB IX/88”.

Distribution. Western Ecuador to extreme north-western Peru.

Remarks. No additional information is available.

Heraclides anchisiades philastrius (Fruhstorfer, 1915)

Papilio anchisiades philastrius (Fruhstorfer, 1915): 70.

Adult Male (Figure 6-27a) *Body*. Similar to the nominate subspecies.

Forewing. Length 39-51 mm (n = 3). Similar to the male of the nominate subspecies but with the tornal spot smaller and with a tinge of yellow.

Hindwing. Similar to the male of the nominate subspecies but with smaller spots.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figure 6-27b) *Body*. As in the male.

Forewing. Length 49-52 mm (n = 3). Similar to the female of the nominate subspecies but with the white tornal spot smaller and not yellow on the ventral.

Hindwing. Similar to the female of the nominate subspecies.

Genitalia. (Figure 6-68d) Similar to the nominate subspecies.

Type(s). “anchisiades / philastrius / Fr. // Trinidad / Fruhstorfer // Type // Fruhstorfer Coll. / M.M. 1937-285”.

Distribution. Trinidad.

Remarks. No additional information is available.

Heraclides isidorus (Doubleday, 1846)

Diagnosis. Similar to *H. anchisiades* but with the white spot on the ventral of the forewing central, around the area where M3 arises from the discal cell, and often diffused into the discal cell. The spots sometimes show on the dorsal of the wing. Where the spot is absent, the ventral of the hindwing has the spots in m3-cu1 and cu1-cu2 white.

Variation. Very variable in the size and color of the spots on the hindwing and the size of the central spot on the forewing.

Natural History. This butterfly flies between 600 and 1400 meters above sea level (Bollino and Onore, 2001). DeVries (1987) places the Costa Rican subspecies above 1200 meters. This butterfly is seldom seen but is known to inhabit pluvial woodland zones and very humid tropical forests where it can be seen along paved roads at the edges of the forest or at muddy pools and the damp sand near streams and rivers.

Life History. DeVries (1987) states that the yellow eggs are laid in clusters and all larval to pupal stages of *H. isidorus isidorus* are similar to those of *H. anchisiades* except that *H. isidorus isidorus* has greater expanses of white on the dorsal surface and at the anal region; the pupa is identical to that of *H. anchisiades*. A survey of the literature yielded no additional information.

Distribution (Figure 6-85). Costa Rica south through Panama to Peru and east to Colombia and Venezuela.

Remarks. Where there were eight subspecies previously, only six are now recognized based on wing patterns, genitalia and distribution.

Heraclides isidorus isidorus (Doubleday, 1846)

Papilio isidorus (Doubleday, 1846): 375.

Papilio isidorus chironis (Rothschild & Jordan, 1906): 610.

Papilio isidorus form pseudoflavescens (Sala, 1992).

Papilio rhodostictus (Butler & Druce, 1874): 364.

Papilio rhodostictus pacificus (Rothschild & Jordan, 1906): 612. **syn. nov.**

Adult Male (Figures 6-27c, 6-27d, 6-29c and 6-29e) *Body*. Similar to *H. anchisiades*.

Forewing. Length 48-50 mm (n = 22). Dark with no markings; the ventral has a central white spot around where M3 arises from the discal cell, often diffusing into the discal cell.

Hindwing. Similar to the male of *H. anchisiades anchisiades* but with a very short tail.

Genitalia. (Figure 6-57) Similar to *H. epenetus*.

Adult Female (6-29d) *Body*.

Forewing. Length 53-55 mm (n = 2). Similar to the female of *H. isidorus flavescens*, but a tinge of yellow in the scales of the spot on the forewing dorsal and ventral; the spot is less confluent, more focused.

Hindwing. Similar to the female of *H. isidorus flavescens* but with the white scales being replaced by red on both the dorsal and ventral.

Genitalia. (Figure 6-68f) Similar to *H. isidorus flavescens*.

Type(s). “Bolivia. / Puriform / Bridges / 46 – 76 / 2609a // Type // isidorus / 22-217. Dbl. // 2609 / a // Bolivia / [label ventral not clear]”; “Rothschild / Bequest / B.M.1939-1. // Chiriqui” “Type / H.T. // P. rhodostictus / Butler type // Costa Rica. / Van Patten. / Druce Coll. // B.C.A. Lep. Rhop. / Papilio / rhodostictus / Butler & Dr. / Godman-Salvin / Coll. 1918.-4.”; “P. rhodostictus / pacificus. Type. / Nov. Zool. 1906. R & J. // R. Dogin[?] / Colombia / W. Rosenberg // Rothschild / Bequest / B.M.1939-1.”

Distribution. . Costa Rica to Panama down the west coast of Colombia and Ecuador and Northern Peru to Bolivia in the Andes

Remarks. New synonym *Papilio rhodostictus pacificus* (Rothschild & Jordan, 1906) based on wing pattern, genitalia, and pattern of distribution.

Heraclides isidorus autana Racheli & Racheli, 1995

Heraclides isidorus autana Racheli & Racheli, 1995: 621.

Adult Male (Not figured) *Body*. not seen.

Forewing. Not examined.

Hindwing. Not examined.

Genitalia. Not dissected.

Adult Female (Figures 6-34e and 6-34f) *Body*. Only a photograph of the type seen.

Forewing. The white spot spans the width of the discal cell and appears bar shaped. The ventral reflects the dorsal.

Hindwing. The spots are large, red on the edges and white in the center; there are three complete spots plus a fourth incomplete spot, the fifth spot formed by the elements of the eye spot. The ventral reflects the dorsal. Very short tail.

Genitalia. Not dissected.

Type(s). Original description states types in collection of author. Photographs of the type was provided by Tommaso Racheli (author). “Holotypus // Venezuela – Barinas / Barimtas, Los Andes / m 1200, 12.1.1983 / T. Racheli leg.”

Distribution. Venezuela.

Remarks. No additional information is available.

Heraclides isidorus brises (Rothschild & Jordan, 1906)

Papilio isidorus brises (Rothschild & Jordan, 1906): 610.

Papilio rhodostictus nymphius (Rothschild & Jordan, 1906): 612. **syn. nov.**

Papilio metrobates (Ehrmann, 1919)

Papilio isidorus variety *leleargei* (Apolinar, 1924)

Papilio rhodostictus nymphius occidentalis (Apolinar, 1924)

Papilio rhodostictus nymphius orientalis (Apolinar, 1924).

Adult Male (Figures 6-27e, 6-27f, 6-28a, 6-28f, 6-29a, and 6-29b) *Body*. Similar to the nominate subspecies.

Forewing. Length 41-50 mm (n = 16). Similar to the nominate subspecies but with the white central spot smaller.

Hindwing. Similar to the nominate subspecies but with the red of the spots sometimes being replaced by light yellow.

Genitalia. Similar to the nominate subspecies.

Adult Female (Not figured) *Body*. Not examined.

Forewing. Not examined.

Hindwing. Not examined.

Genitalia. Not dissected.

Type(s). “Lectotype / *brises* / KB foto 9/88 // Rothschild / Bequest / B.M.1939-1. // Lecto / type // Bogota”; - “Lectotype / *nymphius* / Oxford // Lecto / type // Bogota // *P. rhodostictus* / *nymphius*. Type. / Nov. Zool. 1906. R & J. // Rothschild / Bequest / B.M.1939-1 // Nov. Zool. 1906 / Pl. VII. Fig. 48”; “Ehrman Coll. / Carn. Mus. / Acc. 7815 // Ann. Carn. Mus. / Vol. 1927 / Pl. XXVII. Fig 2. ♂. // Type // *P. metrobates* Ehrm / Type / ♂ Mathan Col. / Muzo Colombia”

Distribution. Eastern and central Colombian Cordillera.

Remarks. A new synonym is assigned to this species based on a comparison of the wing pattern, genitalia and distribution of *Papilio rhodostictus nymphius* and *Papilio isidorus brises*.

Heraclides isidorus flavescens (Oberthür, 1879)

Papilio isidorus aberration *flavescens* (Oberthür, 1879): 79.

Papilio isidorus variety *leucostictus* (Honrath, 1885): 276.

Papilio ceus (Dognin, 1887): 15 – nomen nudum.

Adult Male (Figures 6-28c and 6-28e) *Body*. Similar to the nominate subspecies.

Forewing. Length 43-50 mm (n = 7). Similar to the nominate subspecies but with the white central spot smaller.

Hindwing. Similar to the nominate subspecies but with the spots at m3-cu1 and cu1-cu2 white.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figures 6-28b and 6-28d) *Body*. As in the male.

Forewing. Length 39-59 mm (n = 5). Similar to the female of *H. isidorus autana* but with the spot more confluent and rounder.

Hindwing. Similar to the female of *H. isidorus autana* but with the spots all white except for the most apical sub-marginal spots and the sub-marginal element of the eye spot.

Genitalia. (Figure 6-68e) Similar to *H. pelaus*.

Type(s). “Typicum / Specimen // Levick Bequest / B.M. 1941-83 // Type // aberr. *Flavescens* / Oberthür // Bogota”.

Distribution. Southern Colombia and eastern Ecuador to northern Peru.

Remarks. No additional information is available.

Heraclides isidorus tingo Racheli & Racheli, 1995

Heraclides isidorus tingo Racheli & Racheli, 1995: 620.

Adult Male (Figures 6-30a and 6-30b) *Body*. Similar to the nominate subspecies.

Forewing. Length 48-50 mm (n = 18). Similar to the male of *H. isidorus flavescens*, but without any spots on the upper or ventral.

Hindwing. Similar to the male of *H. isidorus flavescens*, but with the short tail a little longer.

Genitalia. Similar to the nominate subspecies.

Adult Female (Not figured) *Body*. Photographs of the type seen.

Forewing. Similar to the female of *H. isidorus flavescens*.

Hindwing. Similar to the female of *H. isidorus flavescens*, but with the white scales of the spots tinged with yellow scales.

Genitalia. Not dissected.

Type(s). Original description states types in collection of author. Photographs of the types were provided by Tommaso Racheli (author). "Holotypus / *Heraclides isidorus tingo* Racheli & Racheli 1995 // Peru-Amazonas / R. de Mendoza / m 1000 / Rio Hujambo XI.85 / Calderon"; "Paratypus // Tingo Maria / Peru Apr 1986".

Distribution. Peru.

Remarks. No additional information is available.

Heraclides chiansiades (Westwood, 1872)

Papilio chiansiades (Westwood, 1872): 101, plate 5, figures 3-5.

Heraclides chiansiades mossi Brown, 1994: plate 79. **syn. nov.**

Papilio dospassosi (Rütimeyer, 1969): 225.

Papilio maroni (Moreau, 1923): 144.

Diagnosis. Yellowish spot on the forewing dorsal touching the inner margin. The spot hardly shows on the ventral. Mimics of *Mimoides ariariathes gayi*.

Adult Male (Figures 6-30c, 6-30d, 6-31a, 6-33e and 6-33f) *Body*. Similar to the previous species.

Forewing. Length 45-52 mm (n = 22). The yellow spot on the dorsal surface is very low on the wing at a central location, touching the inner margin. The spot hardly shows on the ventral.

Hindwing. Similar to *H. isidorus isidorus* but always with one small sub-marginal spot at m3-cu1.

Genitalia. (Figure 6-58) Similar to *H. epenetus*.

Adult Female (Not figured) *Body*. Not examined.

Forewing. Not examined.

Hindwing. Not examined.

Genitalia. Not dissected.

Variation. Not very variable.

Natural History. A deep forest butterfly (Tyler et al., 1994), this species is similar in appearance to *H. anchisiades* and *Mimoides ariariathes gayi*. Host plant is given as *Citrus* sp. and other Rutaceae (Tyler et al., 1994; Le Crom et al., 2002). A survey of the literature yielded no additional information.

Life History. Unknown.

Type(s). “*Papilio chiansiades* /, / Westw. / Godman-Salvin / Coll. 1918 – 4. // Rio Topo, / Ecuador. / C. Buckley / Cruce Coll. // ♂ // Rio Topo / Ecuador / Buckley // Type / H. T. // *Pap chiansiades* / type Westwood”; “K.B. IX/89 / will be / Holotype // Part 12” “Rio Putu- / mayo. / Columbian. / Sept. 1925 // Photographed / specimen B/CC / Tyler; Brown; & Wilson; / 1992. Swallowtail / Butterflies of the / Americas. / Pl/fig 79/14 // dissection # / 228 Johnson / + Matusik 1985 / 1986 // *Papilio dospassosi* / Rüttimeyer // Holotype”.

Distribution (Figure 6-86). Eastern Andes and upper Amazon to southern Venezuela, south to Rondônia and Bolivia and Belém west to Rio Tapajos and less frequently Rio Madeira. Also Venezuela through Guyana to the lower Amazon, south to Bolivia and east to Rio Tapajos and the upper Amazon and the Andes.

Remarks. A new synonym is assigned to this subspecies. Tyler et al. (1994) named a new subspecies “*mossi*” but the geographic range, morphology and type is consistent with that of the nominate subspecies and is treated as a synonym.

Heraclides rogeri (Boisduval, 1836)

Diagnosis. Red spots on the hindwing never merged and males with a long slender tail.

Variation. The two subspecies are quite distinct. There is often a tail but this can sometimes be short.

Natural History. This species can be found in tropical dry forests. Up to 118 orange-brown eggs are laid in each cluster, similar to *H. anchisiades*, on *Citrus aurantifolia* and other Rutaceae. If not disturbed, females will spend almost one hour depositing eggs on the ventral surface of old leaves on a low branch in the shade. Laying females can be gently touched without interference to the laying process (Einem, 2004).

Life History. Larvae hatch after six days and are rest gregariously during the day and feed at night (Einem, 2004). A survey of the literature yielded no additional information about this butterfly’s habits.

Distribution (Figure 6-86). Eastern and western Mexico down through Yucatan and south to Guatemala.

Remarks. There are two recognized subspecies. Tyler et al. (1994) treated “*rogeri*” as a subspecies of *pharnaces* but this has subsequently been rectified based on the rules of nomenclature (Lamas, 2004).

Heraclides rogeri rogeri (Boisduval, 1836)

Papilio rogeri (Boisduval, 1836): 278.

Adult Male (Figures 6-31c and 6-31e) *Body.* Similar to *H. anchisiades idaeus*.

Forewing. Length 40-50 mm (n = 19). Similar to the male of *H. anchisiades idaeus* but with a little more white suffusion on the ventral that shows through to the dorsal.

Hindwing. With the red proximal post-discal spots more pronounced than the sub-marginal spots.

Genitalia. (Figure 6-59) Similar to *H. epenetus* but with serrations on the distal edge of the harpe near the spine-like point.

Adult Female (Figures 6-31b and 6-31d) *Body.* As in the male.

Forewing. Length 48-57 mm (n = 14). As in the male.

Hindwing. Similar to the male but showing more sub-marginal spots on the upper and ventral.

Genitalia. (Figure 6-67g) Similar to *H. anchisiades*.

Type(s). Probably in Museum National d'Histoire Naturelle, Paris, France (MNHP). A request for information sent and the reply was that the type was not located there. The original description did not provide adequate information about the type. Type presumed lost.

Distribution. All of Yucatan including northern Belize to north-western Guatemala.

Remarks. No additional information is available.

Heraclides rogeri pharnaces (Doubleday, 1846)

Papilio pharnaces (Doubleday, 1846): 374.

Papilio phanostratus (Godman & Salvin, 1890): 232.

Papilio polycharmum (Godman & Salvin, 1890): 66, plate 70, figure 10.

Papilio pharnaces form *paucimaculata* (Vázquez, 1947): 249.

Papilio pharnaces form *dissimilis* (Vázquez, 1957): 478.

Adult Male (Figures 6-32a and 6-32c) *Body*. Similar to the nominate subspecies.

Forewing. Length 38-54 mm (n = 82). Dark, with hardly any markings or suffusion of scales.

Hindwing. With the red post-discal and red sub-marginal spots never merged and in two rows. Always with four or more proximal post-discal spots with the proximal post-discal element of the eye spot forming the most anal spot.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figures 6-31f, 6-32b, and 6-32d) *Body*. As in the male.

Forewing. As in the male.

Hindwing. Similar to the male but with a shorter tail.

Genitalia. (Figure 6-67h) Similar to the nominate subspecies.

Type(s). "B.C.A.Lep.Rhop. / *Papilio* / *phanostratus*, / G. & S. / Godman-Salvin / Coll. 1918.-4. // ♂ // Jalapa, / Mexico. / Hoege. // Type / H.T."; "B.C.A.Lep.Rhop. / *Papilio* / *polycharmum*, / G. & S. / Godman-Salvin / Coll. 1918. -4. // Type / H.T. // Sp. figured. // ♂ // Presidio, / Mexico. / Forrer."; "T. Escalante / Empalme / El Ocotil / IX-73 [?] // F. *paucimaculate* // A. C. Allyn / Acc. 1973-48 // Tipo"; "A. C. Allyn / Acc. 1973-48 // T. Escalante / El Ocotil / XII-55 chis. // *Pharnaces* / F. / *Dissimilis*".

Distribution. Southern Sonora and northern Tamaulipas in Mexico to Tabasco and Chiapas, into north-western Guatemala.

Remarks. No additional information is available.

Heraclides erostratus (Westwood, 1847)

Diagnosis. Males with yellow sub-marginal spots on the hind wing. These spots are red on the ventral and accompanied by red post-discal spots.

Variation. Sexes dimorphic.

Natural History. Other than the larvae being gregarious feeders on *Citrus* sp. (Tyler et al., 1994), a survey of the literature yielded no additional information.

Life History. Unknown.

Distribution (Figure 6-86). Along the western and eastern coast of Mexico and southern Mexico into Guatemala and El Salvador.

Remarks. Three subspecies are recognized.

Heraclides erostratus erostratus (Westwood, 1847)

Papilio erostratus (Westwood, 1847): 36, plate 3, figure 2 & 2*.

Papilio rhetus (Gray, [1853]): 65, plate 11, figure 5 – preoccupied name.

Papilio erostratinus (Vázquez, 1947): 252.

Adult Male (Figure 6-32e and 6-33a) *Body*. Similar to *H. rogeri*.

Forewing. Length 45-55 mm (n = 28). Similar to *H. rogeri*.

Hindwing. With the sub-marginal spots yellow, replaced by red on the ventral and accompanied by red post-discal spots.

Genitalia. (Figure 6-60) Similar to *H. rogeri*.

Adult Female (Figure 6-32f and 6-33b) *Body*. As in the male.

Forewing. Length 50-59 mm (n = 16). As in the male.

Hindwing. Similar to the female of *H. rogeri pharnaces* but always with the most anal marginal spot pink. This spot is white in *H. rogeri pharnaces*.

Genitalia. (Figure 6-68g and 6-68h) Similar to *H. pelaus*.

Type(s). “Type // Guatemala / 48-35. // rhetus / 22-207 Grey // [label with difficult handwriting]” “L. Vázquez det. / Papilio ♂ / erostratinus Váxq. // Tipo // T. Escalante / Necaxa Pue / Ex. Larva / iv-45”.

Distribution. Southern Mexico from Chiapas to Guatemala and El Salvador and Western Mexico in Tamaulipas and Nuevo Leon to northern Puebla and Veracruz.

Remarks. No additional information is available.

Heraclides erostratus vazquezae (Beutelspacher, 1986)

Papilio erostratus vazquezae (Beutelspacher, 1986): 241.

Adult Male (Figure 6-33c) *Body*. Similar to the male of the nominate subspecies.

Forewing. Length 45-55 mm (n = 12). Similar to the male of the nominate subspecies.

Hindwing. Similar to the male of the nominate subspecies.

Genitalia. Similar to the nominate subspecies.

Adult Female (Figure 6-33d) *Body*. As in the male.

Forewing. Length 52 mm (n = 1). Similar to the female of the nominate subspecies.

Hindwing. Similar to the female of the nominate subspecies.

Genitalia. (Figure 6-68i) Similar to the nominate subspecies.

Type(s). “Holotipo // C. Beutelspacher B., det. / Papilio erostratus ♂ / vazquezae Beutelspacher // A. Ibarra / Acahuizotla, / Gre. / 15-X-1982”.

Distribution. Eastern Mexico in Jalisco, Colima, Guerrero and southern Oaxaca into Morelos.

Remarks. No additional information is available.

Synonymic Checklist of *Heraclides*

HERACLIDES Hübner, 1819: 83. Type *Papilio thoas* Linnaeus, 1771.

CALAIDES Hübner, 1819: 86. Type *Papilio androgeus* Cramer, 1775.

PRIAMIDES Hübner, 1819: 87. Type *Priamides hipponous* Hübner, 1819.

TROILIDES Hübner, 1825: pl. 111, 2f. Type *Troilides tros* Hübner, 1825.

THOAS Swainson, 1833: pl. 121. Type *Papilio thoas* Linnaeus, 1771.
anchisiades anchisiades (Esper, 1788)
anchises (Stoll, 1780)
hipponous (Hübner, [1819])
archelaus (Godart, 1819)
theramenes (Felder & Felder, 1861)
matusiki Johnson & Rozycki, 1986
anchisiades capys (Hübner, [1809])
evander (Godart, 1819) preoccupied name
anchisiades idaeus (Fabricius, 1793)
pandion (Bates, 1861) - nomen nudum
anchisiades variety *pandion* (Bates, 1863)
pandion (Felder & Felder, [1865]) name erroneously thought preoccupied
pandonius (Staudinger, 1894) replacement name
anchisiades lamasi Brown, 1994
anchisiades philastrius (Fruhstorfer, 1915)
andraemon andraemon Hübner, [1823]
andraemon hernandezi Torre, 1936
andraemon bonhoti (Sharpe, 1900)
andraemon tailori (Rothschild & Jordan, 1906)
androgeus androgeus (Cramer, 1775)
orestes (Meerburgh, 1777)
polycaon (Cramer, 1779)
piranthus (Cramer, 1779)
acanthus (Gmelin, 1790) misspelling
androgeus bagous (Fruhstorfer, 1907)
androgeus form *mira* (Fassl, 1922)
androgeos form *feyeri* (Niepelt, 1924) original misspelling
androgeus variety *fassli* (Knop, 1925)
androgeus androgeus aberration *decellei* (Krüger, 1934)
hibisci (Fabricius, 1938) replacement name.
altheae (Fabricius, 1938) preoccupied name.
androgeus epidaurus (Godman & Salvin, 1890)
androgeus epidaurus form *ochracea* (Beutelspacher, 1976)
androgeus laodocus (Fabricius, 1793)
laodocus form *limbatus* (Boullet & Le Cerf, 1912)
laodocus form *vollmanni* (Lederer, 1961)
aristodemus aristodemus (Esper, 1794)
cresphontinus (Martyn, 1797)
daphnis (Gray [1853]) preoccupied name
aristodemus bjorndalae (Clench, 1979)
aristodemus majasi Miller, 1987
aristodemus ponceanus (Schaus, 1911)
aristodemus driophilus (Clench, 1979)
aristodemus temenes (Godart, 1819)
aristor (Godart, 1819)

astyalus astyalus (Godart, 1819)
lycophon (Hübner, [1823])
mentor (Dalman, 1823)
pirithous (Boisduval, 1836) preoccupied name
oebalus (Boisduval, 1836)
drepanon (Gray, 1856) nomen nudum
lycophon drepanon (Fruhstorfer, 1907)
lycophon aberration *delunensis* (Niepelt, 1916)
lycophon form *paulina* (Krüger, 1934) preoccupied name
lycophon lycophon form *thersitoides* (Rousseau-Decelle, 1943)
lycophon pirithous form *suffusa* (Rousseau-Decelle, 1943)
astyalus anchicayaensis Constantino, Le Crom & Salazar, 2002
astyalus bajaensis (Brown, Real & Faulkner, 1992)
astyalus occidentalis (Brown & Faulkner, 1984) preoccupied name
astyalus hippomedon (Felder & Felder, 1859)
theophon (Felder & Felder, 1864) nomen nudum
theophon (Felder & Felder, 1865)
hippomedon form *iraidari* (Lichy, 1960)
hippomedon form *taini* (Lichy, 1960)
astyalus pallas (Gray [1853])
pallas (Doubleday [1845]) nomen nudum
hozaus (Ehemann, 1921)
astyalus phanias (Rothschild & Jordan, 1906)
lycophon phanias (Rothschild & Jordan, 1906)
lycophon brunneus (Prüffer, 1922)
caiguanabus (Poey [1852])
numicus (Hopffer, 1856)
chiansiades chiansiades (Westwood, 1872)
chiansiades mossi Brown, 1994. **syn. nov.**
dospassosi (Rütimeyer, 1969)
maroni (Moreau, 1923): 144.
cresphontes (Cramer, 1777)
oxilus (Hübner, [1819]) replacement name.
cresphontes aberration *lurida* (Schultz, 1908)
thoas cresphontes aberration *luxuriosa* (Reiff, 1911)
cresphontes aberration *intacta* (Strand, 1918)
cresphontes variety *maxwelli* (Franck, 1919)
cresphontes transition form *forsythae* (Gunder, 1933)
cresphontes form *melanurus* (Hoffmann, 1940)
cresphontes pennsylvannicus (Chermock & Chermock, 1945)
epenetus (Hewitson, 1861)
erostratus erostratus (Westwood, 1847)
rhetus (Gray, [1853]) preoccupied name
erostratinus (Vázquez, 1947)
erostratus vazquezae (Beutelspacher, 1986)
garleppi garleppi (Staudinger, 1892)

garleppi interruptus (Staudinger, 1892)
garleppi lecerfi Brown & Lamas, 1994
garleppi variety *insidiosus* (Le Cerf, 1923)
hectorides (Esper, 1794)
argentus (Martyn, 1797)
torquatinus (Esper, 1799)
pandrosus (Godart, 1819) preoccupied name
lysithous (Godart, 1819)
chirodamas (Hübner, [1825])
mezentius (Doubleday, 1844)
torquatinus aberration *melania* (Oberthür, 1879)
hectorides form *catamelas* (Rothschild & Jordan, 1906)
hectorides agordus (Fruhstorfer, 1915)
hectorides lysirte (Fruhstorfer, 1915)
himeros himeros (Hopffer, 1865)
mentor (Boisduval, 1836) preoccupied name
herodotus (Capronnier, 1874) nomen nudum
lycophron variety *minor* (Burmeister, 1878) replacement name
herodotus (Oberthür, 1879)
himeros baia (Rothschild & Jordan, 1906)
homothoas (Rothschild & Jordan, 1906)
hyppason (Cramer, 1775)
amosis (Cramer, 1780) preoccupied name.
hyppason variety *paraensis* (Bates, 1861) original misspelling
hyppasonides (Grose-Smith, 1902)
hyppason form *ptilion* (Rothschild & Jordan, 1906)
hyppason rousseau-decellei (Le Moul, 1933) original misspelling
hyppason form *unimaculata* (Rousseau-Decelle, 1943) preoccupied name
hyppason form *modestior* (Varea, 1975)
isidorus isidorus (Doubleday, 1846)
isidorus chironis (Rothschild & Jordan, 1906)
isidorus form *pseudoflavescens* (Sala, 1992)
isidorus rhodostictus (Butler & Druce, 1874)
rhodostictus pacificus (Rothschild & Jordan, 1906) **syn. nov.**

isidorus autana Racheli & Racheli, 1995
isidorus brises (Rothschild & Jordan, 1906)
isidorus nymphius (Rothschild & Jordan, 1906) **syn. nov.**
metrobates (Ehrmann, 1919)
rhodostictus nymphius orientalis (Apolinar, 1924)
isidorus variety *lelargei* (Apolinar, 1924)
rhodostictus nymphius occidentalis (Apolinar, 1924)
isidorus flavescens (Oberthür, 1879)
isidorus variety *leucostictus* (Honrath, 1885)
ceus (Dognin, 1887) nomen nudum.
isidorus tingo Racheli & Racheli, 1995

lamarchei (Staudinger, 1892)
machaonides (Esper, 1796)
lycoraeus (Godart, 1819)
melonius (Rothschild & Jordan, 1906)
thoas melonius (Rothschild & Jordan, 1906)
ornythion (Boisduval, 1836)
oxynius (Geyer, [1827])
oxynius form *niveomarginatus* (Rousseau-Decelle, 1933)
oxynius form *ochracea* (Rousseau-Decelle, 1933)
augustus (Boisduval, 1836)
paeon paeon (Boisduval, 1836)
paon paon perigino (Bryk, 1953) original misspelling
paeon marxi (Möhn, 2001)
paeon escomeli (Cockerell, 1927)
paeon thrason (Felder & Felder, 1865)
thrason (Felder & Felder, 1864) nomen nudum
pelaus pelaus (Fabricius, 1775)
ornofagus (Weidemeyer, 1863) nomen nudum
pelaus atkinsi (Bates, 1935)
pelaus imerius (Godart, 1819)
augias (Ménétries, 1832) preoccupied name
pelaus puertoricensis Möhn, 1999
rogeri rogeri (Boisduval, 1836)
rogeri pharnaces (Doubleday, 1846)
phanostratus (Godman & Salvin, 1890)
polycharmus (Godman & Salvin, 1890)
pharnaces form *paucimaculata* (Vázquez, 1947)
pharnaces form *dissimilis* (Vázquez, 1957)
thersites (Fabricius, 1775)
palamedes (Fabricius, 1775) preoccupied name
acamas (Fabricius, 1793)
thoas thoas (Linnaeus, 1771)
archimedes (Fabricius, 1938)
thoas autocles (Rothschild & Jordan, 1906)
thoas autocles form *nigro-caudata* (Vázquez, 1949) Original misspelling
thoas autocles aberration *nigrimarginata* (Beutelspacher, 1976)
thoas autocles form *ochracea* (Beutelspacher, 1976)
thoas brasiliensis (Rothschild & Jordan, 1906)
thoas impunctata (Boullet & Le Cerf, 1912)
thoas brasiliensis aberration *completa* (Dufrane, 1946)
thoas brasiliensis aberration *reducta* (Dufrane, 1946)
thoas cinyras (Ménétries, 1857)
lampedon (Gray, 1856) nomen nudum.
thoas chamadus (Fruhstorfer, 1907)
cinyras aberration *ridens* (Fassl, 1915)
thoas aberration *flavibrunneus* (Prüffer, 1922)

thoas neacles (Rothschild & Jordan, 1906)
thoas oviedo (Gundlach, 1866)
epithoas (Oberthür, 1897)
thoas thoantiades (Burmeister, 1878)
euclides (Larrañaga, 1923)
thoas brasiliensis aberration *ochracea* (Giacomelli, 1927)
torquatus torquatus (Cramer, 1777)
caudius (Hübner, [1809])
patros (Gray, [1853])
torquatus variety *flavida* (Oberthür, 1879)
tasso (Staudinger [1884]) – regarded as an aberration
torquatus form *theras* (Rothschild & Jordan, 1906)
torquatus form *cleolas* (Rothschild & Jordan, 1906)
torquatus variety *dubia* (Boullet & Le Cerf, 1912) preoccupied name
torquatus aberration *modestus* (Röber, 1927)
garleppi interruptus form *xanthica* (Rousseau-Decelle, 1943)
torquatus aberration *leo* (Okano, 1985)
torquatus atsukoae (Okano, 1985)
torquatus jeani Brown & Lamas, 1994
orchamus (Boisduval, 1836) preoccupied name
torquatus leptalea (Rothschild & Jordan, 1906)
torquatus mazai (Beutelspacher, 1977)
torquatus tolus form *semimaculata* (Vázquez, 1949)
tolus mazai (Beutelspacher, 1977)
torquatus polybius (Swainson, 1823)
trojanus (Boisduval, 1836)
polybius form *albosignata* (Rousseau-Decelle, 1943)
torquatus tolmides (Godman & Salvin, 1890)
torquatus tolus (Godman & Salvin, 1890)
tolus form *prorsus maculata* (Vázquez, 1949) original misspelling
torquatus tolus form *semipunctata* (Vázquez, 1949)

Papilio peleides (Esper, 1793) by Rothschild and Jordan (1906): “Besides Jablonsky’s figure and description there is no evidence of the existence of this insect. Jablonsky expressly states that the figure was carefully drawn from a specimen. The individual may have been an artifact, as suggested by Boisduval, but the figure does not give us that impression. Considering that of many American Papilios only very few specimens are known, it is quite conceivable that *P. peleides* has not been rediscovered”.

Table 6-1. List of host plants for the species of the genus *Heraclides* (Beccaloni et al., 2008).

Host Plant	Family	<i>H. thoas</i>	<i>H. crespontes</i>	<i>H. homothoas</i>	<i>H. melonius</i>	<i>H. paeon</i>	<i>H. aristor</i>	<i>H. caiguanabus</i>	<i>H. thersites</i>	<i>H. androgeus</i>	<i>H. astyalus</i>	<i>H. ornythion</i>	<i>H. aristodemus</i>	<i>H. andraemon</i>	<i>H. machaonides</i>
<i>Arracacia</i> sp.	Apiaceae					✓									
<i>Arracacia xanthorrhiza</i>	Apiaceae					✓									
<i>Conium maculatum</i>	Apiaceae					✓									
<i>Pastinaca sativa</i>	Apiaceae					✓									
<i>Syngonium podophyllum</i>	Araceae	✓													
<i>Piper</i> sp.	Piperaceae	✓													
<i>Piper aduncum</i>	Piperaceae	✓													
<i>Piper amalago</i>	Piperaceae	✓													
<i>Piper arboreum</i>	Piperaceae	✓													
<i>Piper arboreum tuberculatum</i>	Piperaceae	✓													
<i>Piper augustifolium</i>	Piperaceae	✓													
<i>Piper auritum</i>	Piperaceae	✓													
<i>Piper belemense</i>	Piperaceae	✓													
<i>Piper colonense</i>	Piperaceae	✓													
<i>Piper dilatatum</i>	Piperaceae	✓													
<i>Piper emarginatum</i>	Piperaceae	✓													
<i>Piper gaudichaudianum</i>	Piperaceae	✓													
<i>Piper guanacostense</i>	Piperaceae	✓													
<i>Piper hispidum</i>	Piperaceae	✓													
<i>Piper jacquemontianum</i>	Piperaceae	✓													
<i>Piper kerberi</i>	Piperaceae	✓													
<i>Piper lanceifolium</i>	Piperaceae	✓													
<i>Piper marginatum</i>	Piperaceae	✓													
<i>Piper marginatum marginatum</i>	Piperaceae	✓													
<i>Piper mikanianum</i>	Piperaceae														
<i>Piper multiplinervium</i>	Piperaceae	✓													
<i>Piper papantlense</i>	Piperaceae	✓													
<i>Piper peltata</i>	Piperaceae	✓													
<i>Piper pseudofulgineum</i>	Piperaceae	✓													

Table 6-1. (Continued)

Host Plant	Family	<i>H. thoas</i>	<i>H. crespontes</i>	<i>H. homothoas</i>	<i>H. melonius</i>	<i>H. paeon</i>	<i>H. aristor</i>	<i>H. caiguababus</i>	<i>H. thersites</i>	<i>H. androgeus</i>	<i>H. astyalus</i>	<i>H. ornythion</i>	<i>H. aristodemus</i>	<i>H. andraemon</i>	<i>H. machaonides</i>	
<i>Piper reticulatum</i>	Piperaceae	✓														
<i>Piper sanctifelicis</i>	Piperaceae	✓														
<i>Piper umbellatum</i>	Piperaceae	✓														
<i>Piper urostachyum</i>	Piperaceae	✓														
<i>Piper villiramulum</i>	Piperaceae	✓														
<i>Amyris</i> sp.	Rutaceae															✓
<i>Amyris balsamifera</i>	Rutaceae												✓			
<i>Amyris elemifera</i>	Rutaceae												✓			
<i>Amyris pinnata</i>	Rutaceae								✓	✓						
<i>Balfourodendron riedelianum</i>	Rutaceae									✓						
<i>Casimora</i> sp.	Rutaceae								✓							
<i>Casimora edulis</i>	Rutaceae	✓							✓							
<i>Casimora tetrameria</i>	Rutaceae	✓														
<i>Choisya ternata</i>	Rutaceae	✓									✓					
<i>Citrus</i> sp.	Rutaceae	✓	✓	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Citrus aurantiifolia</i>	Rutaceae	✓	✓					✓		✓	✓			✓		
<i>Citrus aurantium</i>	Rutaceae	✓	✓	✓		✓			✓	✓				✓		
<i>Citrus limetta</i>	Rutaceae								✓							
<i>Citrus limon</i>	Rutaceae	✓	✓					✓	✓	✓						
<i>Citrus maxima</i>	Rutaceae	✓								✓						
<i>Citrus medica</i>	Rutaceae								✓							
<i>Citrus paradisi</i>	Rutaceae	✓									✓					
<i>Citrus reticulata</i>	Rutaceae	✓		✓				✓	✓	✓						
<i>Citrus sinensis</i>	Rutaceae	✓	✓	✓		✓			✓	✓				✓		
<i>Dictamnus</i> sp.	Rutaceae	✓														
<i>Esenbeckia</i> sp.	Rutaceae	✓						✓								
<i>Esenbeckia berlandieri</i>	Rutaceae	✓									✓					
<i>Esenbeckia febrifuga</i>	Rutaceae	✓							✓	✓						
<i>Esenbeckia leiocarpa</i>	Rutaceae	✓							✓	✓						
<i>Esenbeckia pentaphylla</i>	Rutaceae	✓									✓					

Table 6-1. (Continued)

Host Plant	Family	<i>H. thoas</i>	<i>H. crespontes</i>	<i>H. homothoas</i>	<i>H. melonius</i>	<i>H. paeon</i>	<i>H. aristor</i>	<i>H. caiguanabus</i>	<i>H. thersites</i>	<i>H. androgeus</i>	<i>H. asfyalus</i>	<i>H. orrythion</i>	<i>H. aristodemus</i>	<i>H. andraemon</i>	<i>H. machaonides</i>
<i>Esenbeckia pilocarpoides</i>	Rutaceae										✓				
<i>Esenbeckia pumila</i>	Rutaceae	✓													
<i>Fortunella marginata</i>	Rutaceae	✓													
<i>Galipea jasminiflora</i>	Rutaceae										✓				
<i>Murraya paniculata</i>	Rutaceae	✓													
<i>Pilocarpus pennatifolius pennatifolius</i>	Rutaceae										✓				
<i>Ptelea</i> sp.	Rutaceae	✓	✓												
<i>Ptelea trifoliata</i>	Rutaceae		✓												
<i>Ruta</i> sp.	Rutaceae			✓		✓									✓
<i>Ruta chalepensis</i>	Rutaceae		✓												
<i>Ruta graveolens</i>	Rutaceae	✓	✓			✓					✓				✓
<i>Skimmia japonica</i>	Rutaceae										✓				
<i>Swinglea glutinosa</i>	Rutaceae									✓					
<i>Zanthoxylum</i> sp.	Rutaceae	✓	✓						✓	✓	✓		✓	✓	✓
<i>Zanthoxylum americanum</i>	Rutaceae		✓										✓		
<i>Zanthoxylum caribaeum</i>	Rutaceae	✓	✓							✓					
<i>Zanthoxylum coco</i>	Rutaceae									✓	✓				
<i>Zanthoxylum culantrillo</i>	Rutaceae		✓								✓				
<i>Zanthoxylum ekmanii</i>	Rutaceae														
<i>Zanthoxylum fagara</i>	Rutaceae	✓			✓				✓	✓			✓		
<i>Zanthoxylum flavum</i>	Rutaceae												✓		
<i>Zanthoxylum martinicense</i>	Rutaceae	✓									✓				
<i>Zanthoxylum rhoifolium</i>	Rutaceae	✓								✓	✓				
<i>Zanthoxylum riedelianum</i>	Rutaceae	✓								✓					
<i>Zanthoxylum setulosum</i>	Rutaceae	✓				✓				✓	✓				

Table 6-1. (Continued)

Host Plant	Family	<i>H. lamarchei</i>	<i>H. himeros</i>	<i>H. hectorides</i>	<i>H. garleppi</i>	<i>H. torquatus</i>	<i>H. hyppason</i>	<i>H. epenetus</i>	<i>H. oxynius</i>	<i>H. pelaus</i>	<i>H. anchisiades</i>	<i>H. isidorus</i>	<i>H. chiansiades</i>	<i>H. rogeri</i>	<i>H. erostratus</i>
<i>Piper</i> sp.	Piperaceae		✓												
<i>Piper amalago</i>	Piperaceae		✓												
<i>Piper belemense</i>	Piperaceae					✓									
<i>Piper mikanianum</i>	Piperaceae		✓												
<i>Piper umbellatum</i>	Piperaceae		✓												
<i>Piper xylosteoides</i>	Piperaceae		✓												
<i>Amyris pinnata</i>	Rutaceae										✓				
<i>Angostura nicaraguensis</i>	Rutaceae					✓									
<i>Casimora</i> sp.	Rutaceae									✓					
<i>Casimora edulis</i>	Rutaceae									✓	✓		✓	✓	
<i>Casimora tetrameria</i>	Rutaceae										✓				
<i>Choisya ternata</i>	Rutaceae					✓					✓				
<i>Citrus</i> sp.	Rutaceae		✓		✓	✓	✓		✓	✓	✓	✓	✓	✓	✓
<i>Citrus aurantiifolia</i>	Rutaceae										✓				
<i>Citrus aurantium</i>	Rutaceae										✓				✓
<i>Citrus limetta</i>	Rutaceae														
<i>Citrus limon</i>	Rutaceae		✓			✓			✓	✓		✓			✓
<i>Citrus maxima</i>	Rutaceae		✓								✓				
<i>Citrus medica</i>	Rutaceae										✓				
<i>Citrus mitis</i>	Rutaceae			✓											
<i>Citrus paradisi</i>	Rutaceae					✓					✓				
<i>Citrus reticulata</i>	Rutaceae			✓		✓					✓				
<i>Citrus sinensis</i>	Rutaceae			✓		✓					✓				✓
<i>Dictamnus</i> sp.	Rutaceae														
<i>Esenbeckia</i> sp.	Rutaceae					✓				✓					
<i>Esenbeckia berlandieri</i>	Rutaceae										✓				
<i>Esenbeckia febrifuga</i>	Rutaceae					✓					✓				
<i>Esenbeckia leiocarpa</i>	Rutaceae		✓	✓		✓					✓				
<i>Esenbeckia pentaphylla</i>	Rutaceae					✓									

Table 6-1. (Continued)

Host Plant	Family	<i>H. lamarchei</i>	<i>H. himeros</i>	<i>H. hectorides</i>	<i>H. garleppi</i>	<i>H. torquatus</i>	<i>H. hyppason</i>	<i>H. epenetus</i>	<i>H. oxynius</i>	<i>H. pelaus</i>	<i>H. anchisiades</i>	<i>H. isidorus</i>	<i>H. chiansiades</i>	<i>H. rogeri</i>	<i>H. erostratus</i>
<i>Esenbeckia pilocarpoides</i>	Rutaceae					✓									
<i>Euxylophora paraensis</i>	Rutaceae					✓									
<i>Fortunella japonica</i>	Rutaceae											✓			
<i>Fortunella marginata</i>	Rutaceae											✓			
<i>Galipea jasminiflora</i>	Rutaceae			✓											
<i>Helietta</i> sp.	Rutaceae			✓											
<i>Monnieria trifolia</i>	Rutaceae					✓									
<i>Pilocarpus</i> sp.	Rutaceae			✓											
<i>Skimmia japonica</i>	Rutaceae											✓			
<i>Swinglea glutinosa</i>	Rutaceae											✓			
<i>Zanthoxylum</i> sp.	Rutaceae			✓	✓			✓	✓	✓	✓	✓	✓		
<i>Zanthoxylum coco</i>	Rutaceae	✓										✓			
<i>Zanthoxylum culantrillo</i>	Rutaceae														
<i>Zanthoxylum ekmanii</i>	Rutaceae											✓			
<i>Zanthoxylum fagara</i>	Rutaceae			✓								✓			
<i>Zanthoxylum martinicense</i>	Rutaceae							✓	✓						
<i>Zanthoxylum melanostictum</i>	Rutaceae											✓			
<i>Zanthoxylum rhoifolium</i>	Rutaceae			✓								✓			
<i>Zanthoxylum riedelianum</i>	Rutaceae											✓			
<i>Zanthoxylum setulosum</i>	Rutaceae											✓			

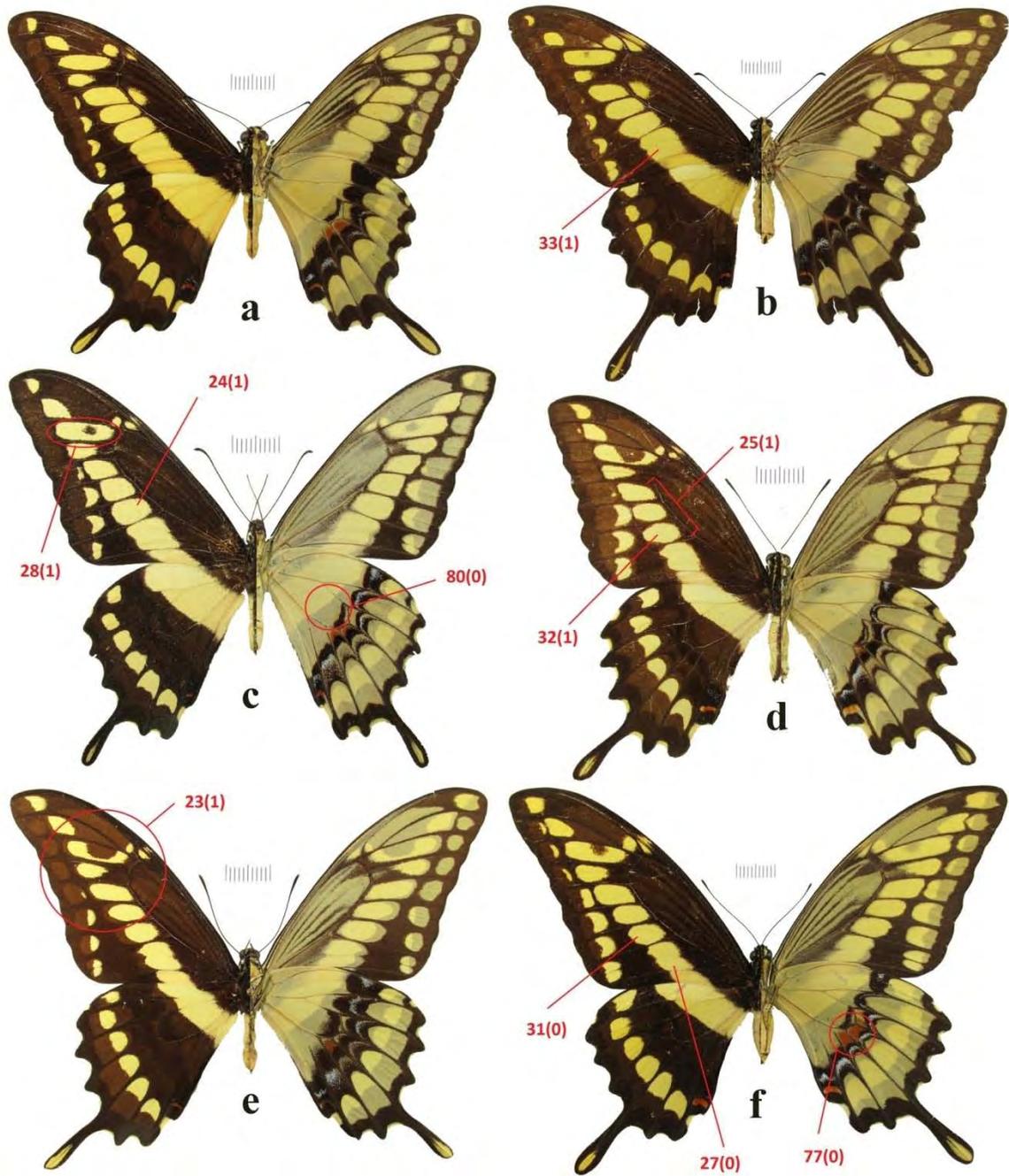


Figure 6-1. *Heraclides* adults dorsal and ventral: (a) *H. thoas thoas* ♂, (b) *H. thoas thoas* ♀, (c) *H. thoas autocles* ♂, (d) *H. thoas autocles* ♀, (e) *H. thoas brasiliensis* ♂, (f) *H. thoas brasiliensis* ♀. Scale bar in 1 mm segments.

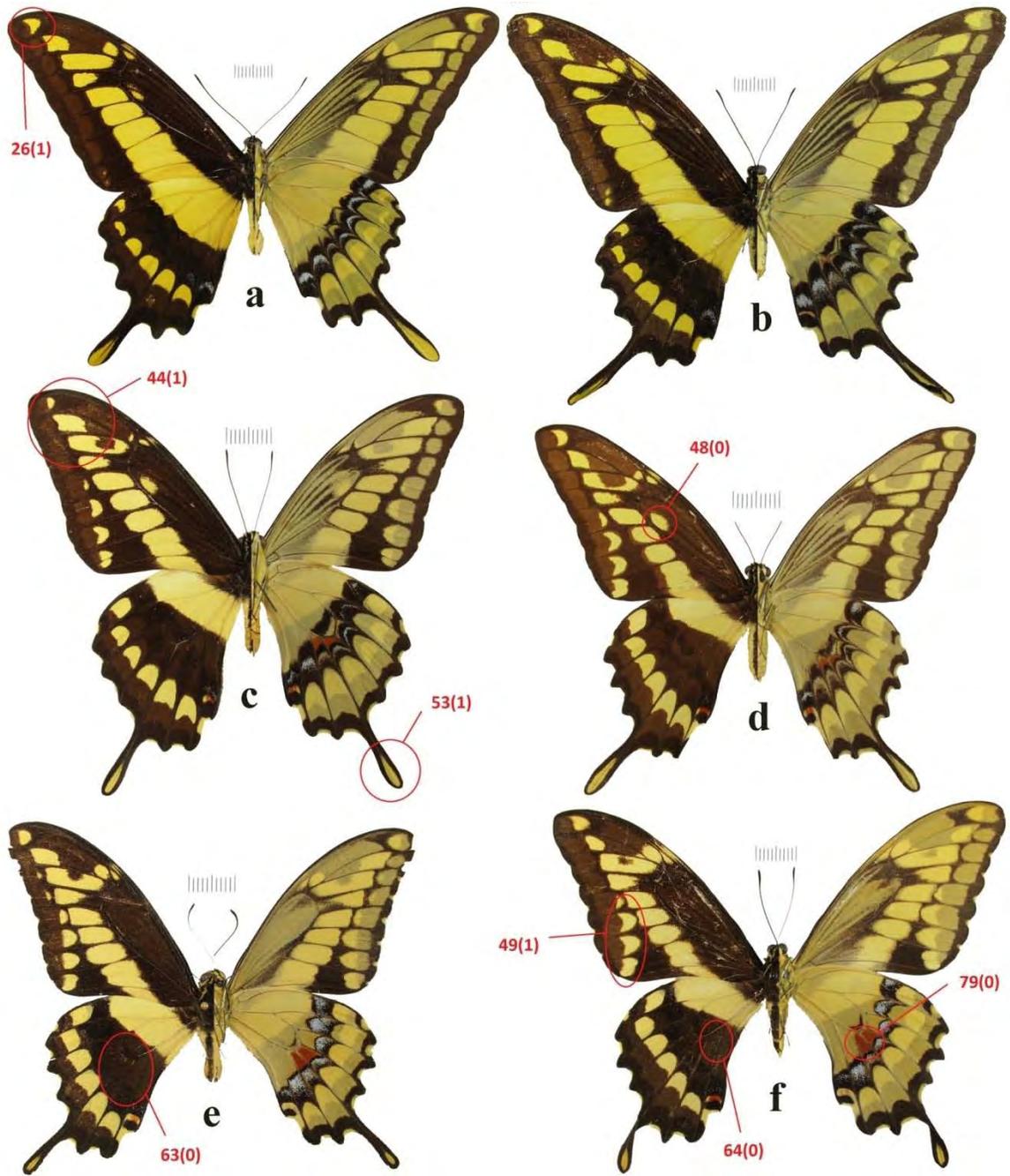


Figure 6-2. *Heraclides* adults dorsal and ventral: (a) *H. thoas cinyras* ♂, (b) *H. thoas cinyras* ♀, (c) *H. thoas neacles* ♂, (d) *H. thoas neacles* ♀, (e) *H. thoas oviedo* ♂, (f) *H. thoas oviedo* ♀. Scale bar in 1 mm segments.

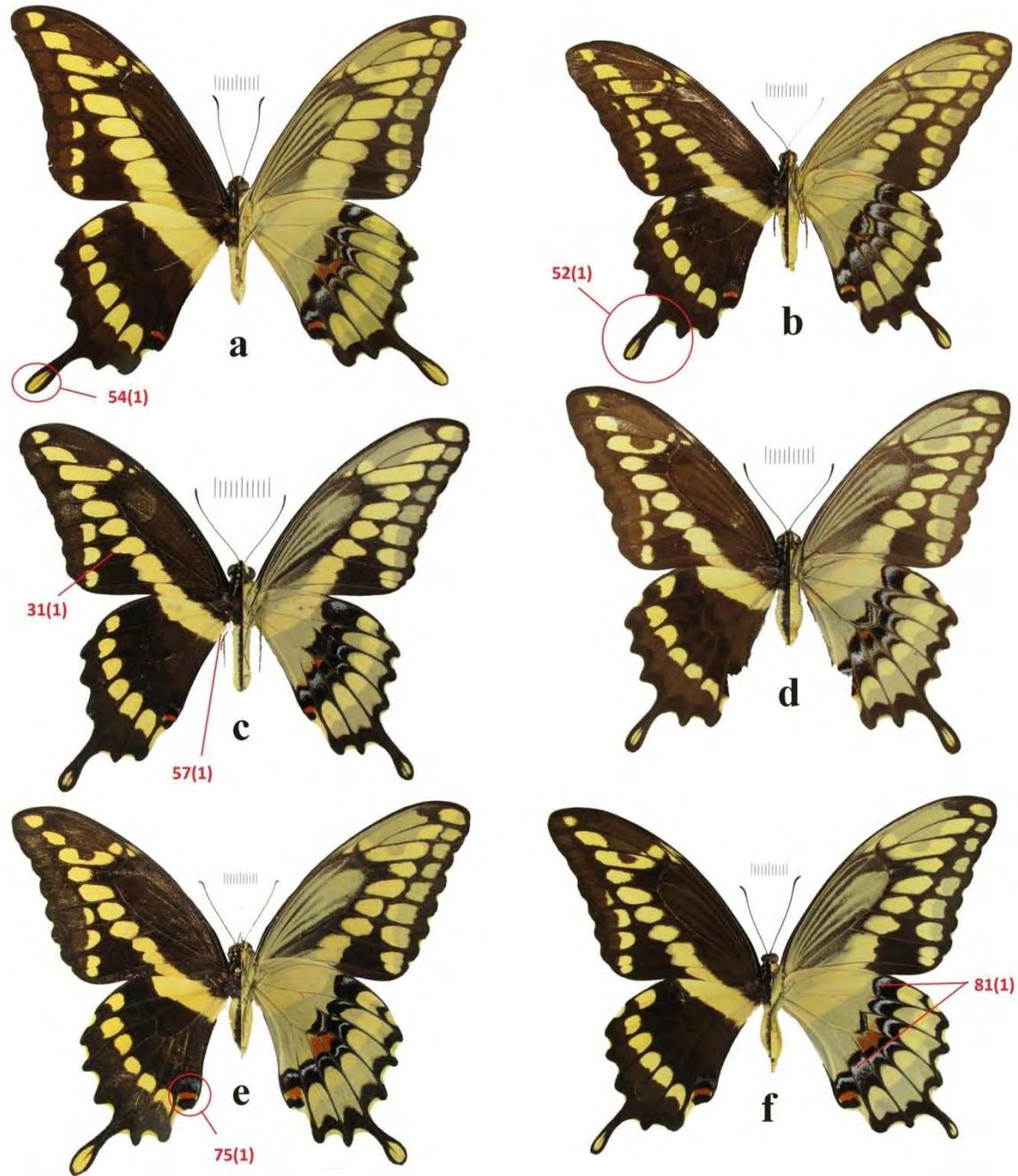


Figure 6-3. *Heraclides* adults dorsal and ventral: (a) *H. thoas thoantiades* ♂, (b) *H. thoas thoantiades* ♀, (c) *H. crespontes* ♀, (d) *H. crespontes* ♀, (e) *H. crespontes* ♂, (f) *H. crespontes* ♀. Scale bar in 1 mm segments.

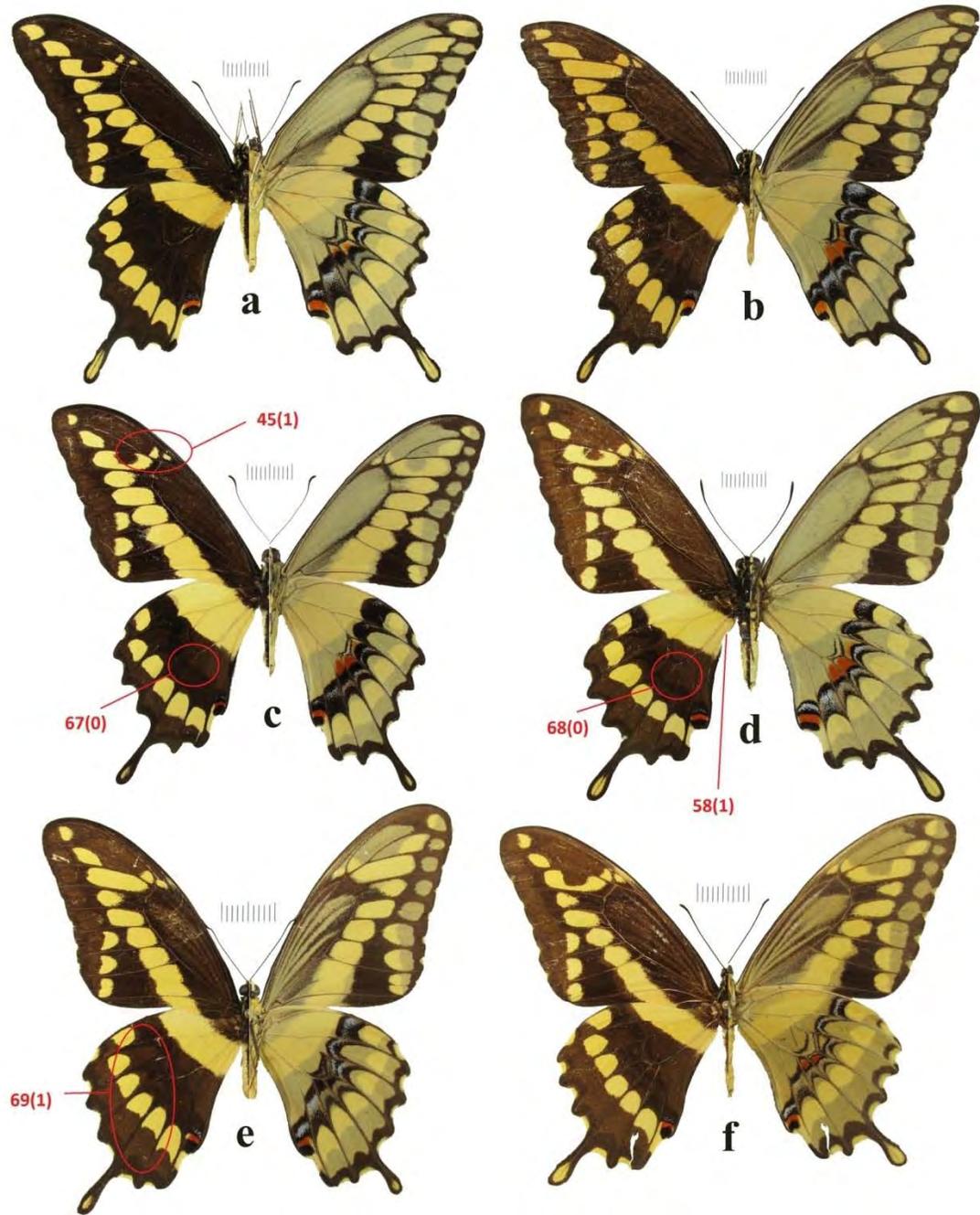


Figure 6-4. *Heraclides* adults dorsal and ventral: (a) *H. crespontes* ♂, (b) *H. crespontes* ♂, (c) *H. crespontes* ♂, (d) *H. crespontes* ♀, (e) *H. homothoas* ♂, (f) *H. homothoas* ♀. Scale bar in 1 mm segments.

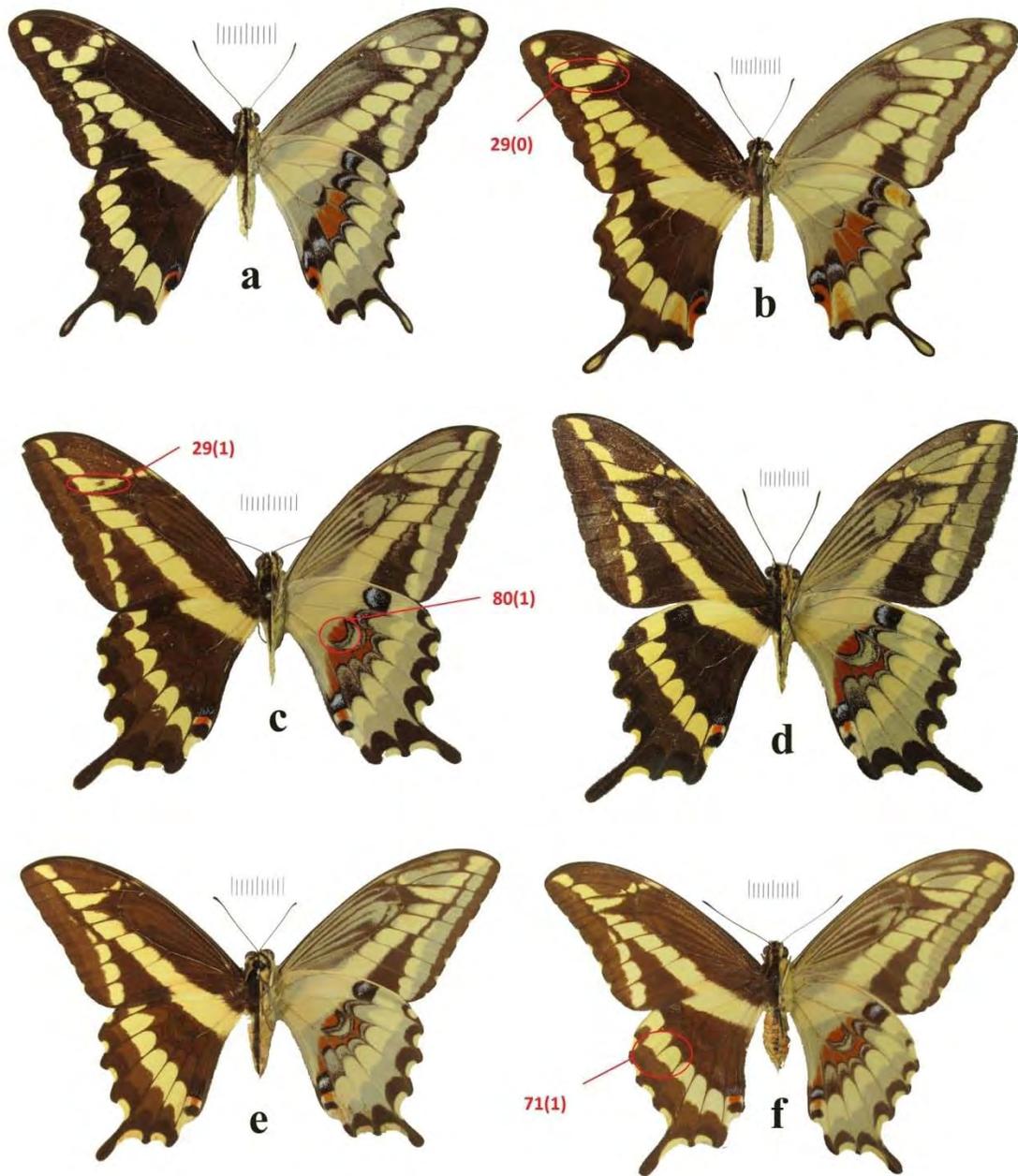


Figure 6-5. *Heraclides* adults dorsal and ventral: (a) *H. melonius* ♂, (b) *H. melonius* ♀, (c) *H. paeon paeon* ♂, (d) *H. paeon paeon* ♀, (e) *H. paeon escomeli* ♂, (f) *H. paeon escomeli* ♀. Scale bar in 1 mm segments.

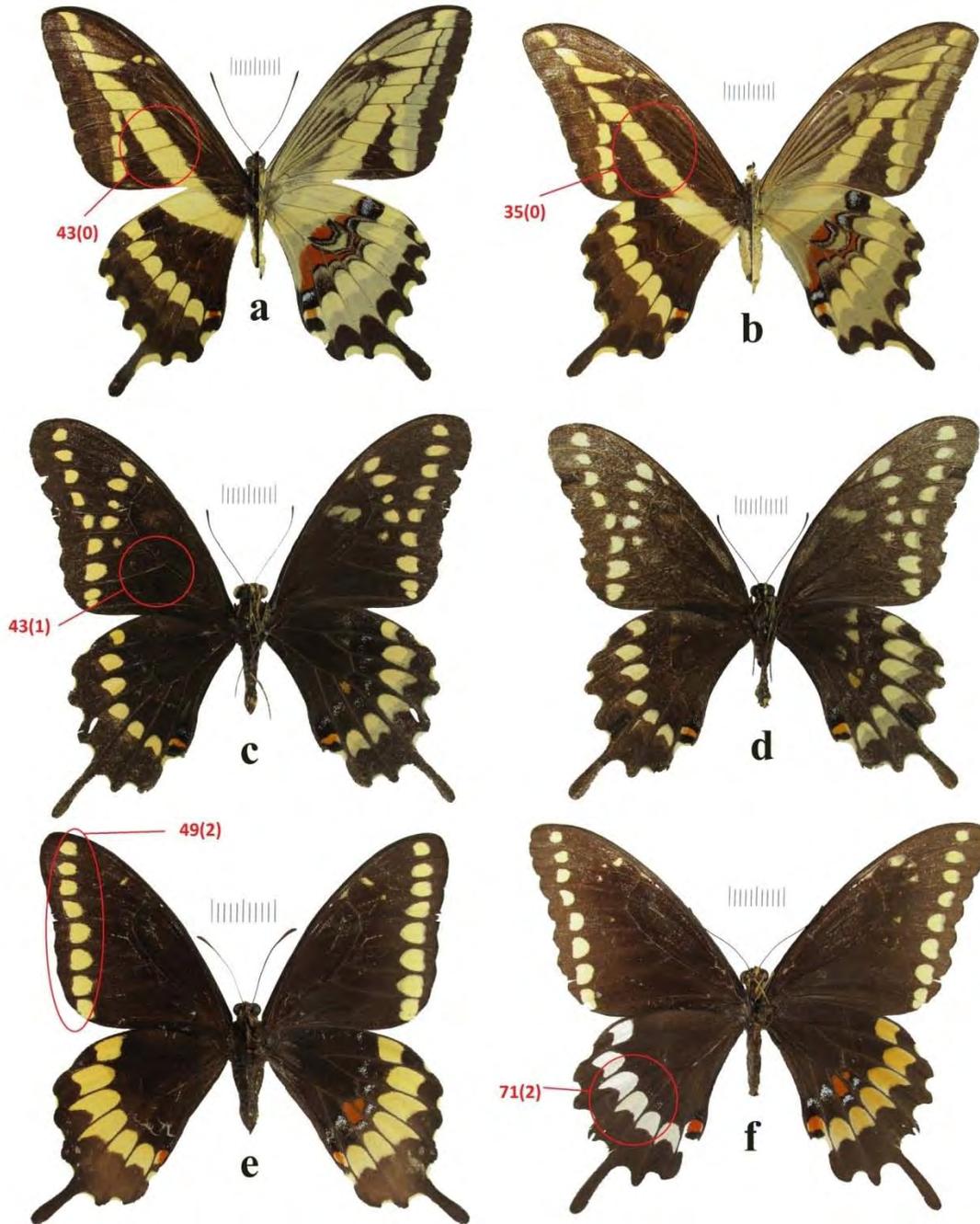


Figure 6-6. *Heraclides* adults dorsal and ventral: (a) *H. paeon thrason* ♂, (b) *H. paeon thrason* ♀, (c) *H. aristor* ♂, (d) *H. aristor* ♀, (e) *H. caiguanabus* ♂, (f) *H. caiguanabus* ♀. Scale bar in 1 mm segments.

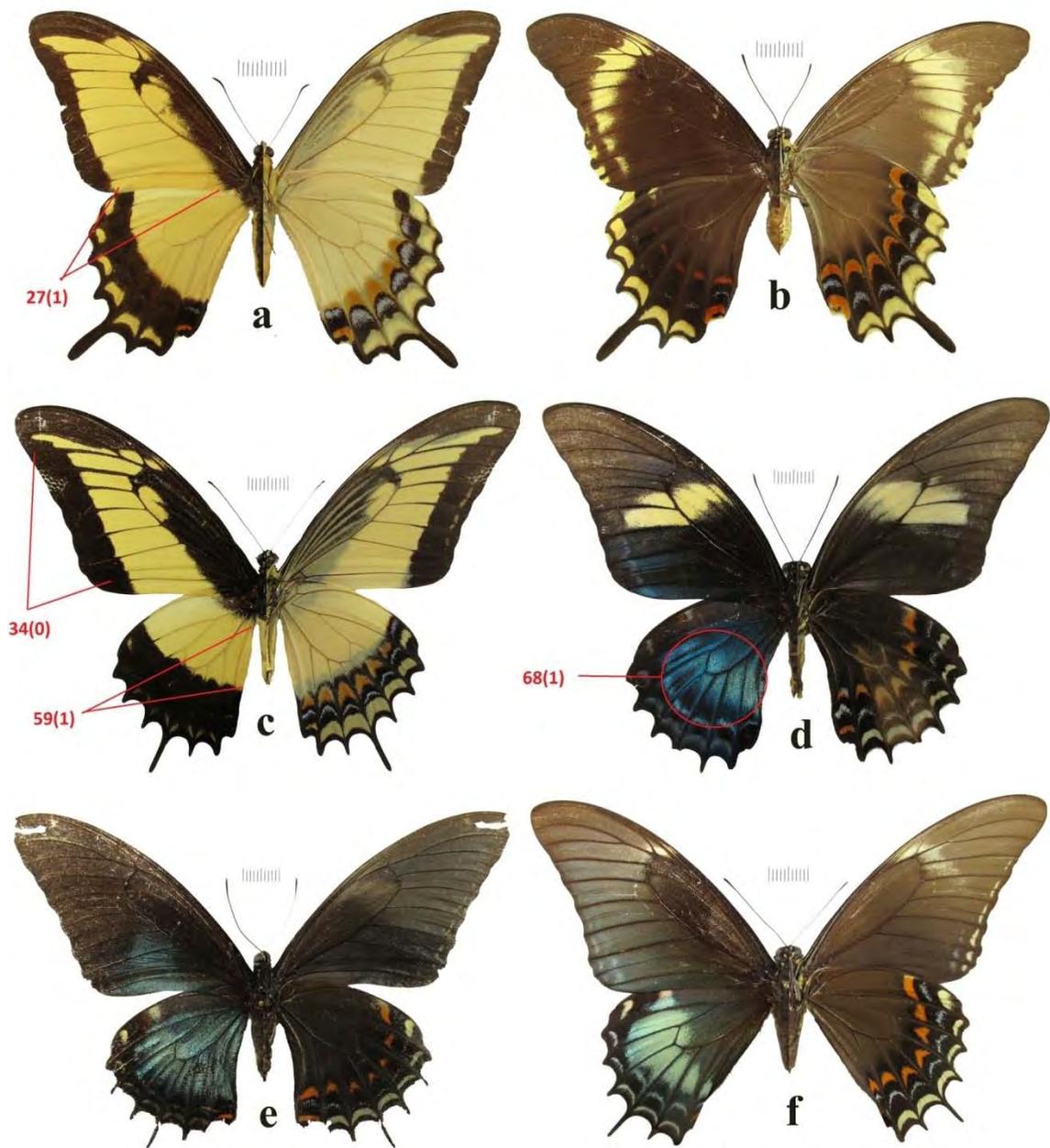


Figure 6-7. *Heraclides* adults dorsal and ventral: (a) *H. thersites* ♂, (b) *H. thersites* ♀, (c) *H. androgeus androgeus* ♂, (d) *H. androgeus androgeus* ♀, (e) *H. androgeus androgeus* ♀, (f) *H. androgeus epidaurus* ♀. Scale bar in 1 mm segments.

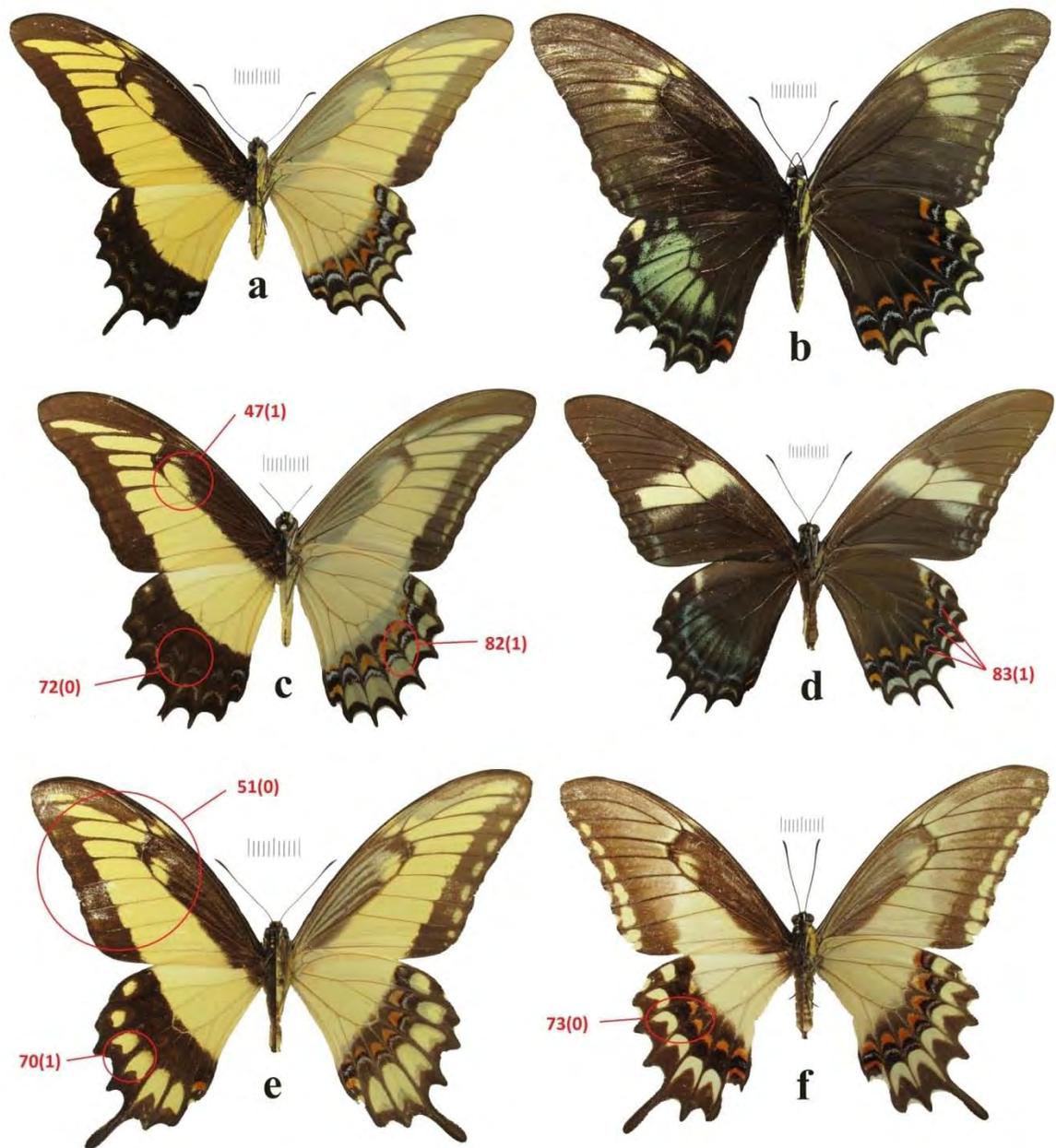


Figure 6-8. *Heraclides* adults dorsal and ventral: (a) *H. androgeus epidaurus* ♂, (b) *H. androgeus epidaurus* ♀, (c) *H. androgeus laodocus* ♂, (d) *H. androgeus laodocus* ♀, (e) *H. astyalus astyalus* ♂, (f) *H. astyalus astyalus* ♀. Scale bar in 1 mm segments.

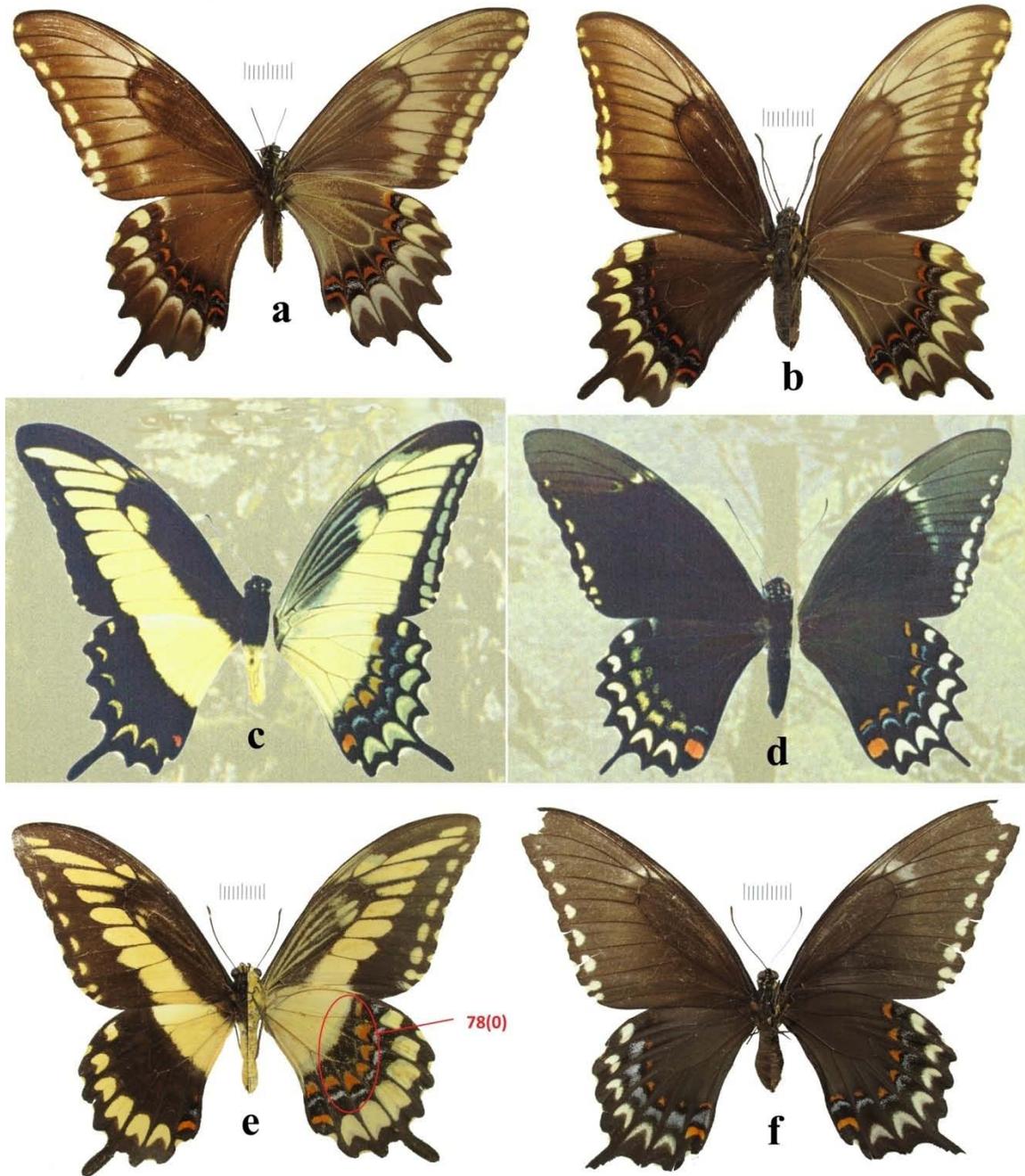


Figure 6-9. *Heraclides* adults dorsal and ventral: (a) *H. astyalus astyalus* ♀, (b) *H. astyalus astyalus* ♀, (c) *H. astyalus anchicayaensis* ♂, (Le Crom et al., 2002) (d) *H. astyalus anchicayaensis* ♀, (Le Crom et al., 2002) (e) *H. astyalus bajaensis* ♂, (f) *H. astyalus bajaensis* ♀. Scale bar in 1 mm segments.

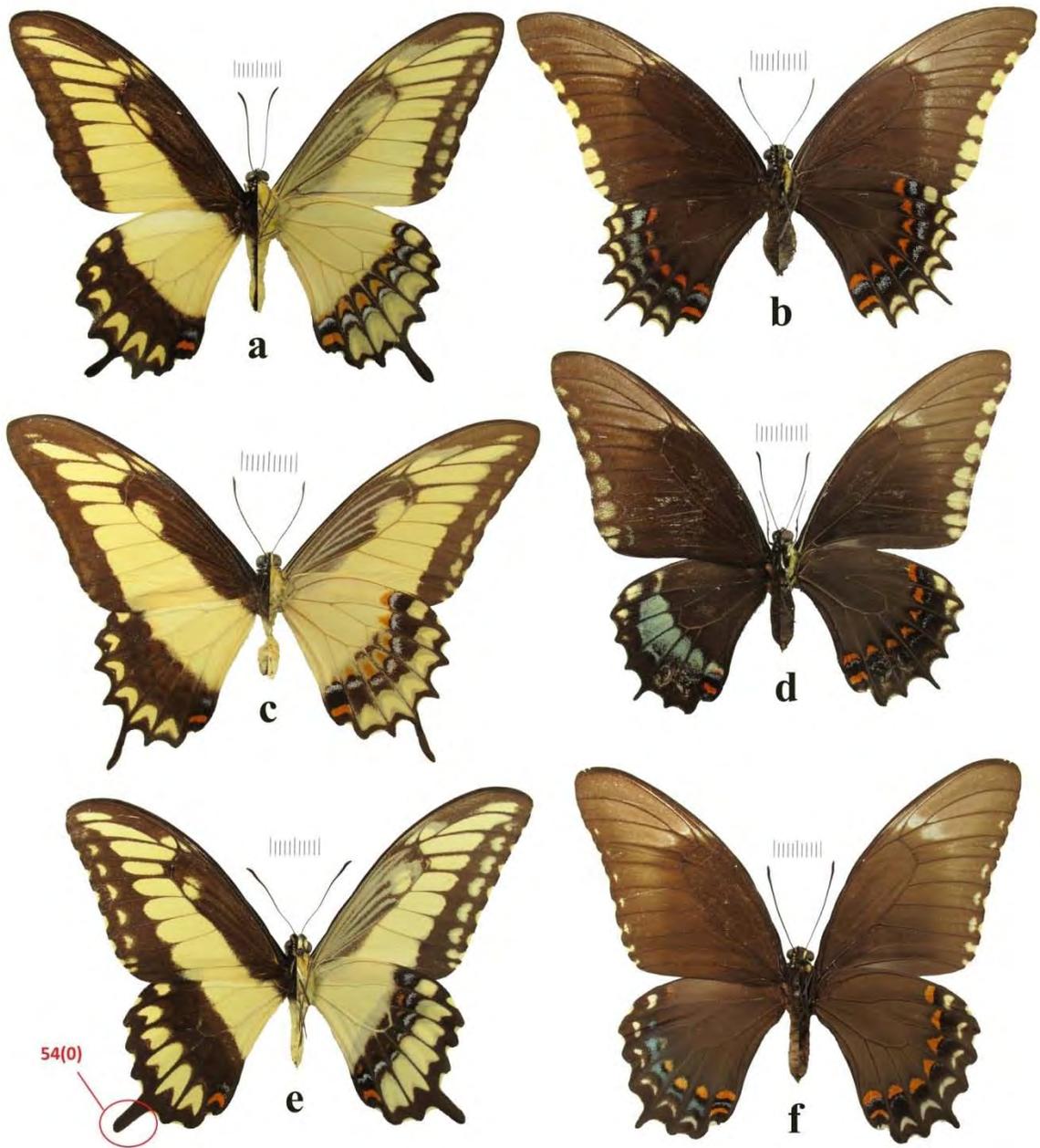


Figure 6-10. *Heraclides* adults dorsal and ventral: (a) *H. astyalus hippomedon* ♂, (b) *H. astyalus hippomedon* ♀, (c) *H. astyalus hippomedon* ♂, (d) *H. astyalus hippomedon* ♀, (e) *H. astyalus pallas* ♂, (f) *H. astyalus pallas* ♀. Scale bar in 1 mm segments.

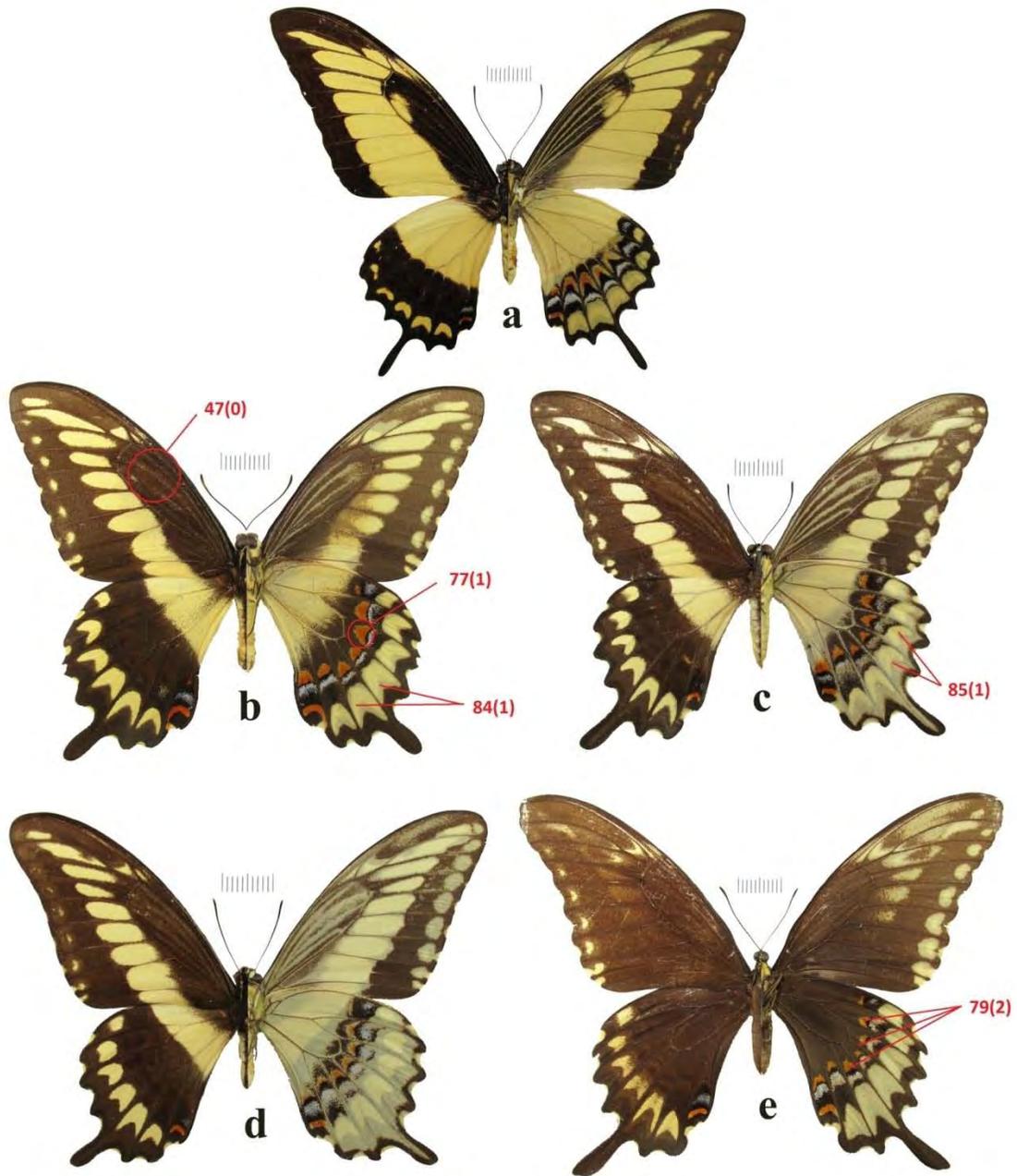


Figure 6-11. *Heraclides* adults dorsal and ventral: (a) *H. astyalus phanias* ♂, (b) *H. ornythion* ♂, (c) *H. ornythion* ♀, (d) *H. ornythion* ♂, (e) *H. ornythion* ♀. Scale bar in 1 mm segments.

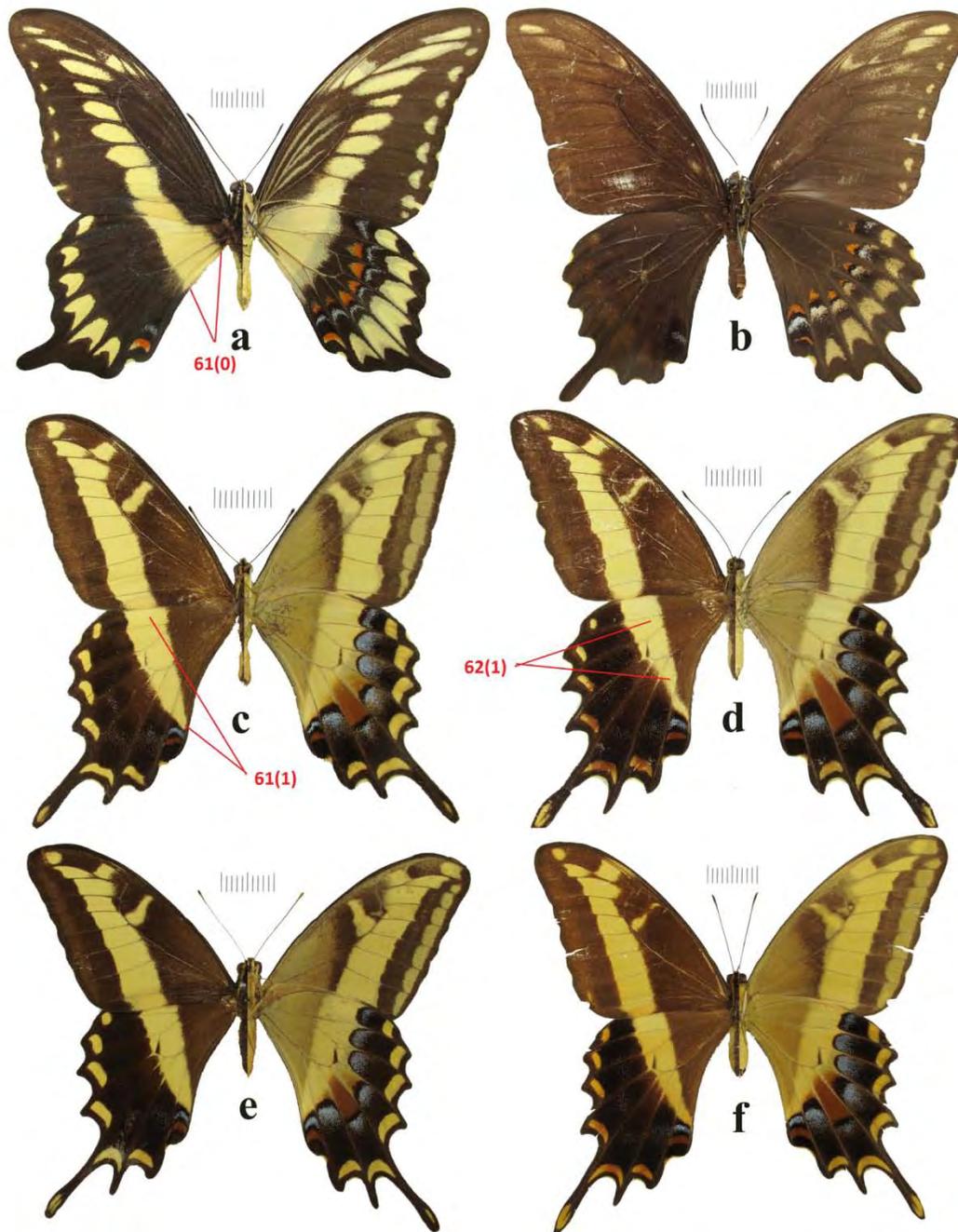


Figure 6-12. *Heraclides* adults dorsal and ventral: (a) *H. ornythion* ♂, (b) *H. ornythion* ♀, (c) *H. andraemon andraemon* ♂, (d) *H. andraemon andraemon* ♀, (e) *H. andraemon andraemon* ♂, (f) *H. andraemon andraemon* ♀. Scale bar in 1 mm segments.

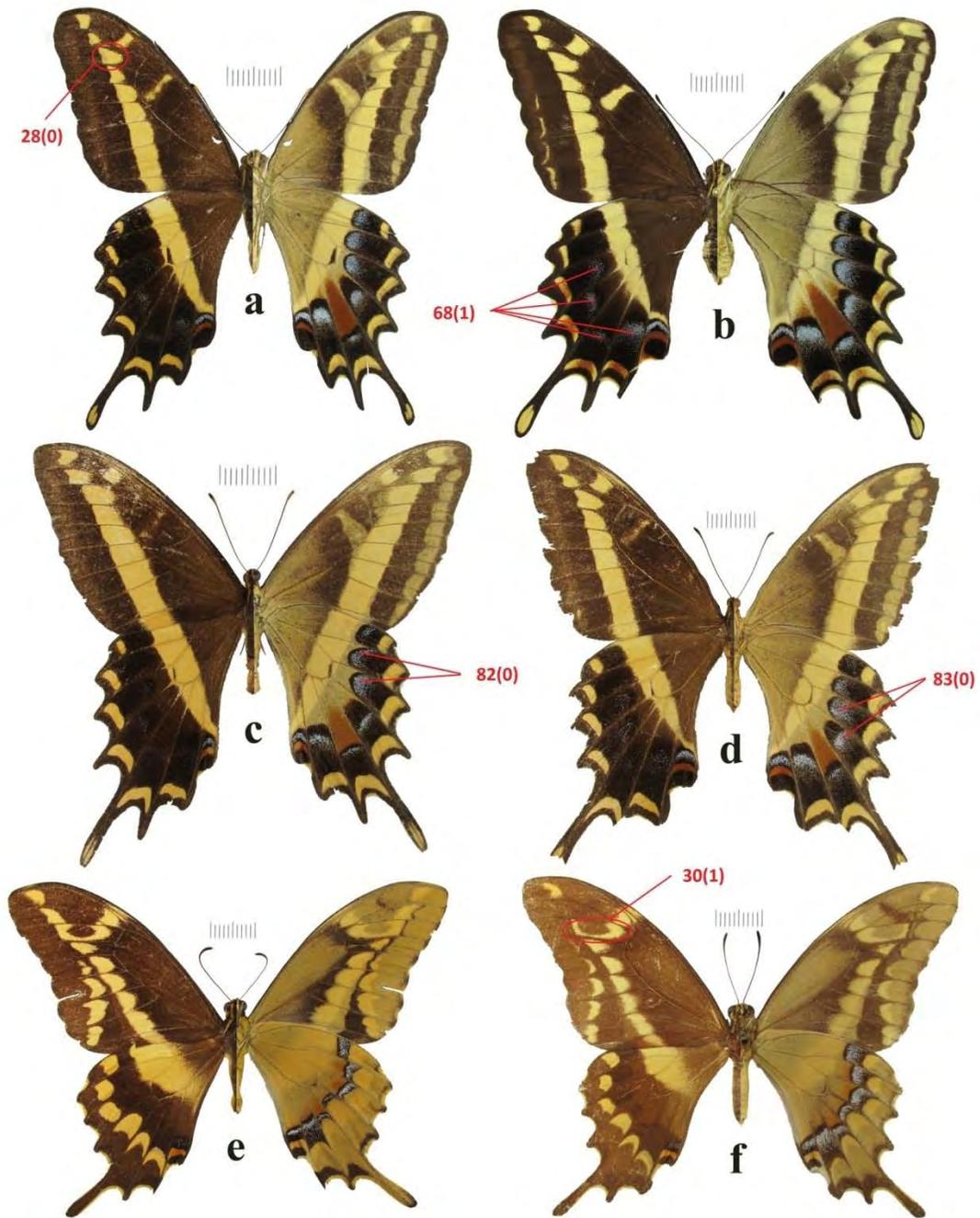


Figure 6-13. *Heraclides* adults dorsal and ventral: (a) *H. andraemon bonhotei* ♂, (b) *H. andraemon bonhotei* ♀, (c) *H. andraemon tailori* ♂, (d) *H. andraemon tailori* ♀, (e) *H. aristodemus aristodemus* ♂, (f) *H. aristodemus aristodemus* ♀. Scale bar in 1 mm segments.

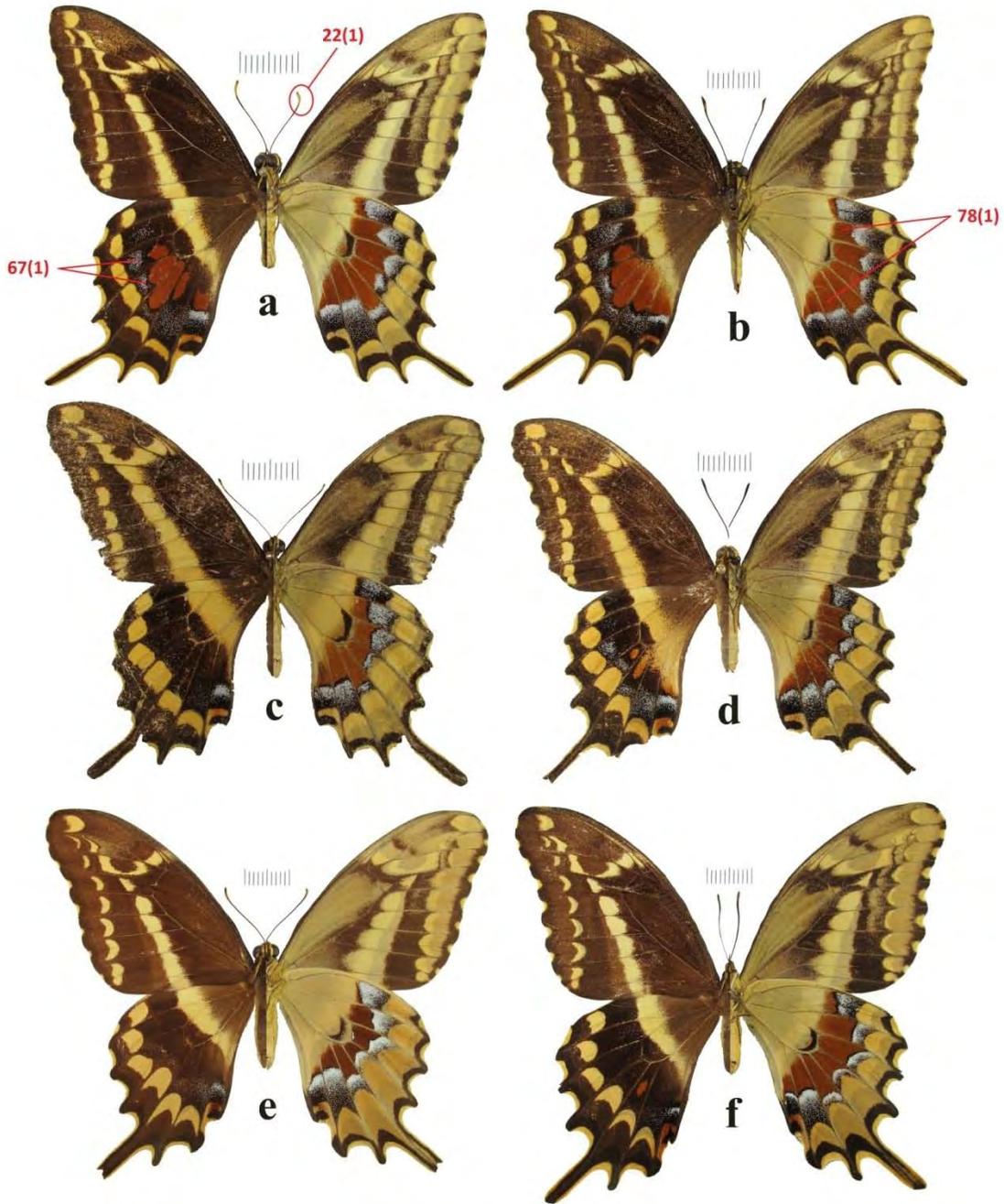


Figure 6-14. *Heraclides* adults dorsal and ventral: (a) *H. aristodemus bjordalae* ♂, (b) *H. aristodemus bjordalae* ♀, (c) *H. aristodemus majasi* ♂, (d) *H. aristodemus majasi* ♀, (e) *H. aristodemus ponceanus* ♂, (f) *H. aristodemus ponceanus* ♀. Scale bar in 1 mm segments.

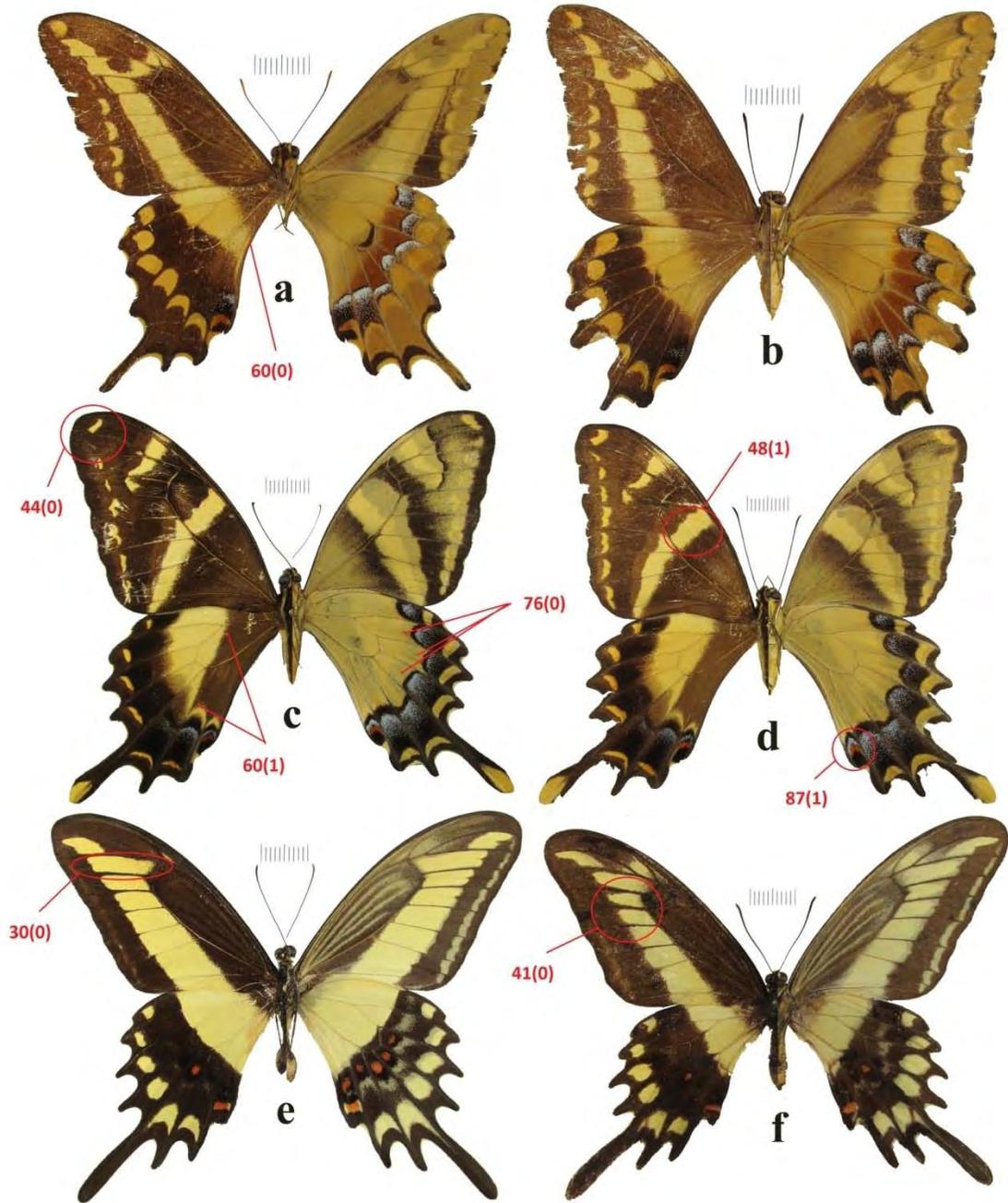


Figure 6-15. *Heraclides* adults dorsal and ventral: (a) *H. aristodemus temenes* ♂, (b) *H. aristodemus temenes* ♀, (c) *H. machaonides* ♂, (d) *H. machaonides* ♀, (e) *H. lamarchei* ♂, (f) *H. lamarchei* ♀. Scale bar in 1 mm segments.

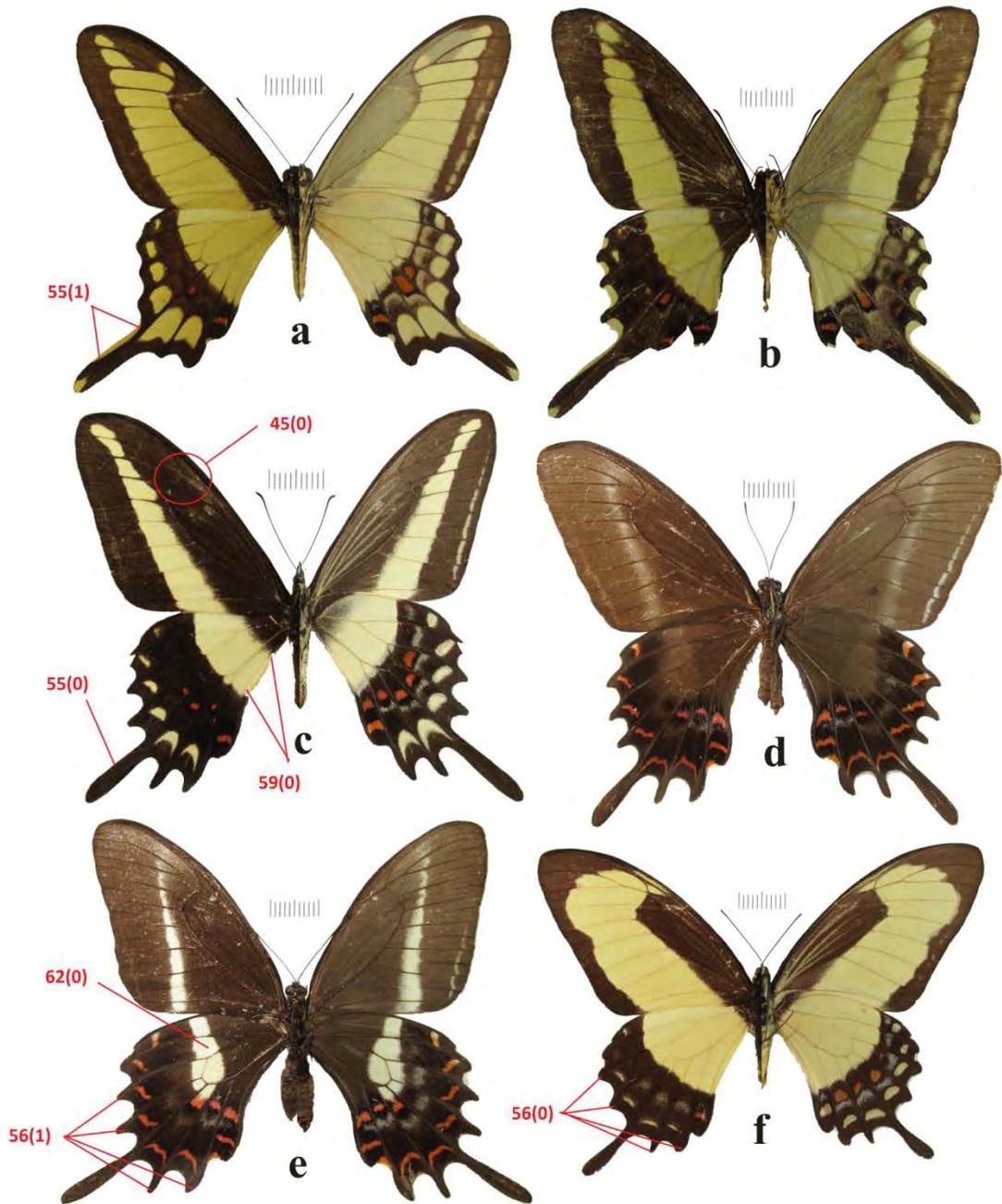


Figure 6-16. *Heraclides* adults dorsal and ventral: (a) *H. himeros himeros* ♂, (b) *H. himeros himeros* ♀, (c) *H. hectorides* ♂, (d) *H. hectorides* ♀, (e) *H. hectorides* ♀, (f) *H. garleppi garleppi* ♂. Scale bar in 1 mm segments.



Figure 6-17. *Heraclides* adults dorsal and ventral: (a) *H. garleppi garleppi* ♂, (b) *H. torquatus torquatus* ♀, (c) *H. garleppi interruptus* ♂, (d) *H. garleppi interruptus* ♀, (e) *H. garleppi lecerfi* ♂, (f) *H. garleppi lecerfi* ♀. Scale bar in 1 mm segments.

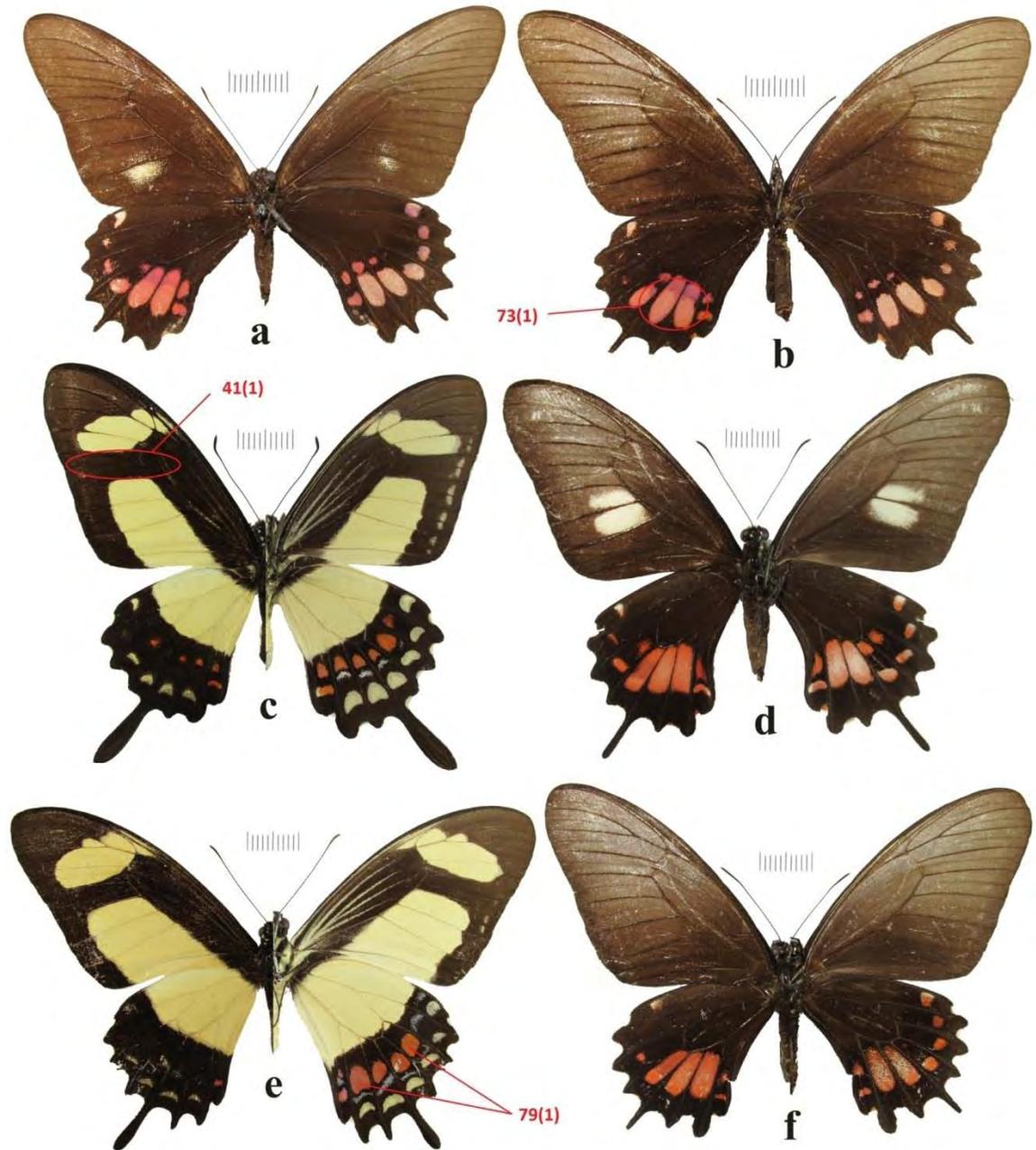


Figure 6-18. *Heraclides* adults dorsal and ventral: (a) *H. garleppi lecerfi* ♀, (b) *H. garleppi lecerfi* ♀, (c) *H. torquatus torquatus* ♂, (d) *H. torquatus torquatus* ♀, (e) *H. garleppi interruptus* ♂, (f) *H. torquatus torquatus* ♀. Scale bar in 1 mm segments.

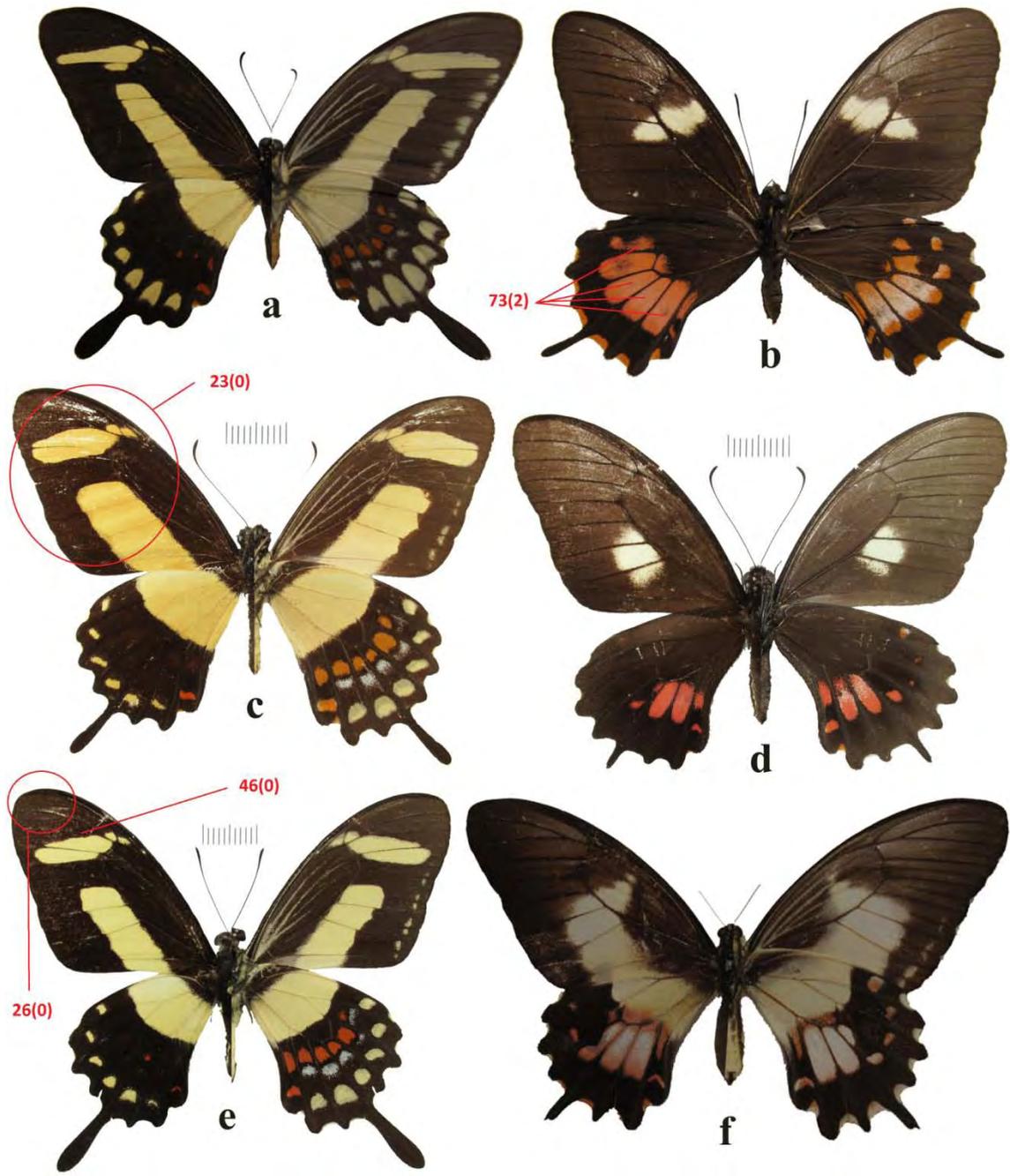


Figure 6-19. *Heraclides* adults dorsal and ventral: (a) *H. torquatus atsukoae* ♂, (b) *H. torquatus atsukoae* ♀, (c) *H. torquatus jeani* ♂, (d) *H. torquatus leptalea* ♀, (e) *H. torquatus leptalea* ♂, (f) *H. tasso-like* ♀. Scale bar in 1 mm segments.



Figure 6-20. *Heraclides* adults dorsal and ventral: (a) *H. torquatus tolus* ♂, (b) *H. torquatus mazai* ♀, - from www.butterfliesofamerica.com, (c) *H. torquatus polybius* ♂, (d) *H. torquatus polybius* ♀, (e) *H. torquatus tolmidis* ♂, (f) *H. torquatus tolmidis* ♀. Scale bar in 1 mm segments.

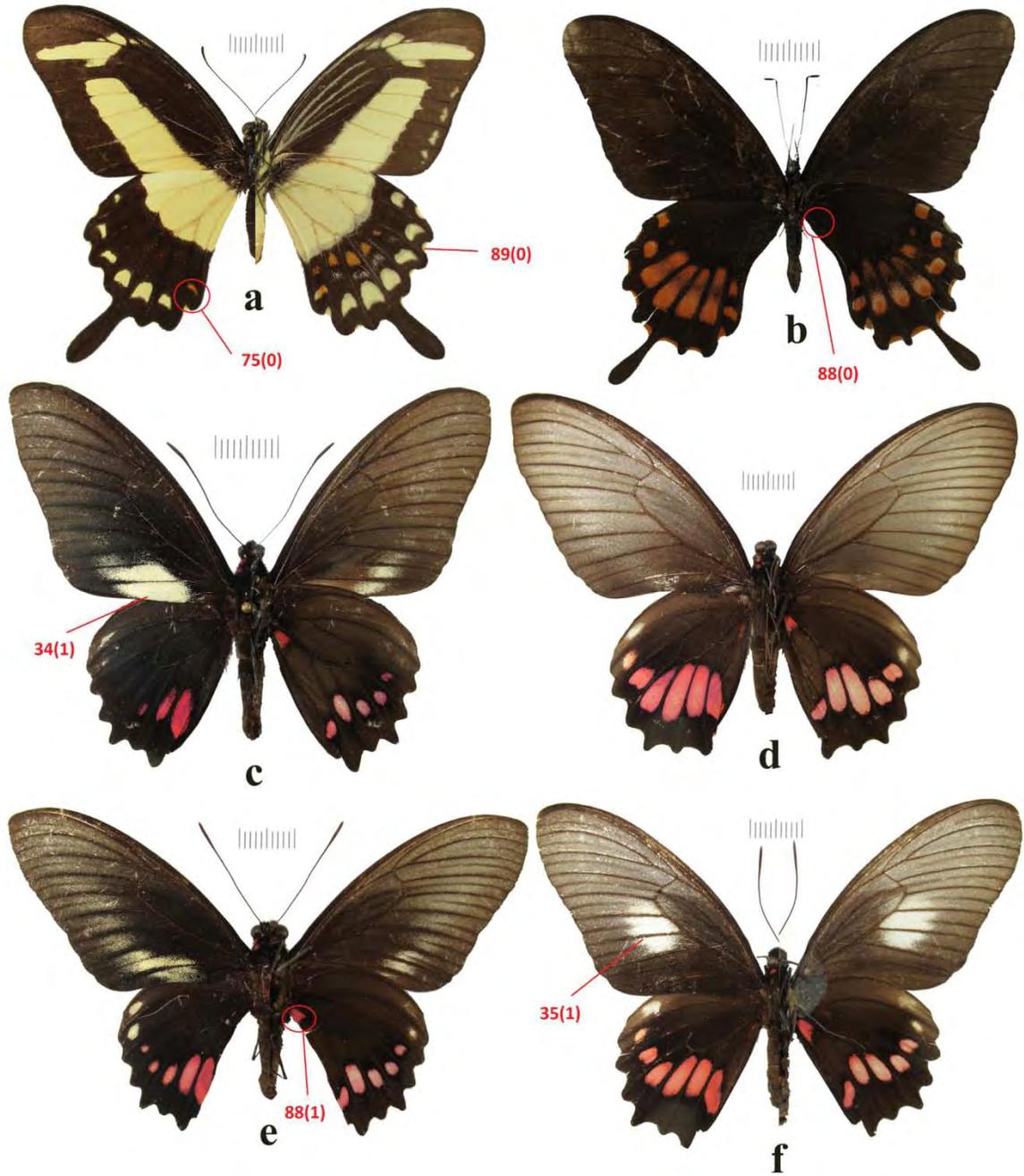


Figure 6-21. *Heraclides* adults dorsal and ventral: (a) *H. torquatus tolus* ♂, (b) *H. torquatus tolus* ♀, (c) *H. hyppason* ♂, (d) *H. hyppason* ♀, (e) *H. hyppason* ♂, (f) *H. hyppason* ♀. Scale bar in 1 mm segments.

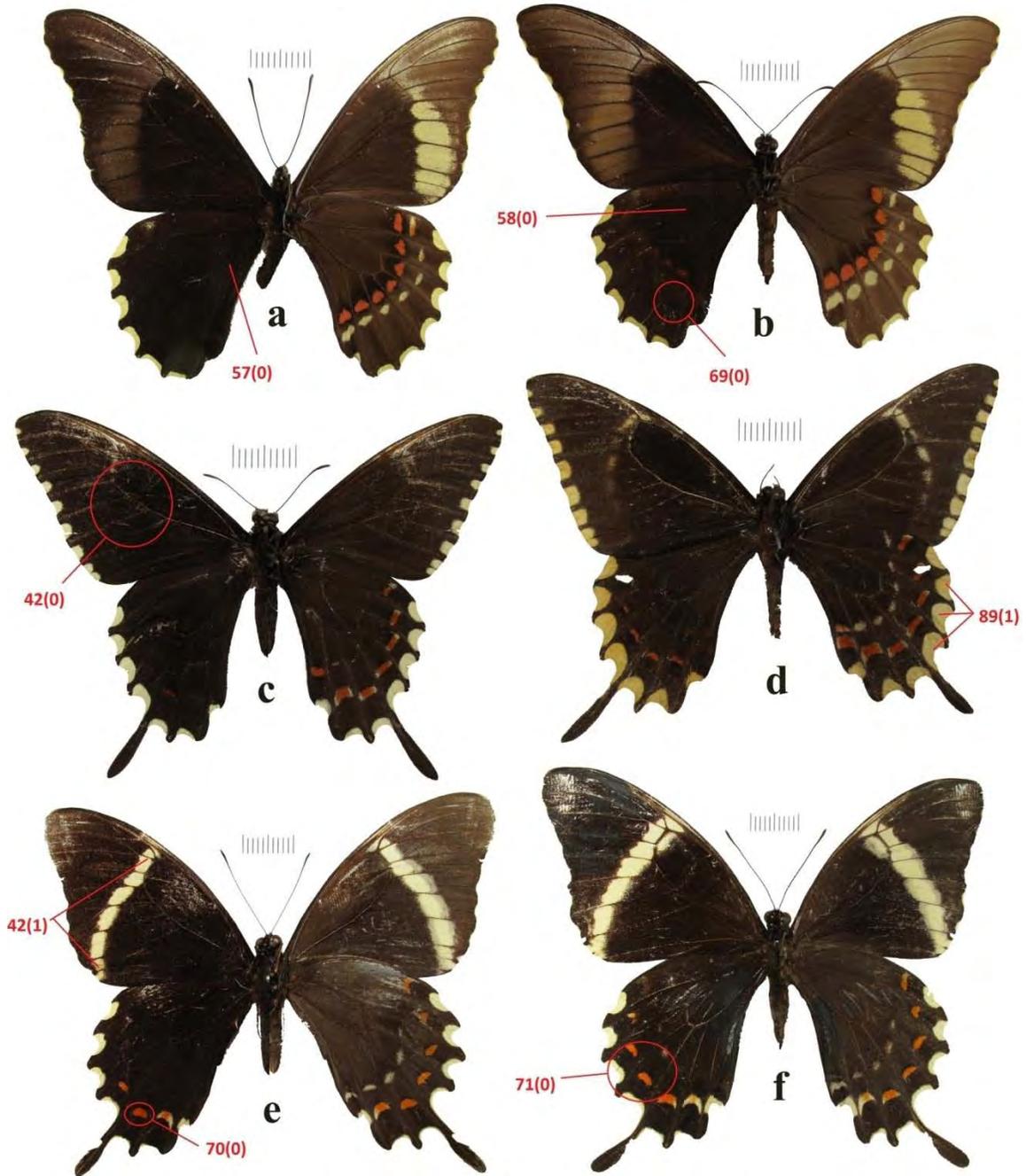


Figure 6-22. *Heraclides* adults dorsal and ventral: (a) *H. epenetus* ♂, (b) *H. epenetus* ♀, (c) *H. oxynius* ♂, (d) *H. oxynius* ♀, (e) *H. pelaus pelaus* ♂, (f) *H. pelaus pelaus* ♀. Scale bar in 1 mm segments.

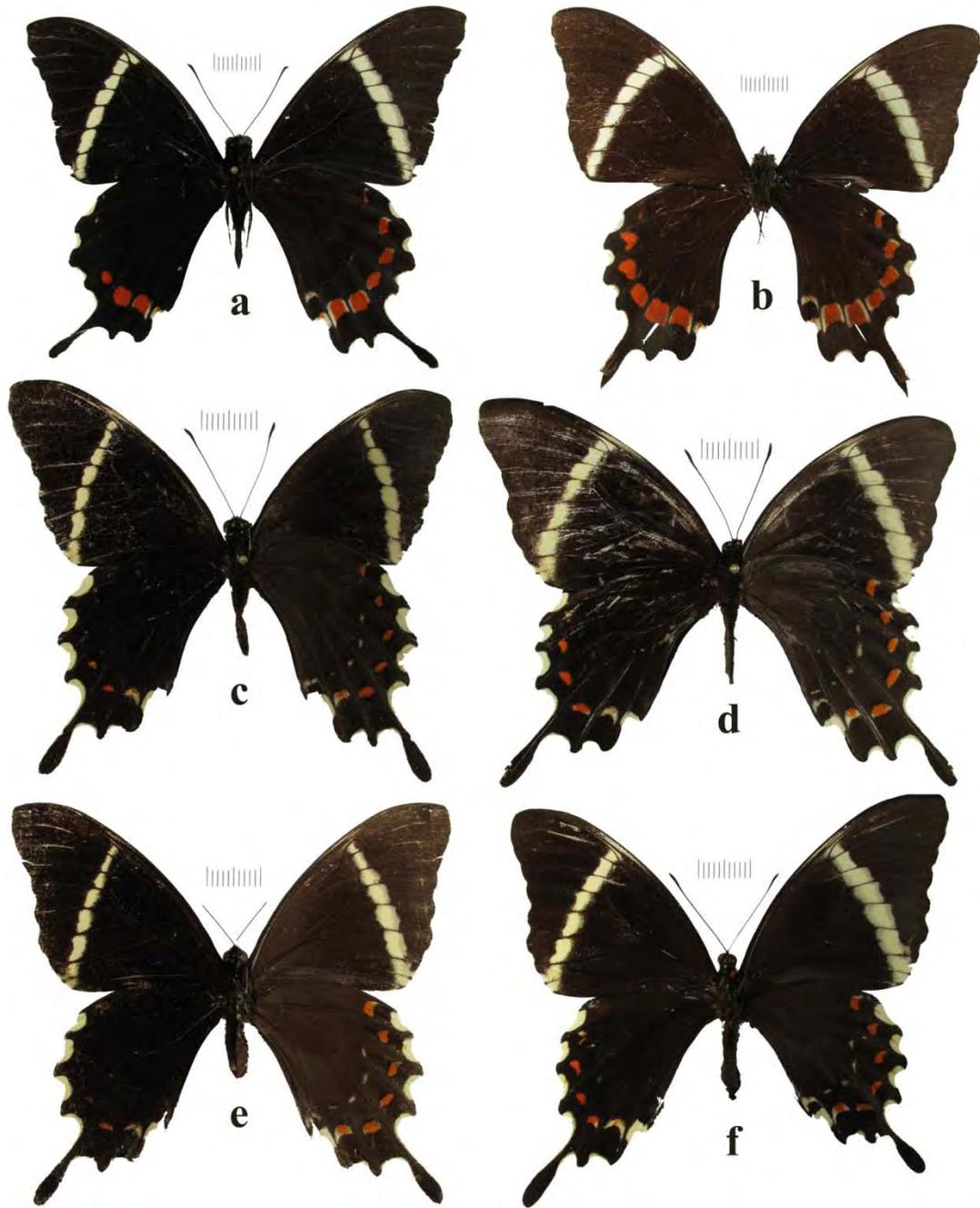


Figure 6-23. *Heraclides* adults dorsal and ventral: (a) *H. pelaus atkinsi* ♂, (b) *H. pelaus atkinsi* ♀, (c) *H. pelaus imerius* ♂, (d) *H. pelaus imerius* ♀, (e) *H. pelaus puertoricensis* ♂, (f) *H. pelaus puertoricensis* ♀. Scale bar in 1 mm segments.

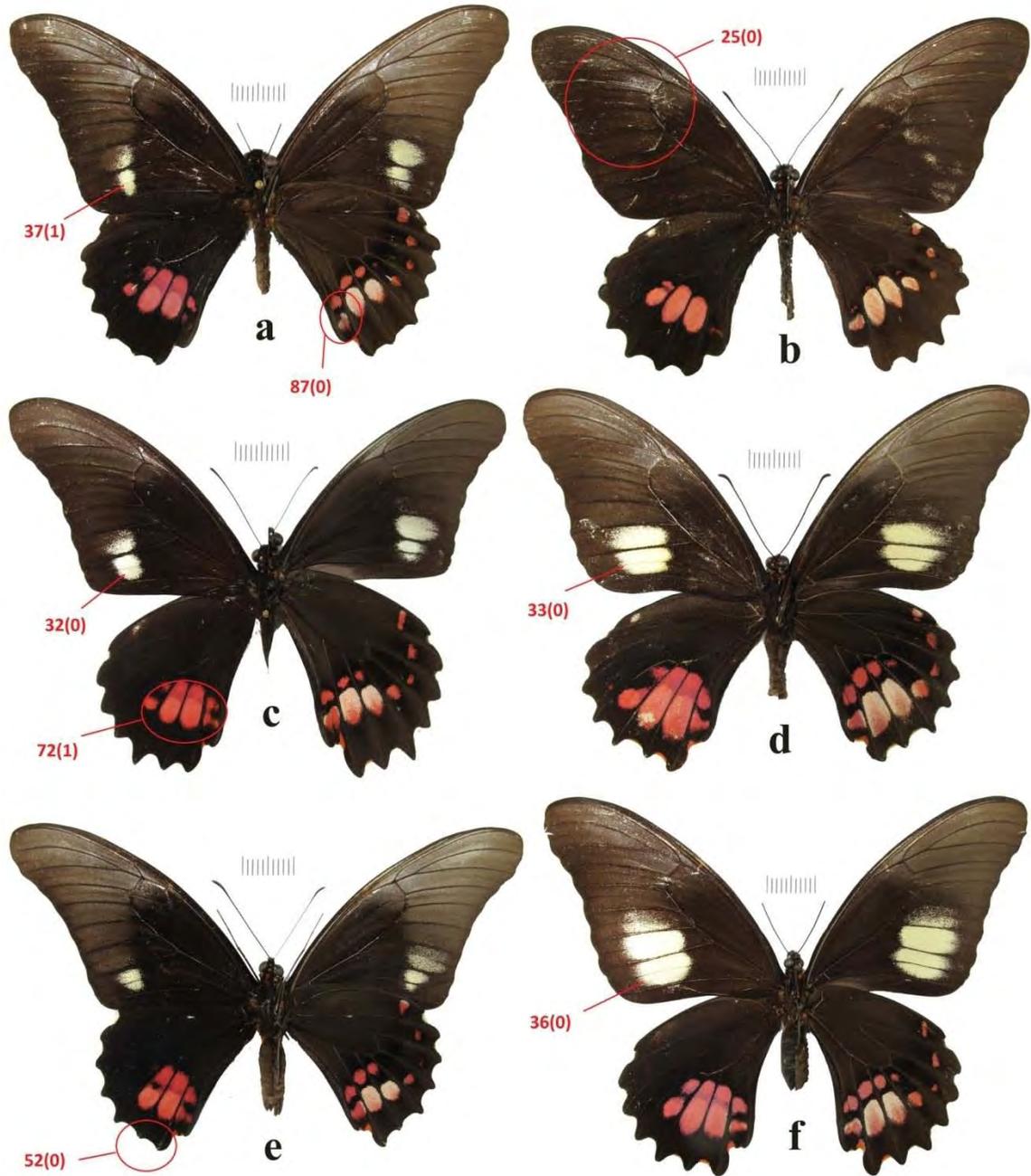


Figure 6-24. *Heraclides* adults dorsal and ventral: (a) *H. anchisiades anchisiades* ♂, (b) *H. anchisiades anchisiades* ♀, (c) *H. anchisiades anchisiades* ♂, (d) *H. anchisiades anchisiades* ♀, (e) *H. anchisiades anchisiades* ♂, (f) *H. anchisiades anchisiades* ♀. Scale bar in 1 mm segments.



Figure 6-25. *Heraclides* adults dorsal and ventral: (a) *H. anchisiades capys* ♂, (b) *H. anchisiades capys* ♀, (c) *H. anchisiades capys* ♂, (d) *H. anchisiades idaeus* ♀, (e) *H. anchisiades idaeus* ♂, (f) *H. anchisiades idaeus* ♀. Scale bar in 1 mm segments.



Figure 6-26. *Heraclides* adults dorsal and ventral: (a) *H. anchisiades idaeus* ♂, (b) *H. anchisiades idaeus* ♀, (c) *H. anchisiades idaeus* ♂, (d) *H. anchisiades idaeus* ♀, (e) *H. anchisiades idaeus* ♂, (f) *H. anchisiades lamasi* ♀. Scale bar in 1 mm segments.



Figure 6-27. *Heraclides* adults dorsal and ventral: (a) *H. anchisiades philastrus* ♂, (b) *H. anchisiades philastrus* ♀, (c) *H. isidorus isidorus* ♂, (d) *H. isidorus isidorus* ♂, (e) *H. isidorus brises* ♂, (f) *H. isidorus brises* ♂. Scale bar in 1 mm segments.

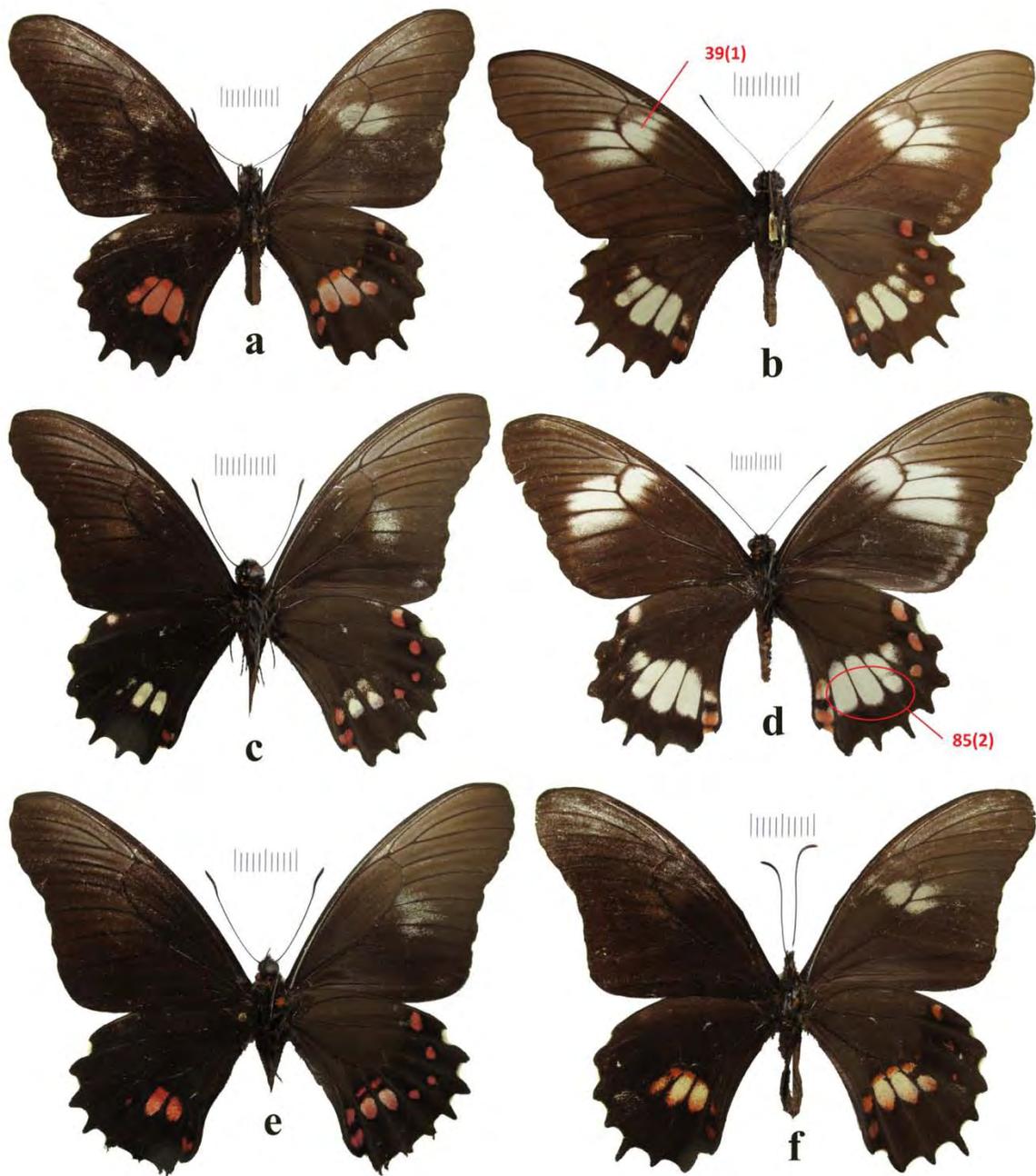


Figure 6-28. *Heraclides* adults dorsal and ventral: (a) *H. isidorus brises* ♂, (b) *H. isidorus flavescens* ♀, (c) *H. isidorus flavescens* ♂, (d) *H. isidorus flavescens* ♀, (e) *H. isidorus flavescens* ♂, (f) *H. isidorus brises* (formerly *nymphius*) ♂. Scale bar in 1 mm segments.



Figure 6-29. *Heraclides* adults dorsal and ventral: (a) *H. isidorus brises* (formerly *nymphius*) ♂, (b) *H. isidorus brises* (formerly *nymphius*) ♂, (c) *H. isidorus isidorus* (formerly *isidorus pacificus*) ♂, (d) *H. isidorus isidorus* (formerly *isidorus pacificus*) ♀, (e) *H. isidorus isidorus* ♂, (f) *H. unknown* ♂, from José María Caro, Calera, Chile. Scale bar in 1 mm segments.

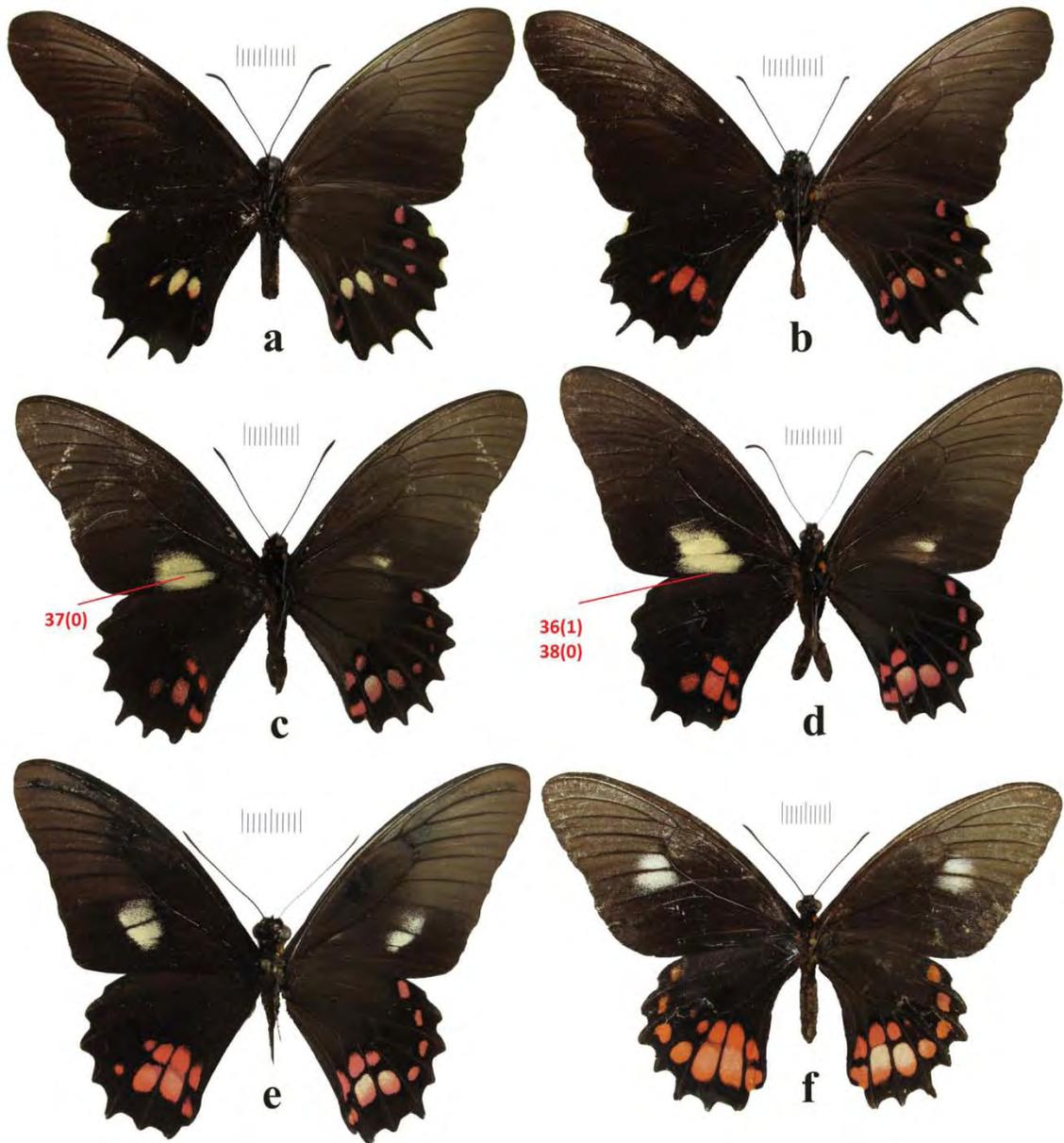


Figure 6-30. *Heraclides* adults dorsal and ventral: (a) *H. isidorus tingo* ♂, (b) *H. isidorus tingo* ♀, (c) *H. chiansiades chiansiades* ♂, (d) *H. chiansiades chiansiades* ♂, (e) *H. anchisiades anchisiades* (formerly *H. chainsiades maroni*) ♂, (f) *H. anchisiades anchisiades* (formerly *H. chainsiades maroni*) ♀. Scale bar in 1 mm segments.

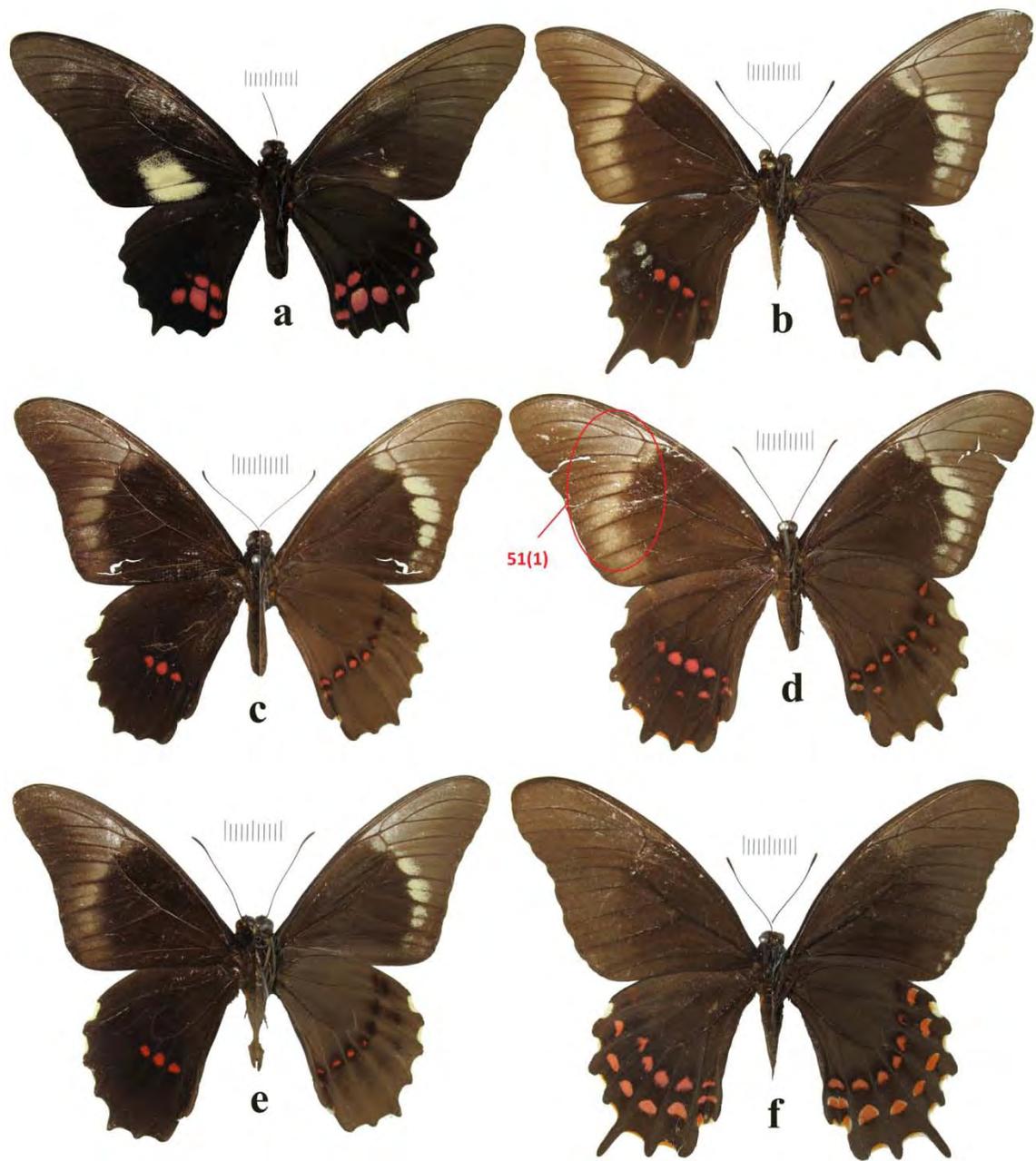


Figure 6-31. *Heraclides* adults dorsal and ventral: (a) *H. chiansiades chiansiades* (formerly *H. chiansiades mossi*) ♂, (b) *H. rogeri rogeri* ♀, (c) *H. rogeri rogeri* ♂, (d) *H. rogeri rogeri* ♀, (e) *H. rogeri rogeri* ♂, (f) *H. rogeri pharnaces* ♀. Scale bar in 1 mm segments.

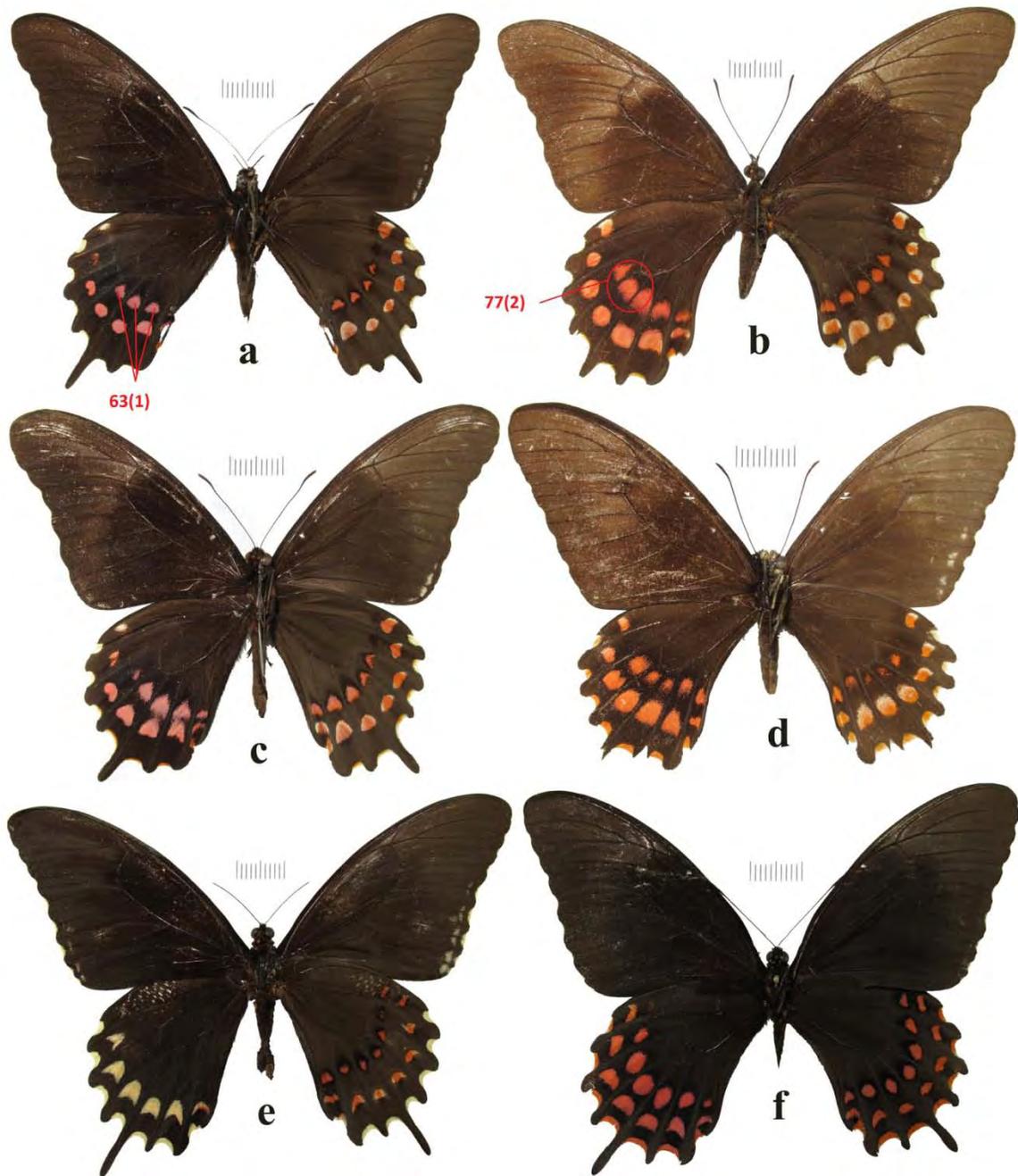


Figure 6-32. *Heraclides* adults dorsal and ventral: (a) *H. rogeri pharnaces* ♂, (b) *H. rogeri pharnaces* ♀, (c) *H. rogeri pharnaces* ♂, (d) *H. rogeri pharnaces* ♀, (e) *H. erostratus erostratus* ♂, (f) *H. erostratus erostratus* ♀. Scale bar in 1 mm segments.



Figure 6-33. *Heraclides* adults dorsal and ventral: (a) *H. erostratus erostratus* ♂, (b) *H. erostratus erostratus* ♀, (c) *H. erostratus vazquezae* ♂, (d) *H. erostratus vazquezae* ♀, (e) *H. chiansiades dospassosi* - HOLOTYPE (dorsal) (f) *H. chiansiades dospassosi* - HOLOTYPE (ventral). Scale bar in 1 mm segments.

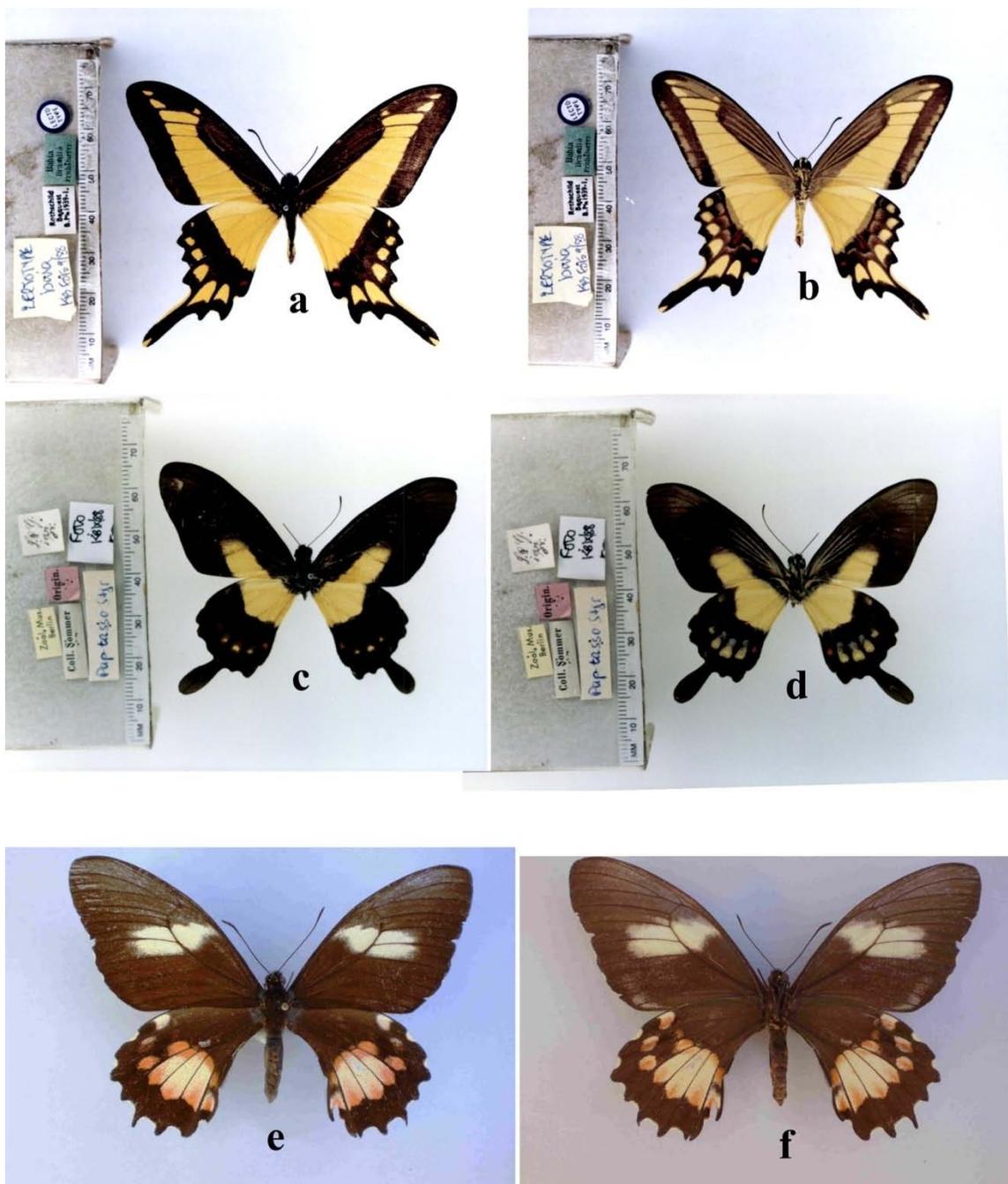


Figure 6-34. *Heraclides* adults dorsal and ventral: (a) *H. himeros baia* – LECTOTYPE (dorsal) (b) *H. himeros baia* – LECTOTYPE (ventral) (c) *H. tasso* – HOLOTYPE (dorsal) (d) *H. tasso* – HOLOTYPE (ventral) (e) *H. isidorus autana* – HOLOTYPE (dorsal) (f) *H. isidorus autana* – HOLOTYPE (ventral)

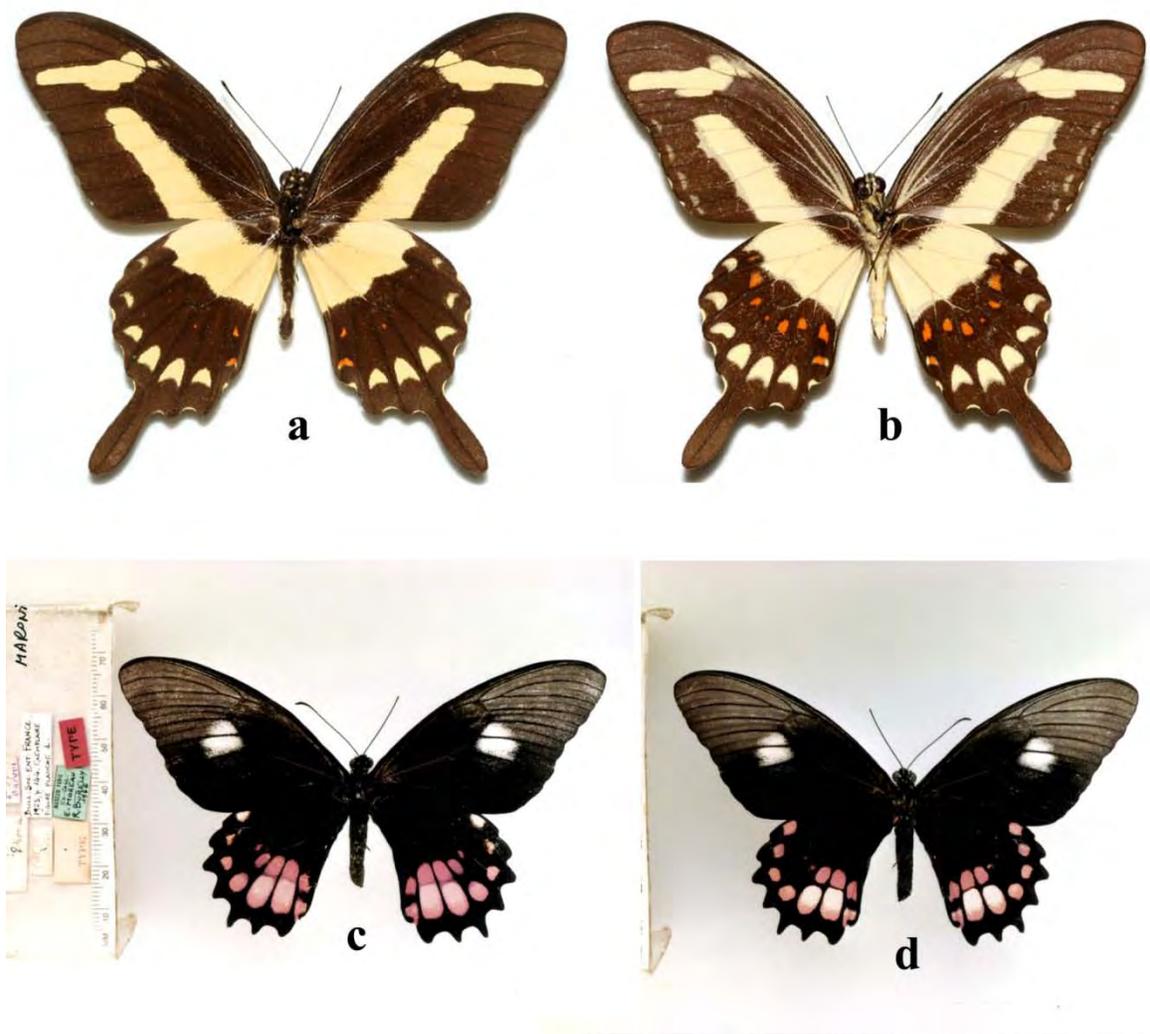


Figure 6-35. *Heraclides* adults dorsal and ventral: (a) *Heraclides torquatus mazai* ♂, - from www.butterfliesofamerica.com (dorsal) (b) *Heraclides torquatus mazai* (ventral) ♂, - from www.butterfliesofamerica.com (c) *Papilio maroni* - HOLOTYPE (dorsal) (d) *Papilio maroni* - HOLOTYPE (ventral)

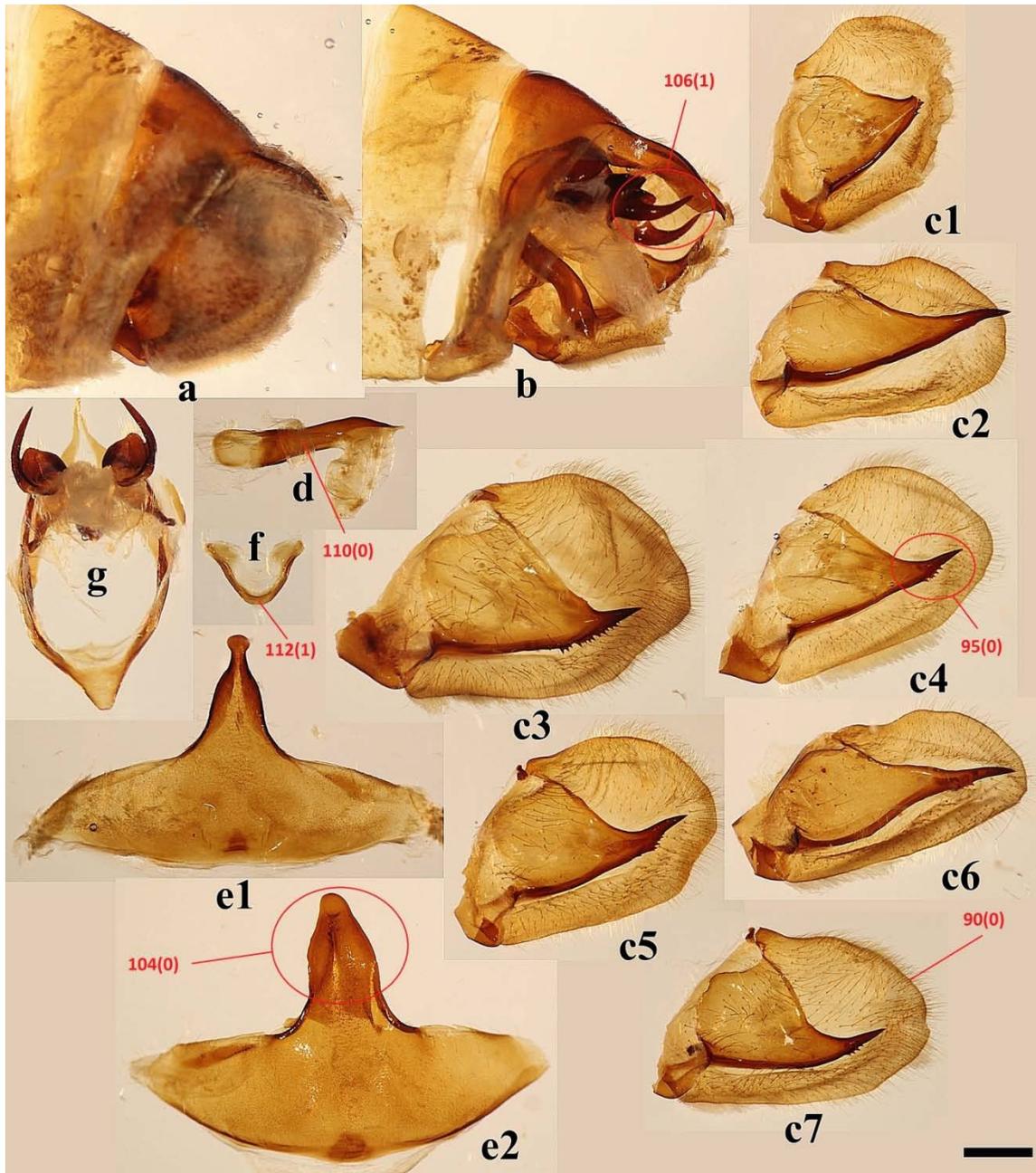


Figure 6-36. *Heraclides thoas* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. t. thoas* valve, (c2) *H. t. autocles* valve, (c3) *H. t. brasiliensis* valve, (c4) *H. t. cinyras* valve, (c5) *H. t. neacles* valve, (c6) *H. t. oviedo* valve, (c7) *H. t. thoantiades* valve, (d) aedeagus, (e1) *H. t. thoas* 8th tergite, (e2) *H. t. autocles* 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

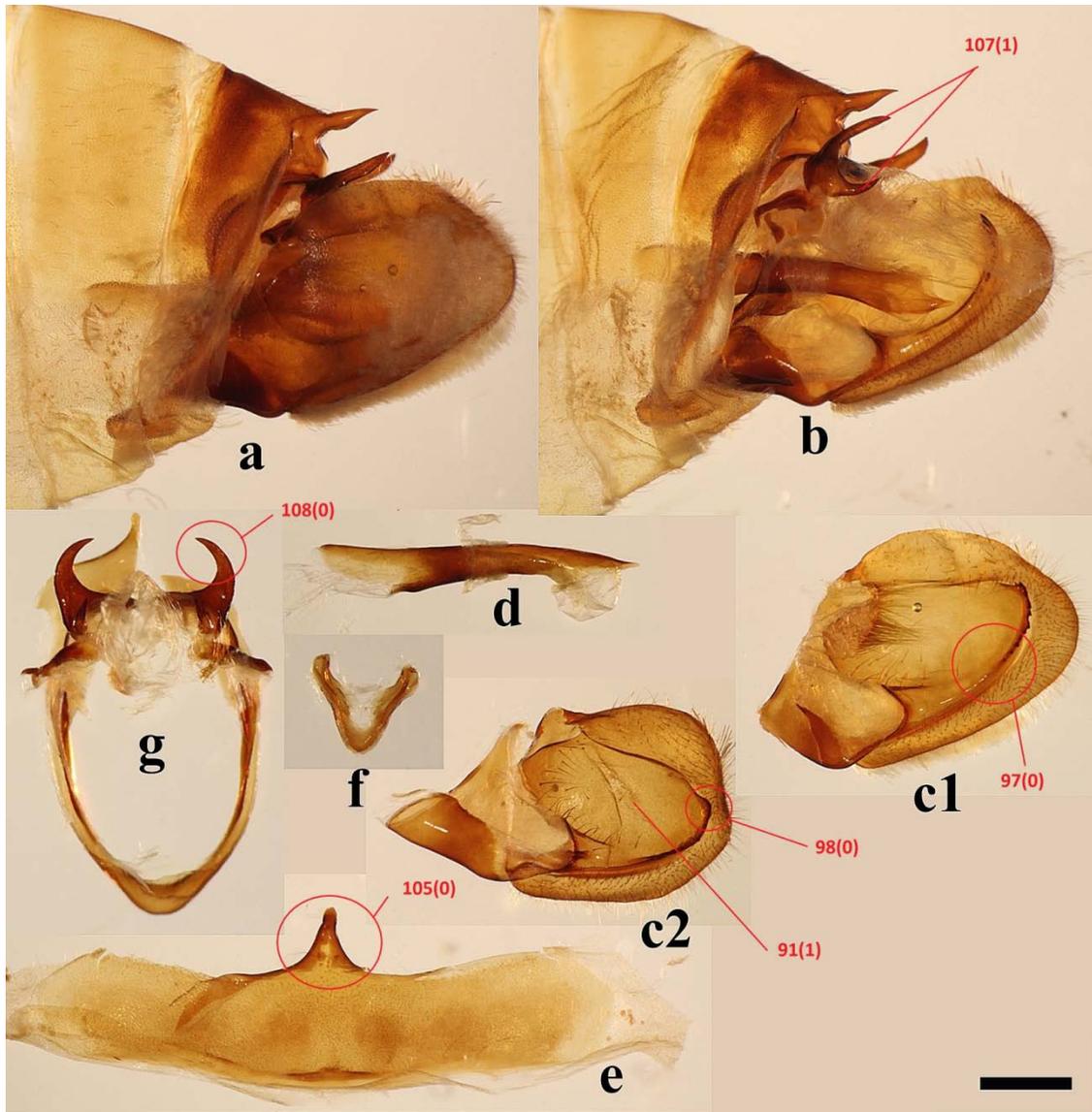


Figure 6-37. *Heraclides crespontes* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. crespontes* valve (Florida), (c2) *H. crespontes* valve (Costa Rica), (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

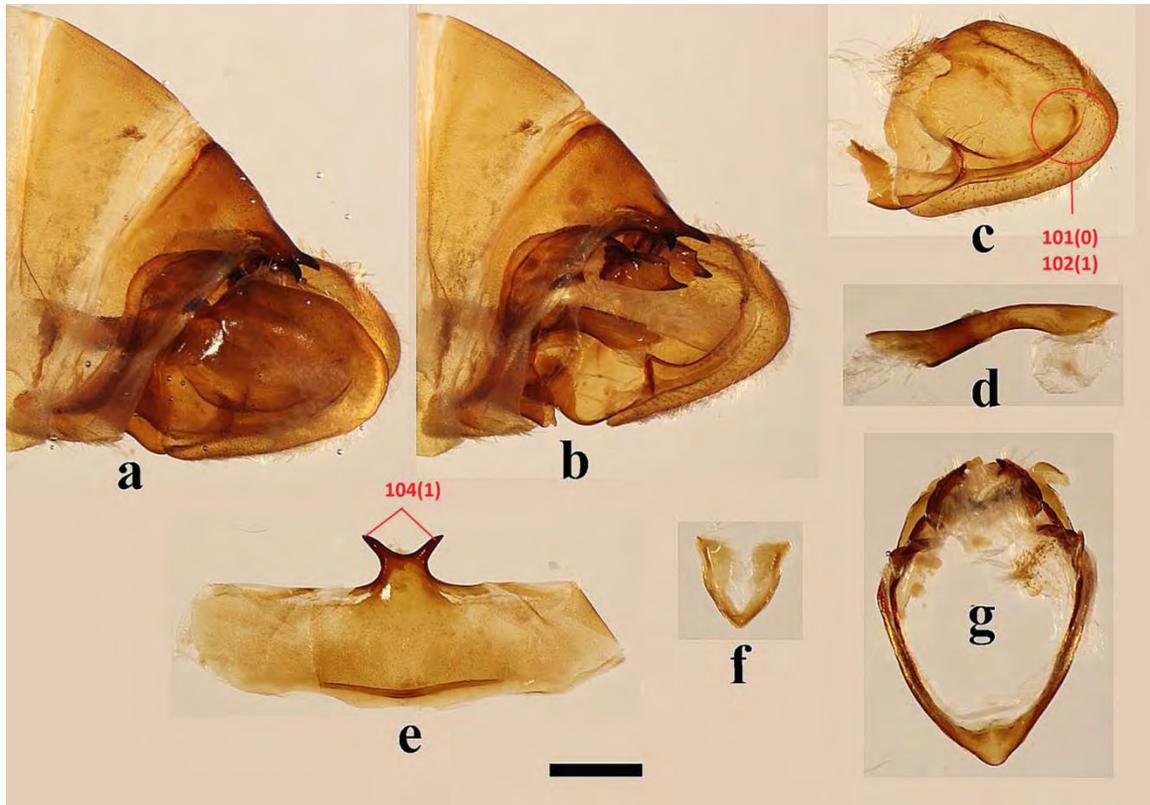


Figure 6-38. *Heraclides homothoas* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

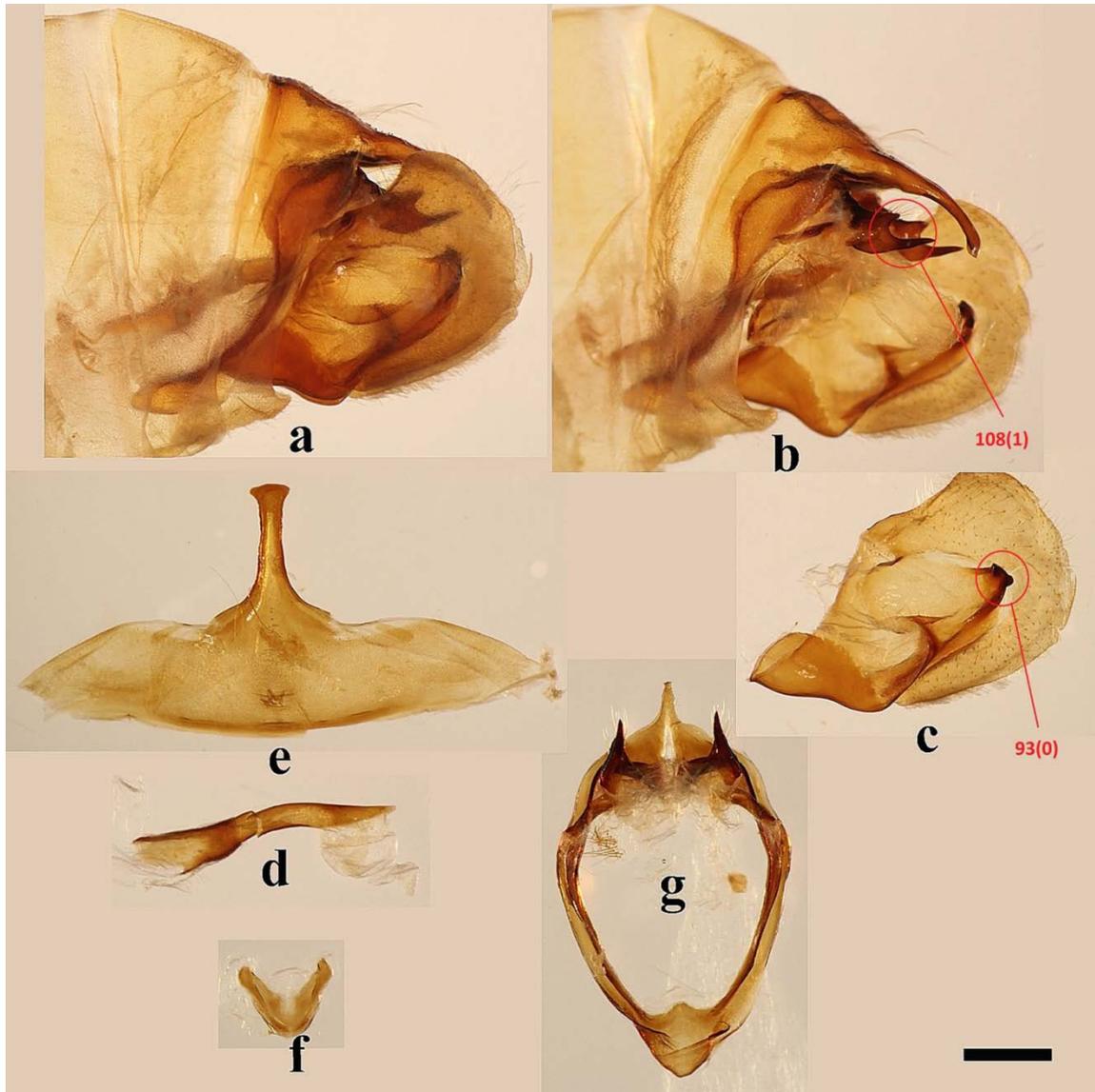


Figure 6-39. *Heraclides melonius* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

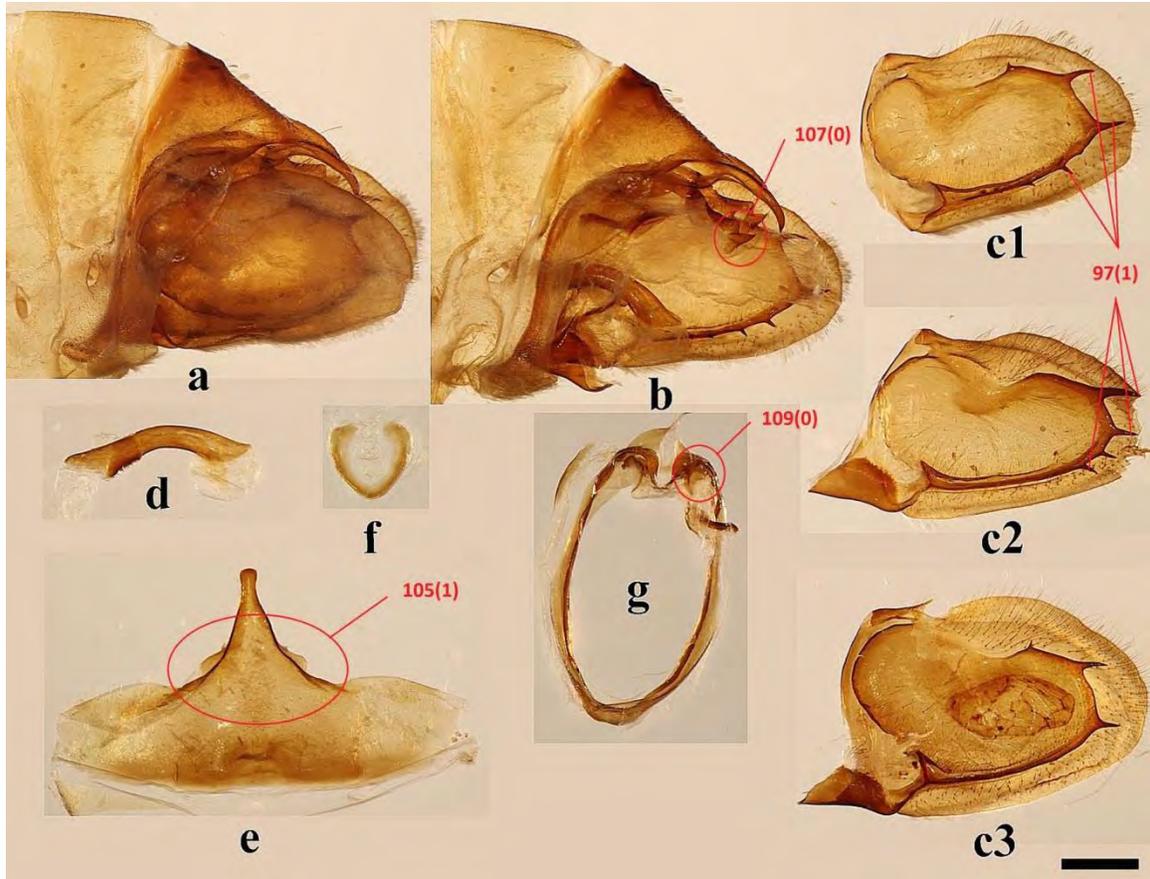


Figure 6-40. *Heraclides paeon* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. p. paeon* valve, (c2) *H. p. escomeli* valve, (c3) *H. p. thrason* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

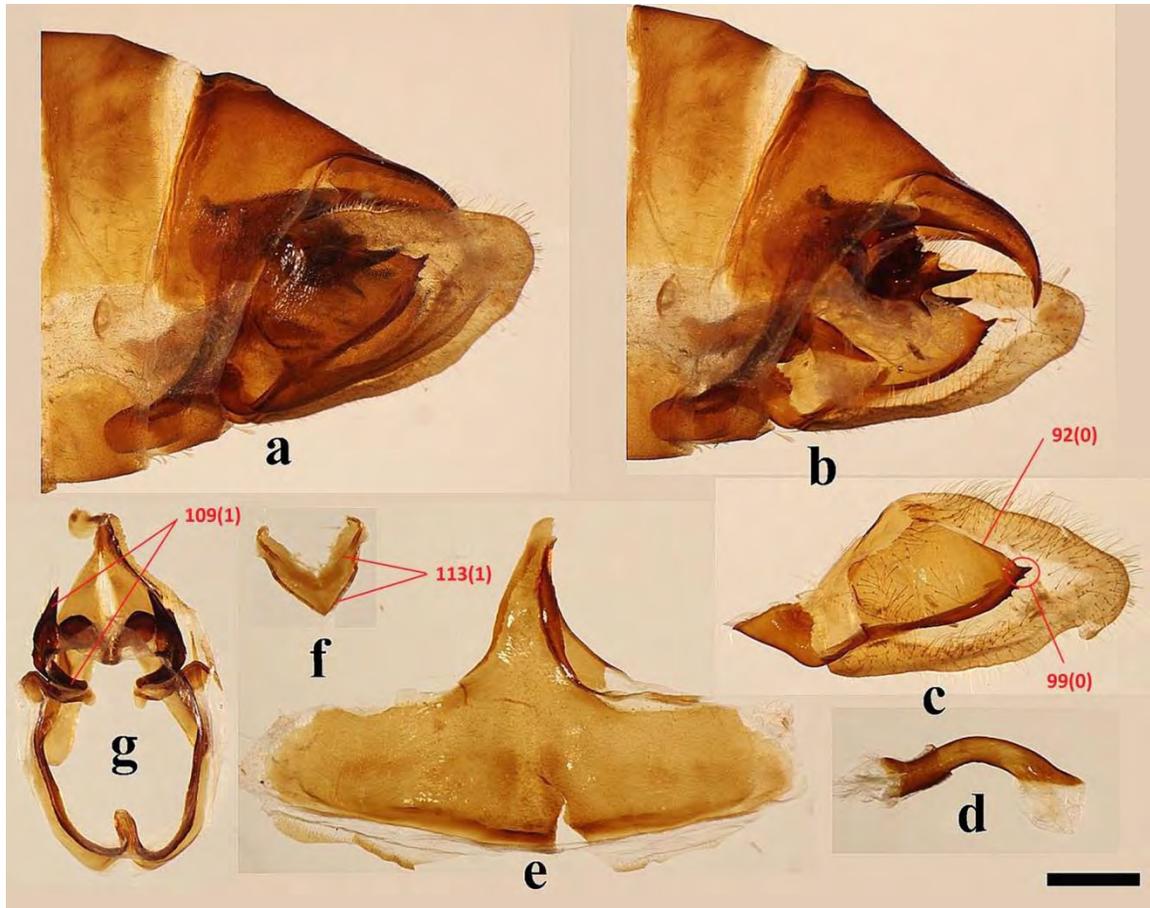


Figure 6-41. *Heraclides aristor* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

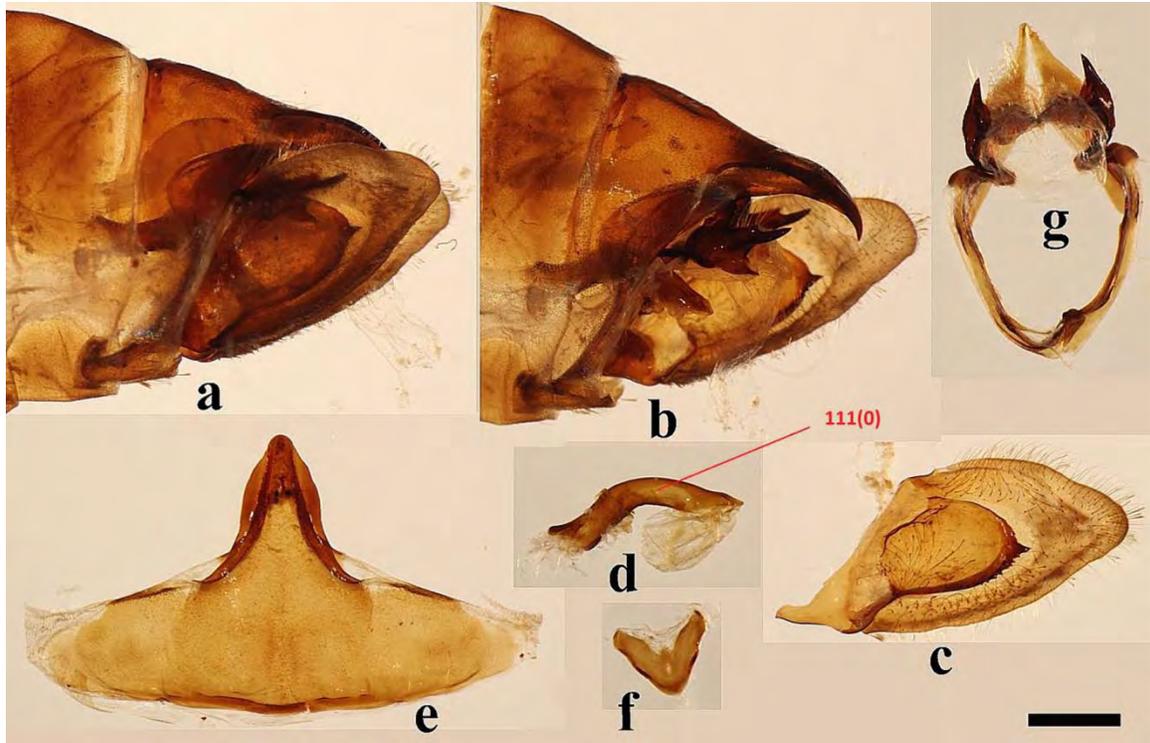


Figure 6-42. *Heraclides caiguanabus* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

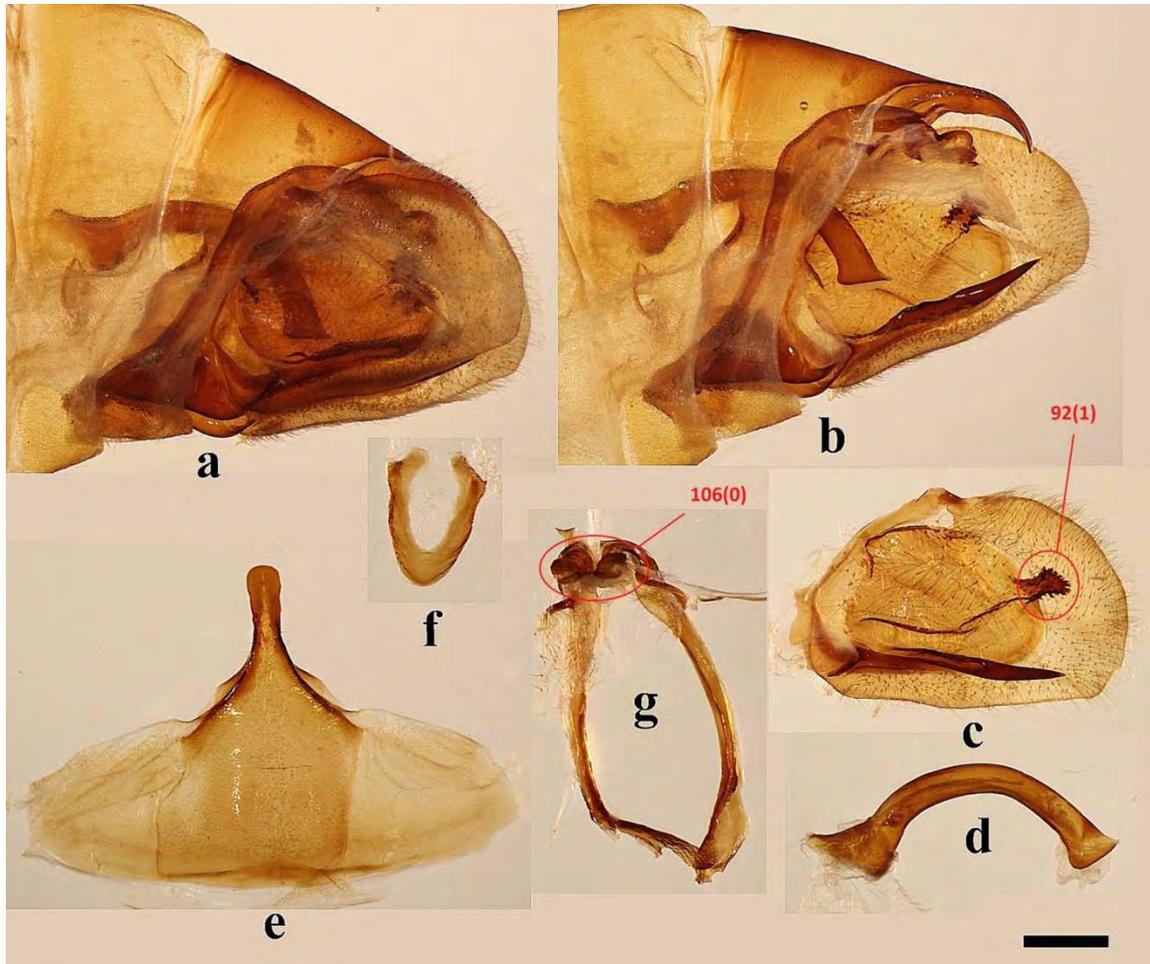


Figure 6-43. *Heraclides thersites* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

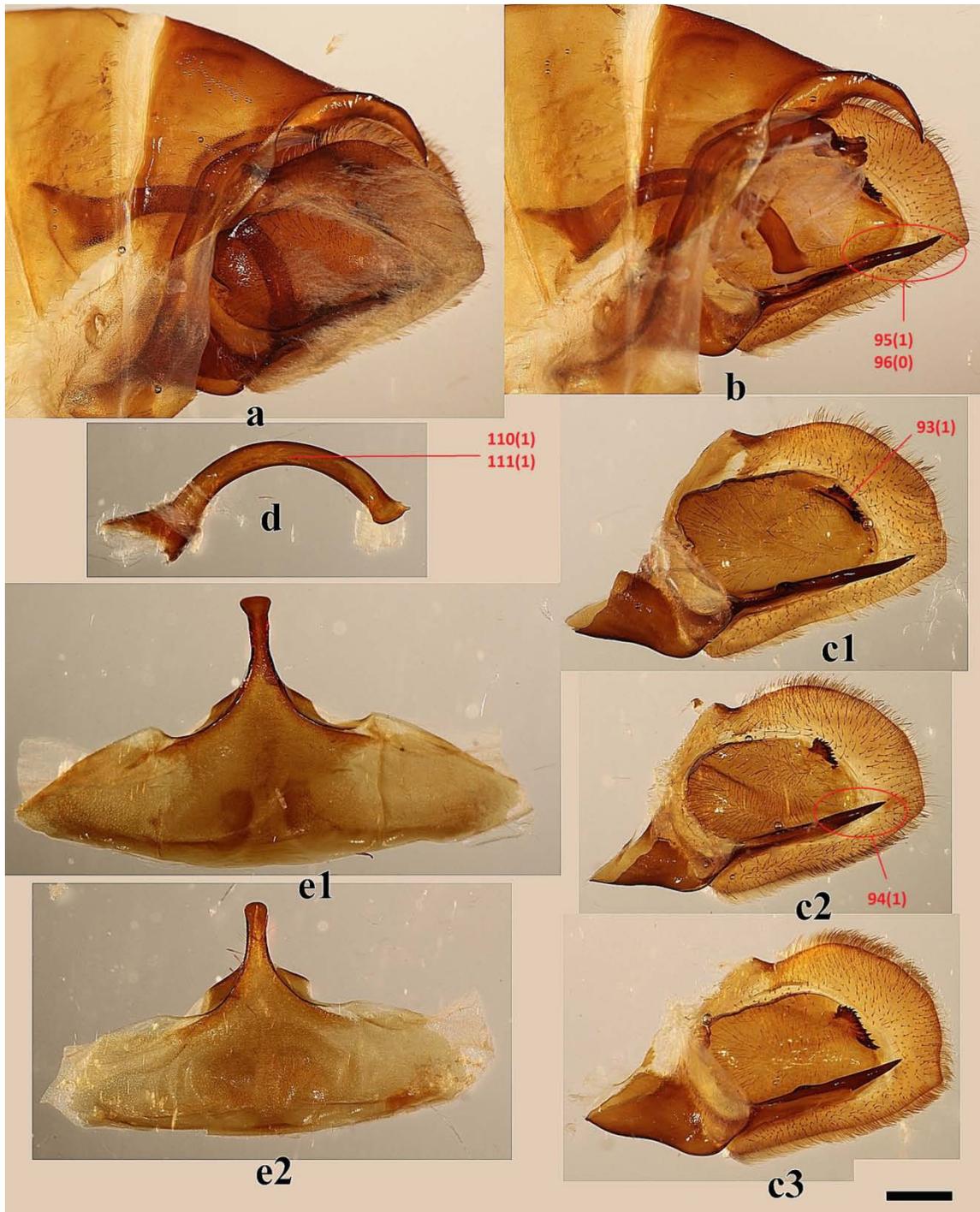


Figure 6-44. *Heraclides androgeus* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. a. androgeus* valve, (c2) *H. a. epidaurus* valve, (c3) *H. a. laodocus* valve, (d) aedeagus, (e1) *H. androgeus androgeus* 8th tergite, (e2) *H. a. epidaurus* 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

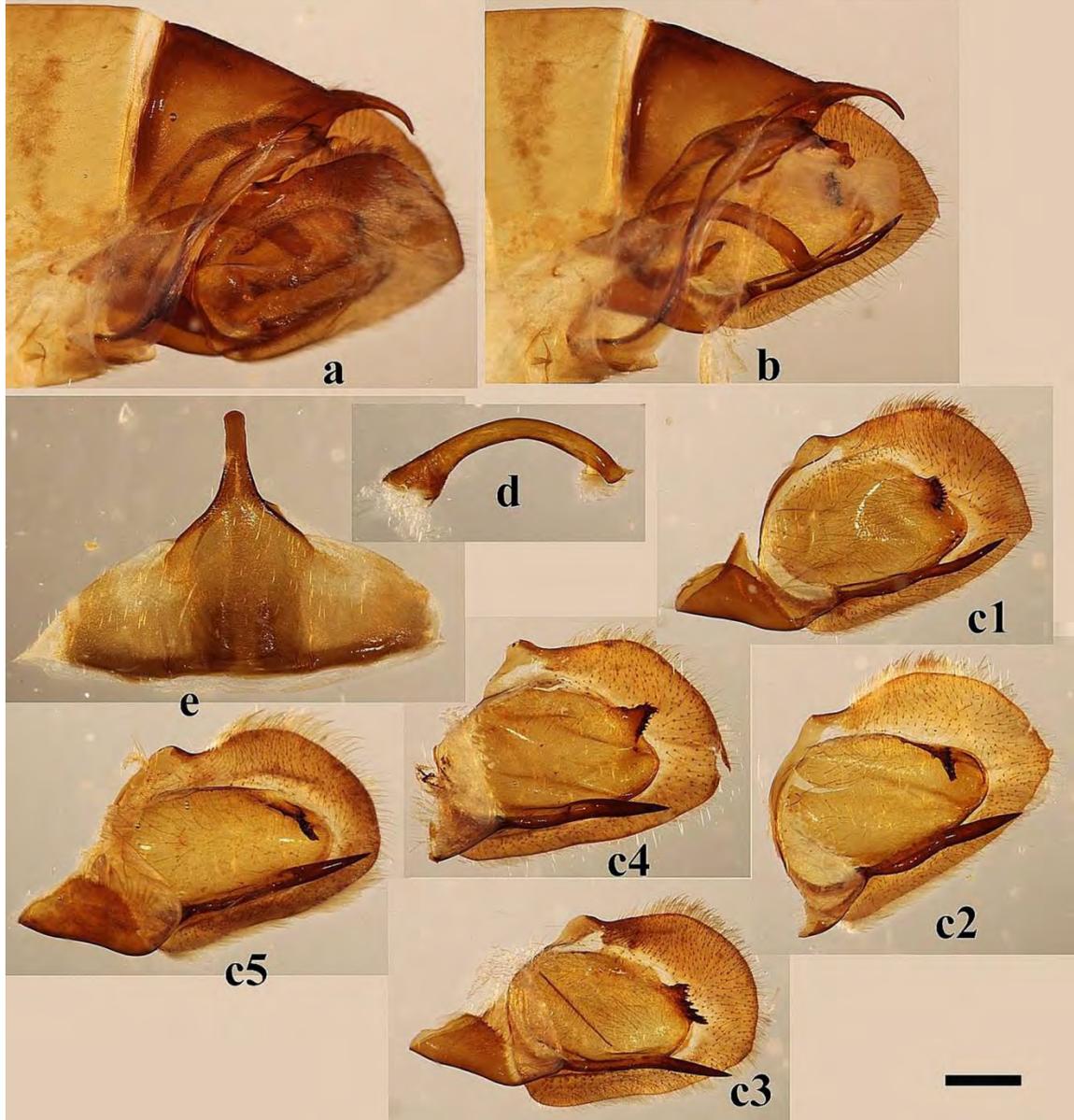


Figure 6-45. *Heraclides astyalus* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. a. astyalus* valve, (c2) *H. a. bajaensis* valve, (c3) *H. a. hippomedon* valve, (c4) *H. a. pallas* valve, (c5) *H. a. phanias* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

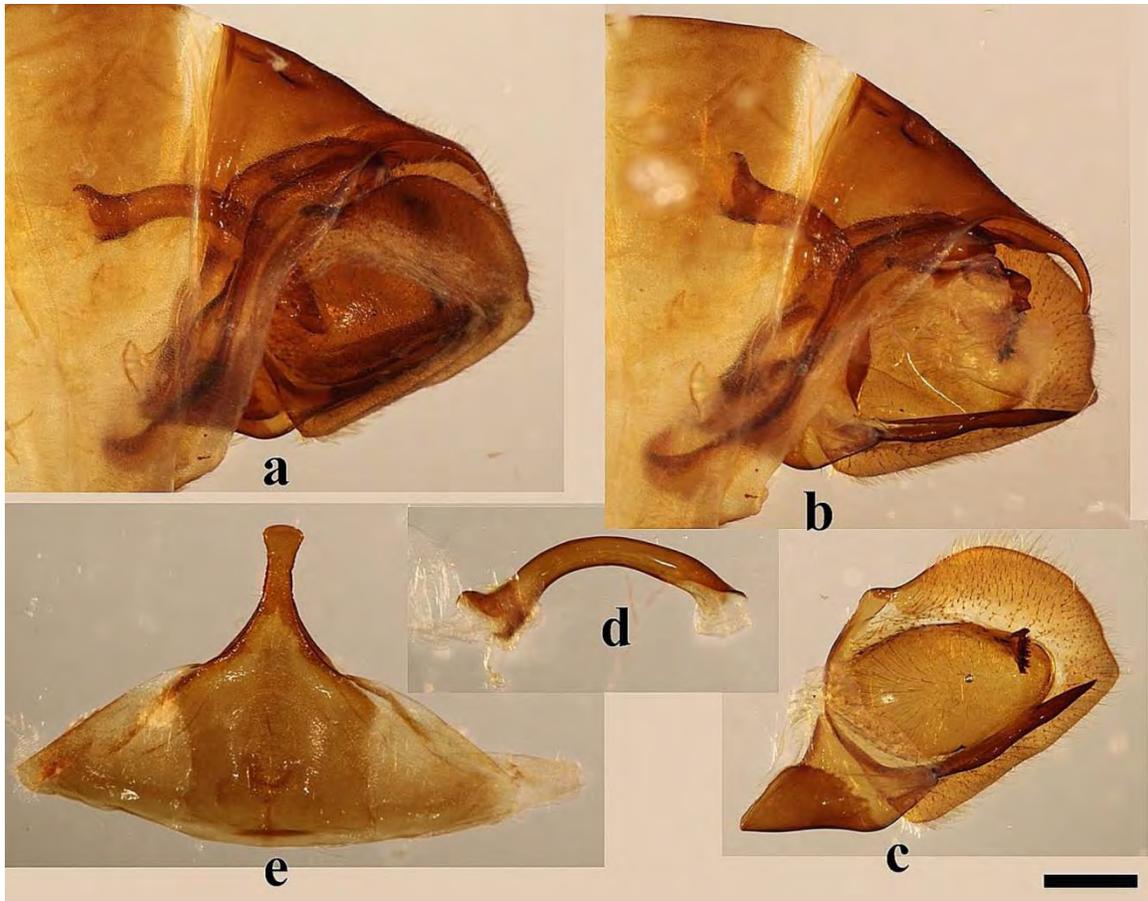


Figure 6-46. *Heraclides ornythion* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

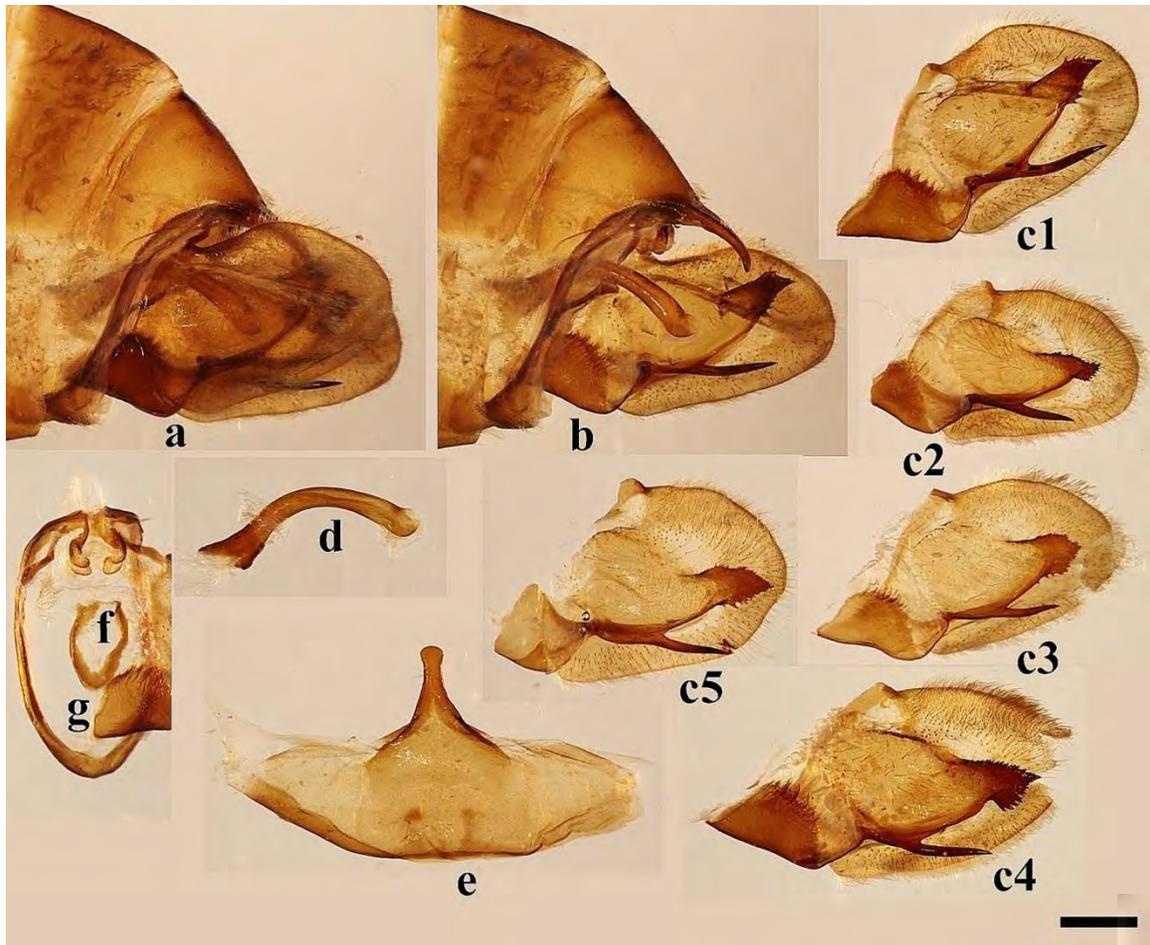


Figure 6-47. *Heraclides aristodemus* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. a. aristodemus* valve, (c2) *H. a. bjoerndalae* valve, (c3) *H. a. majasi* valve, (c4) *H. a. ponceanus* valve, (c5) *H. a. temenes* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

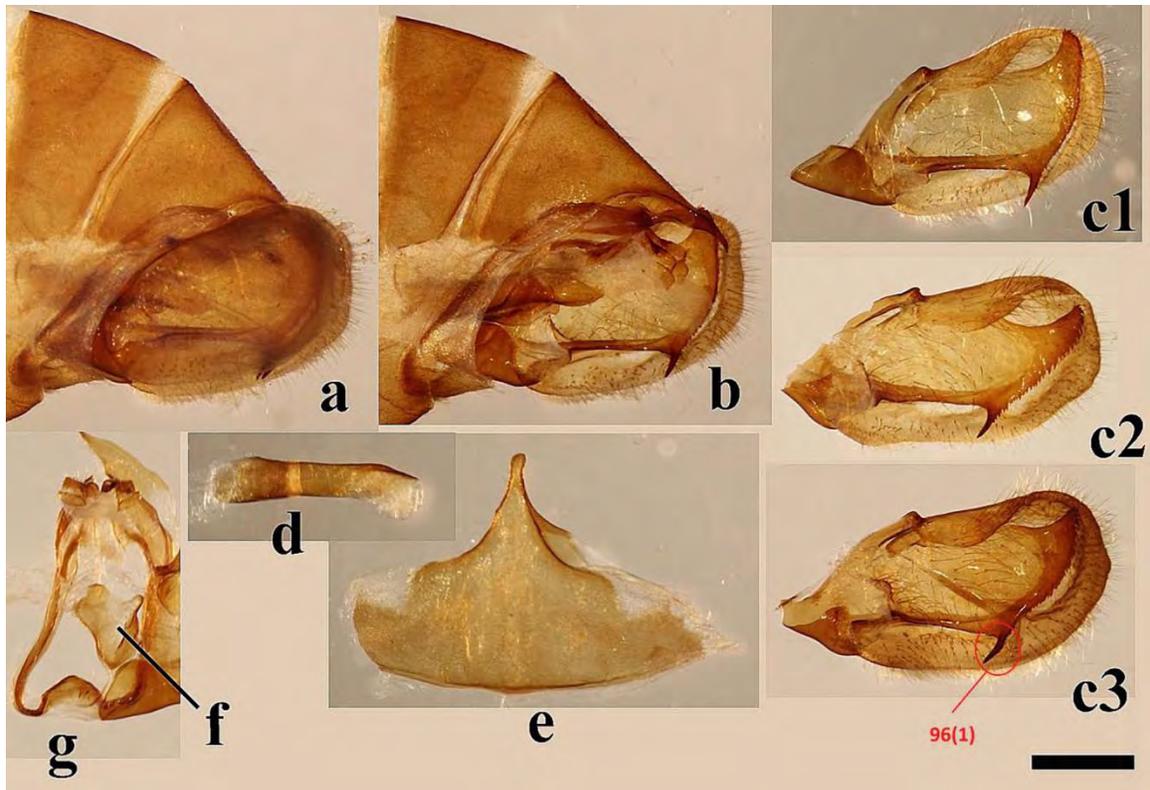


Figure 6-48. *Heraclides andraemon* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. a. andraemon* valve, (c2) *H. a. bonhotei* valve, (c3) *H. a. tailori* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

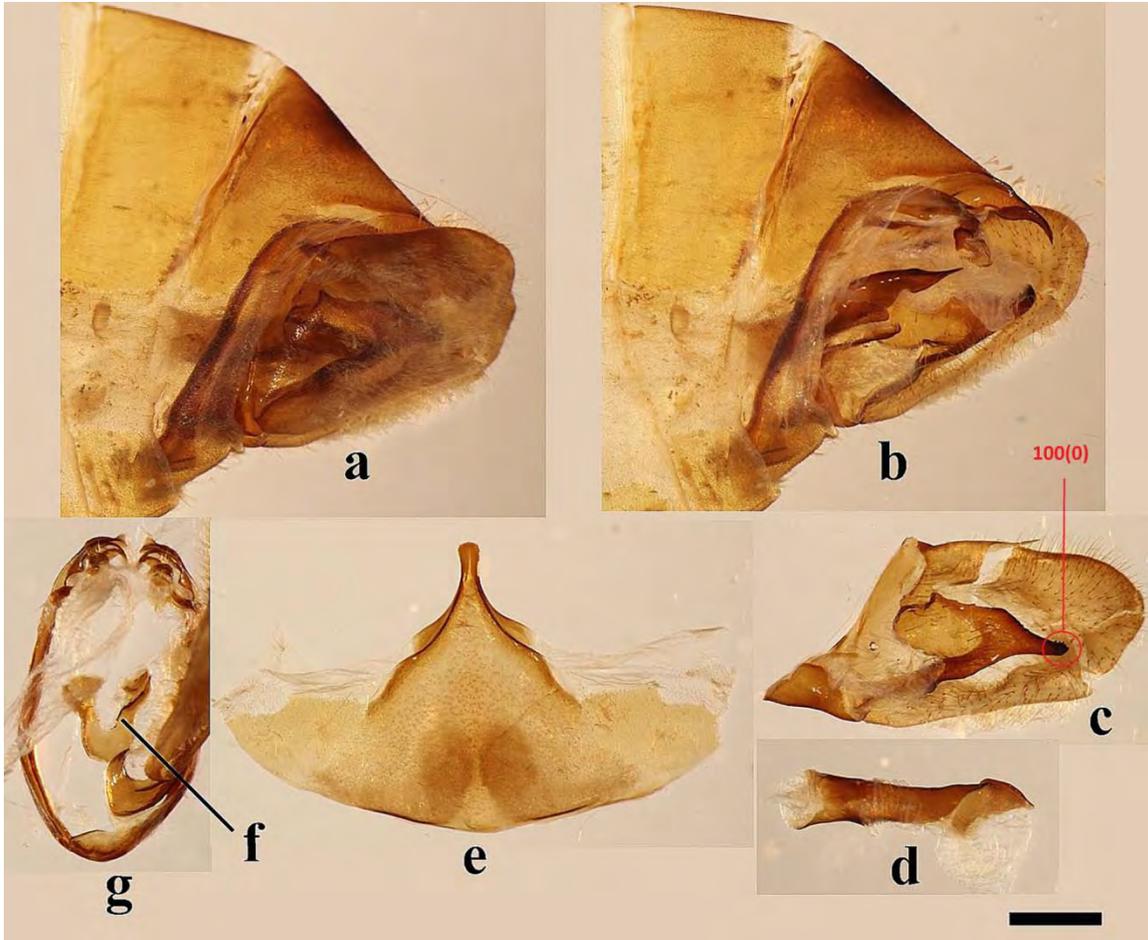


Figure 6-49. *Heraclides machaonides* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

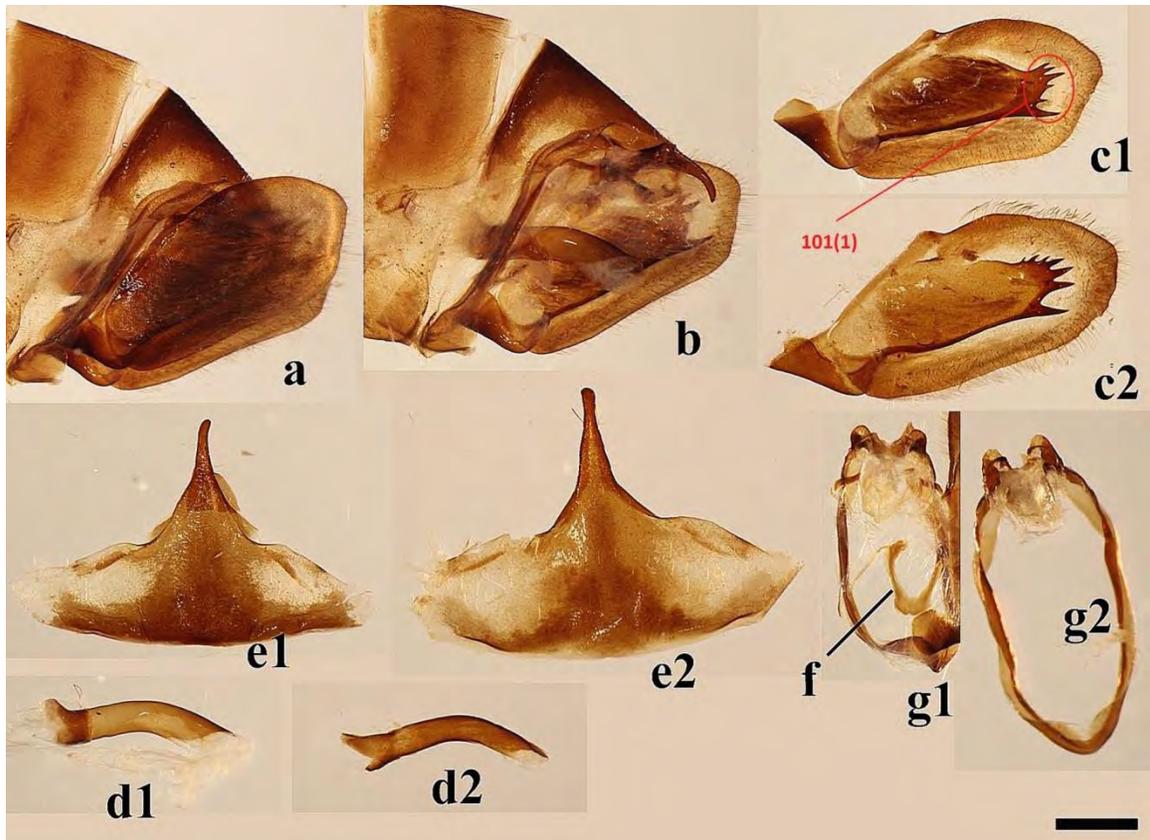


Figure 6-50. *Heraclides lamarchei* and *H. Hectorides* male genitalia: (a) *H. Hectorides* abdomen, (b) *H. Hectorides* abdomen with left valve removed, (c1) *H. Hectorides* valve, (c2) *H. lamarchei* valve, (d1) *H. Hectorides* aedeagus, (d2) *H. lamarchei* aedeagus, (e1) *H. Hectorides* 8th tergite, (e2) *H. lamarchei* 8th tergite, (f) *H. Hectorides* juxta, (g1) *H. Hectorides* uncus, vinculum and saccus, (g2) *H. lamarchei* uncus, vinculum and saccus. Scale bar approximately 1 mm.

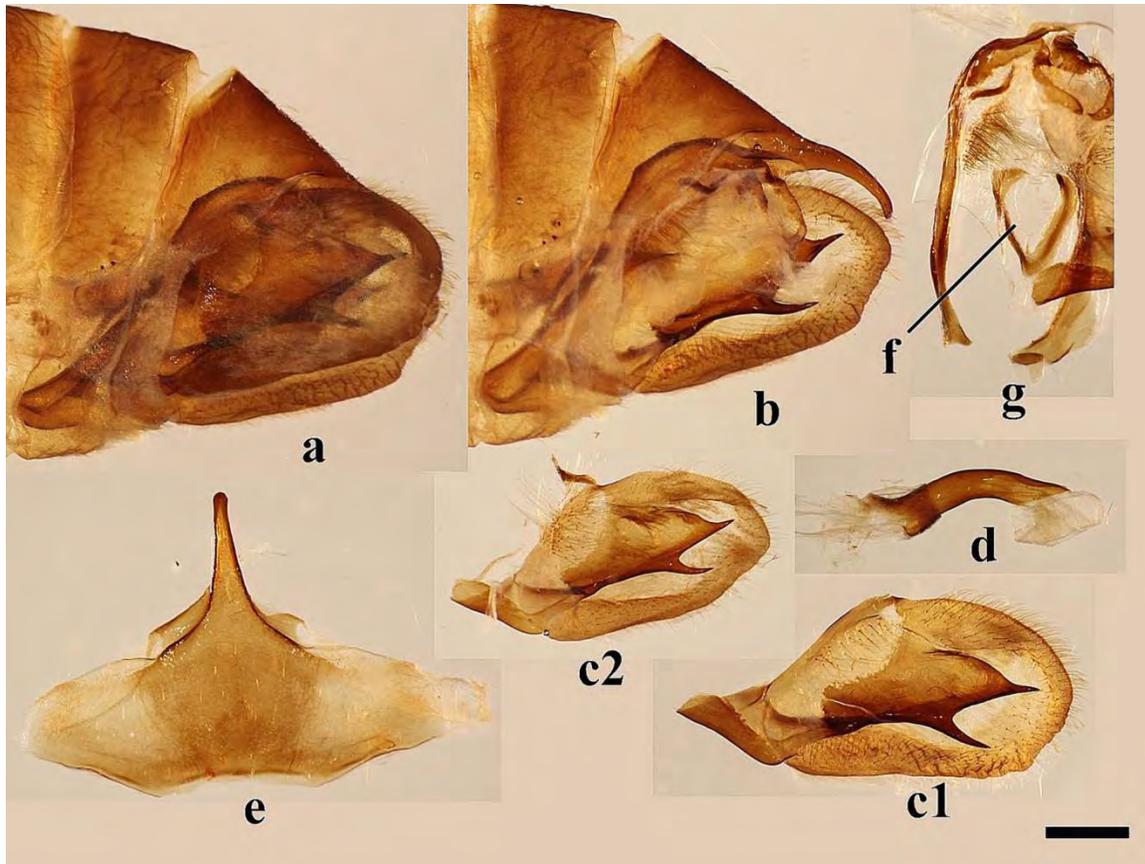


Figure 6-51. *Heraclides garleppi* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. garleppi garleppi* valve, (c2) *H. g. lecerfi* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

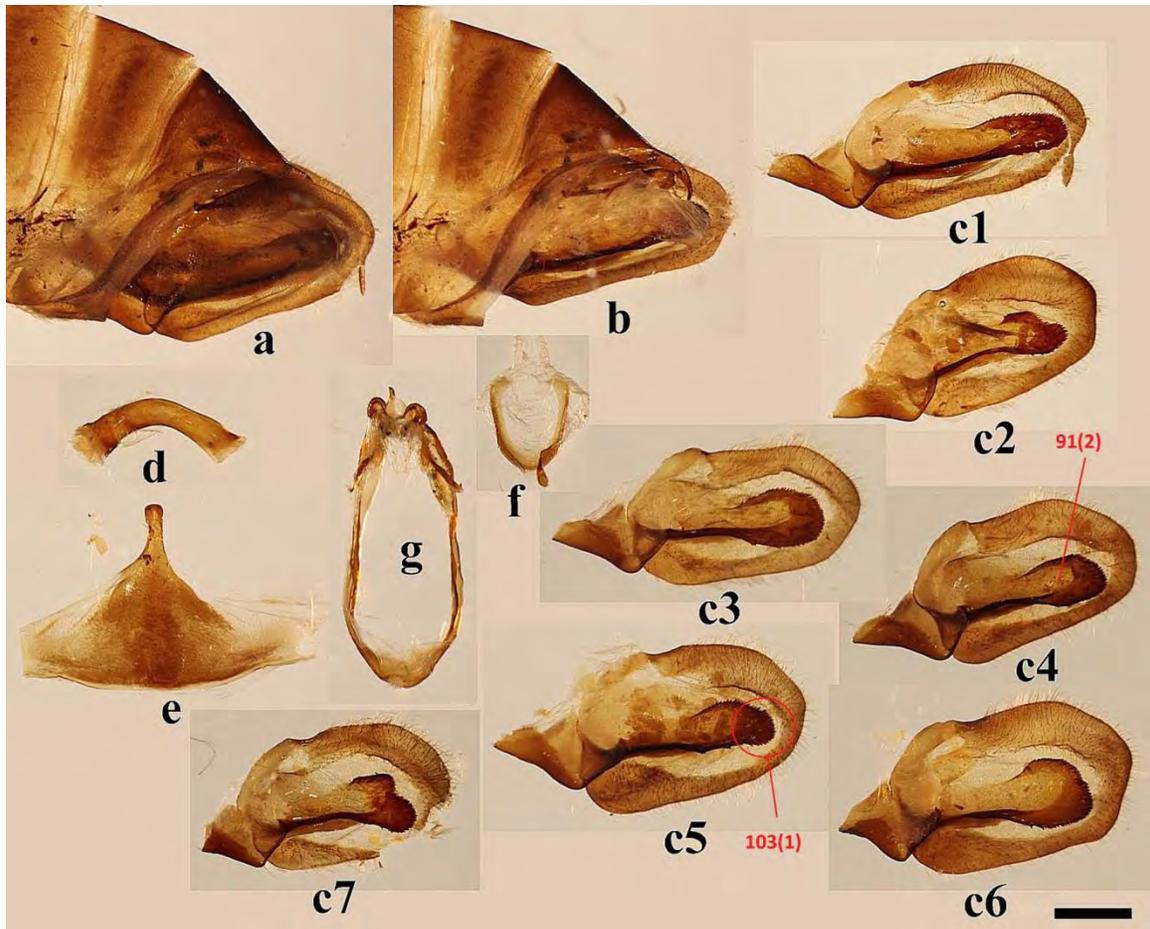


Figure 6-52. *Heraclides torquatus* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. t. torquatus* valve, (c2) *H. t. atsukoa* valve, (c3) *H. t. jeani* valve, (c4) *H. t. leptalea* valve, (c5) *H. t. polybius* valve, (c6) *H. to. tolmidis* valve, (c7) *H. t. tolus* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

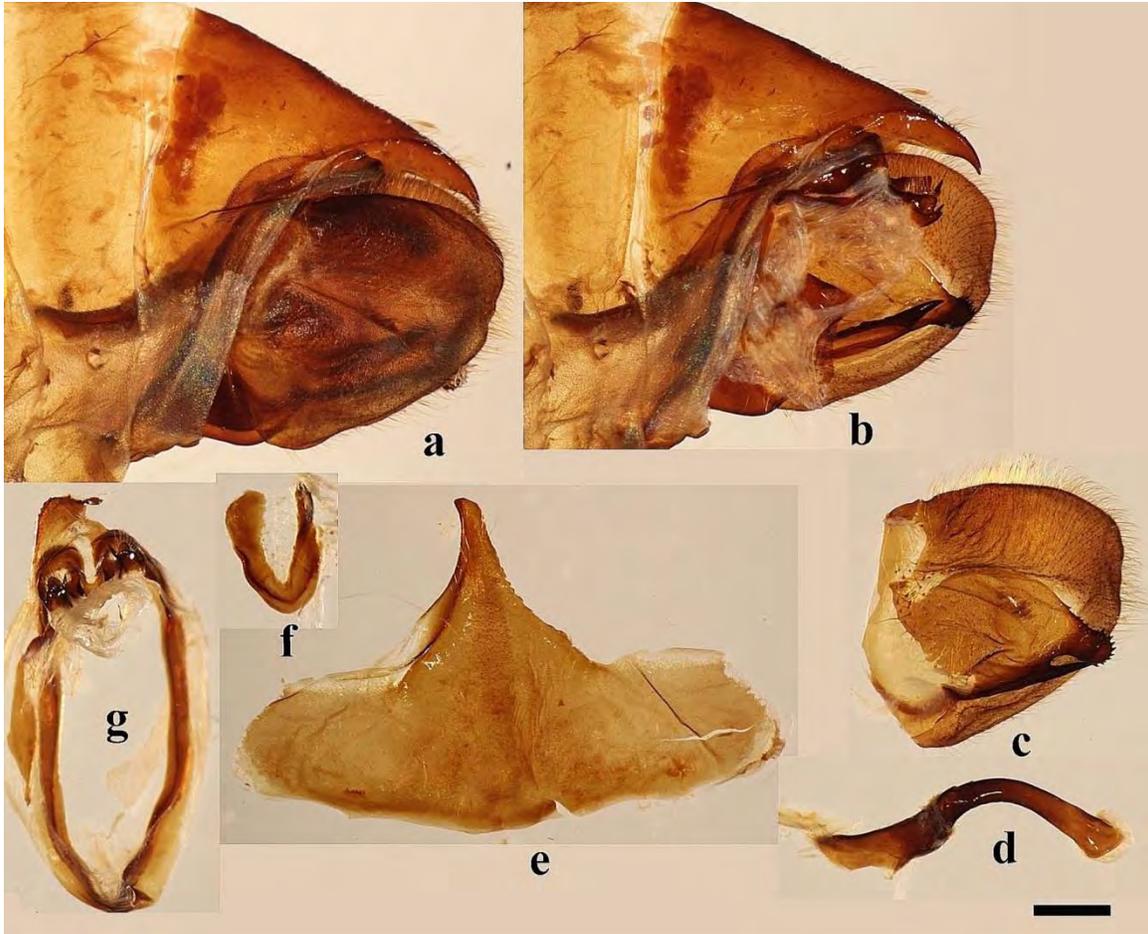


Figure 6-53. *Heraclides hyppason* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

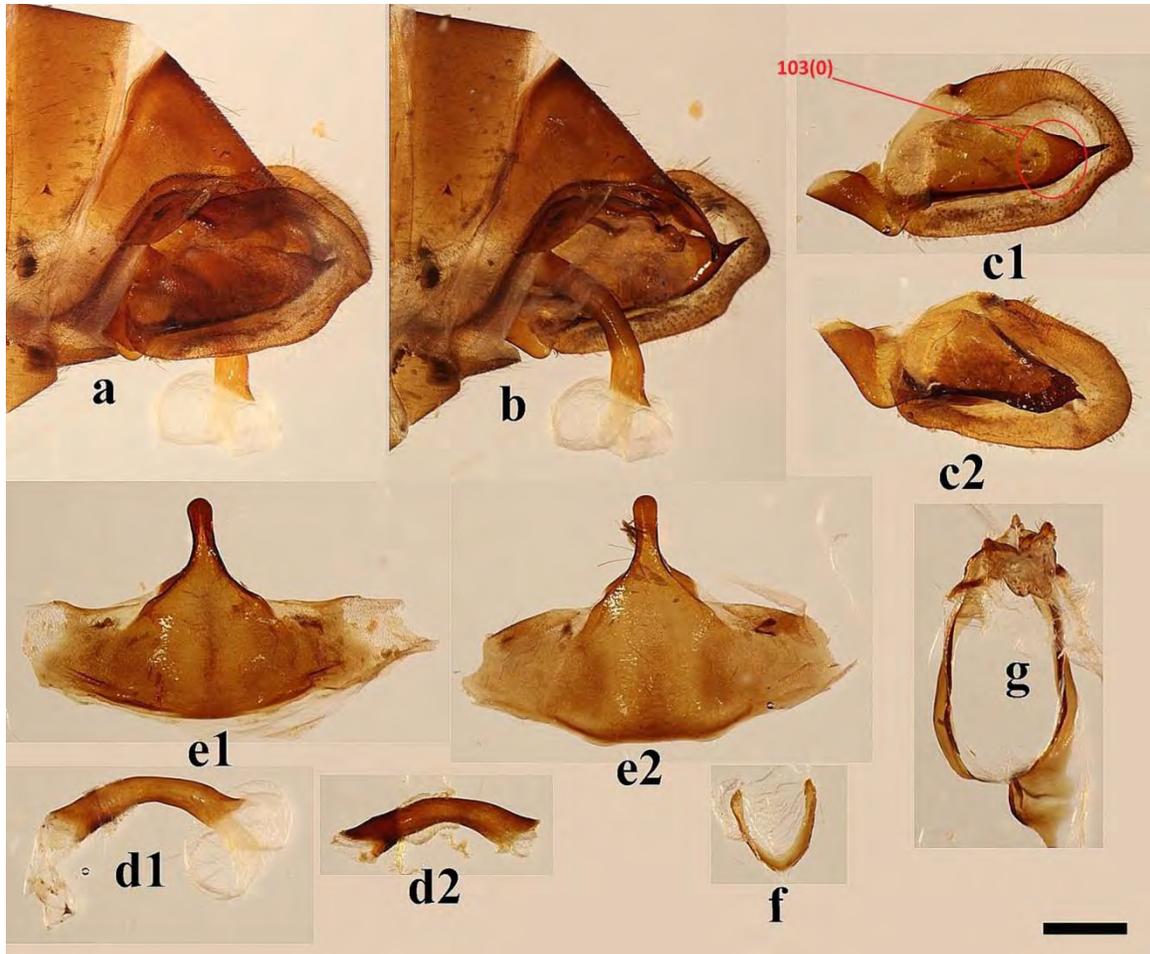


Figure 6-54. *Heraclides epenetus* and *oxynius* male genitalia: (a) *H. epenetus* abdomen, (b) *H. epenetus* abdomen with left valve removed, (c1) *H. epenetus* valve, (c2) *H. oxynius* valve, (d1) *H. epenetus* aedeagus, (d2) *H. oxynius* aedeagus, (e1) *H. epenetus* 8th tergite, (e2) *H. oxynius* 8th tergite, (f) *H. epenetus* juxta, (g) *H. epenetus* uncus, vinculum and saccus. Scale bar approximately 1 mm.

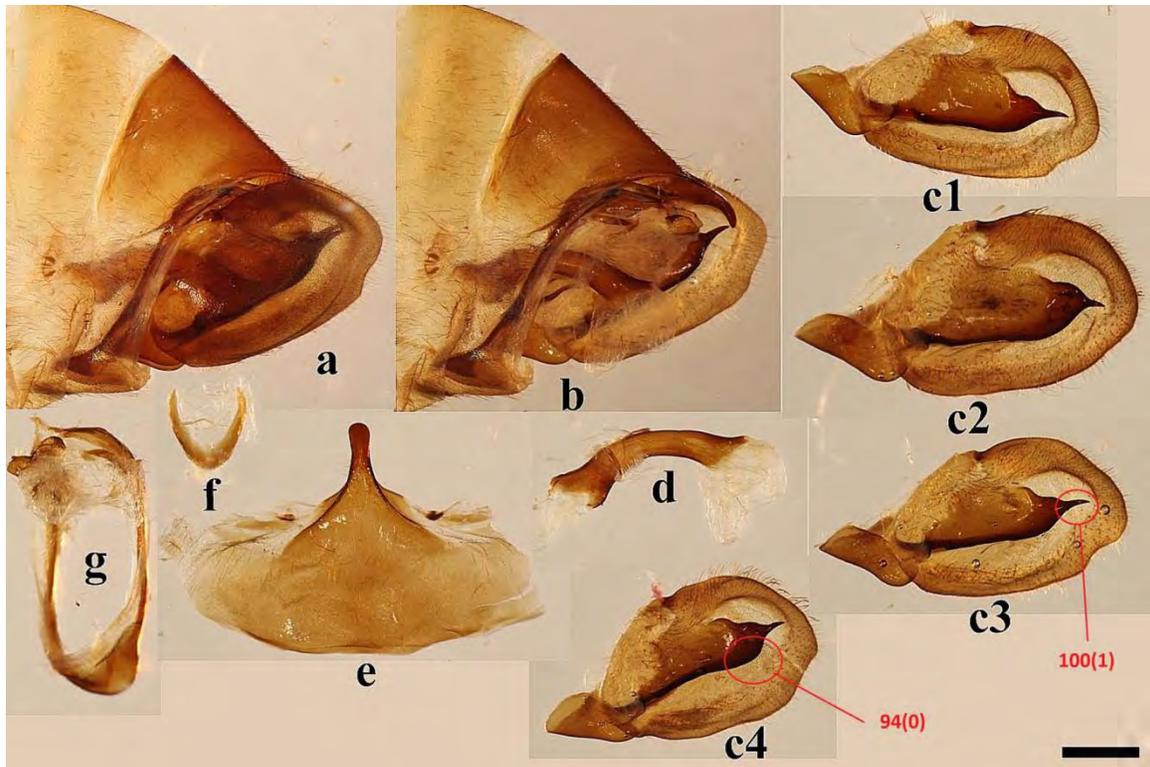


Figure 6-55. *Heraclides pelaus* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. p. pelaus* valve, (c2) *H. p. atkinsi* valve, (c3) *H. p. imerius* valve, (c4) *H. p. puertoricensis* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

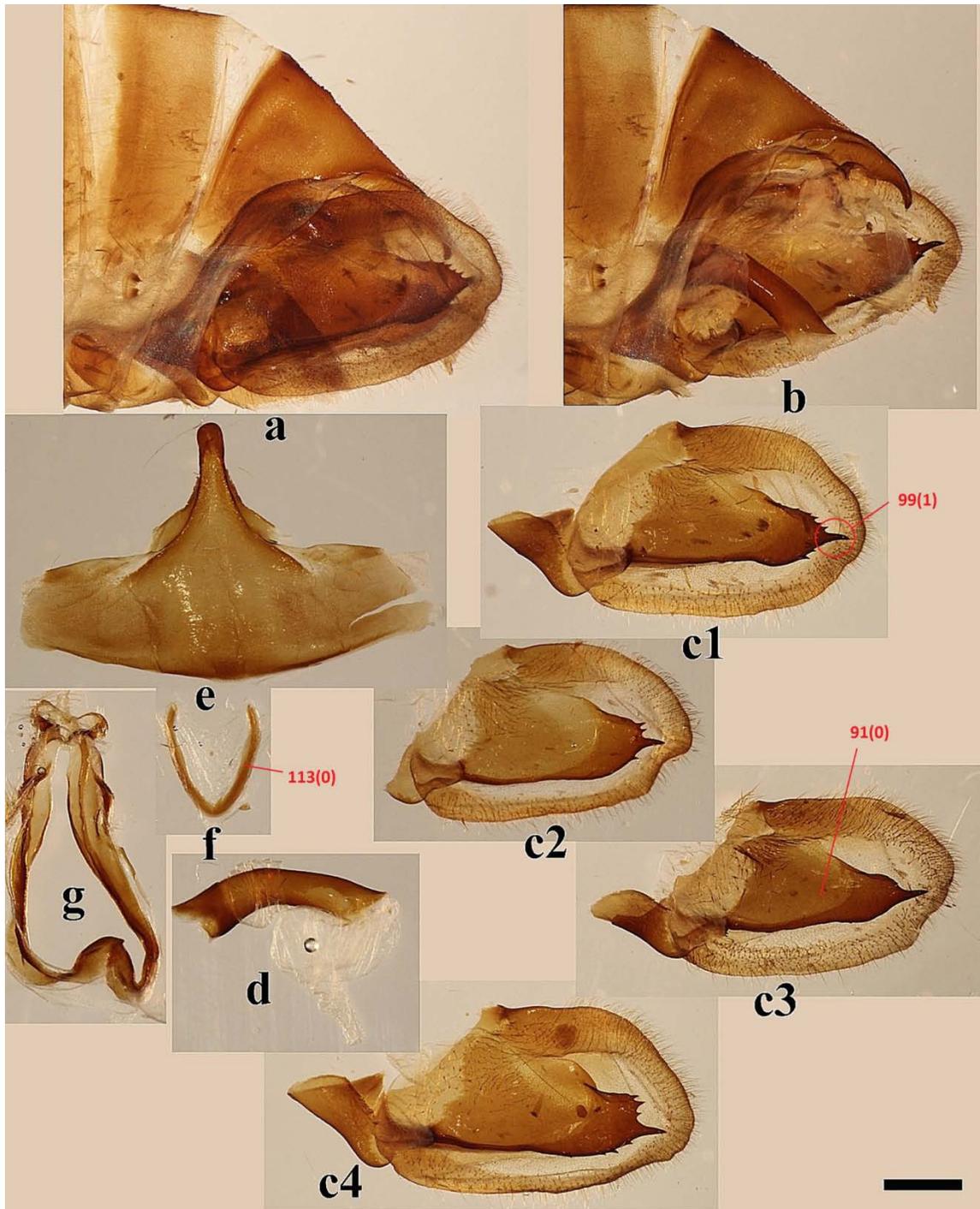


Figure 6-56. *Heraclides anchisiades* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. a. anchisiades* valve, (c2) *H. a. capys* valve, (c3) *H. a. idaeus* valve, (c4) *H. a. philastrius* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

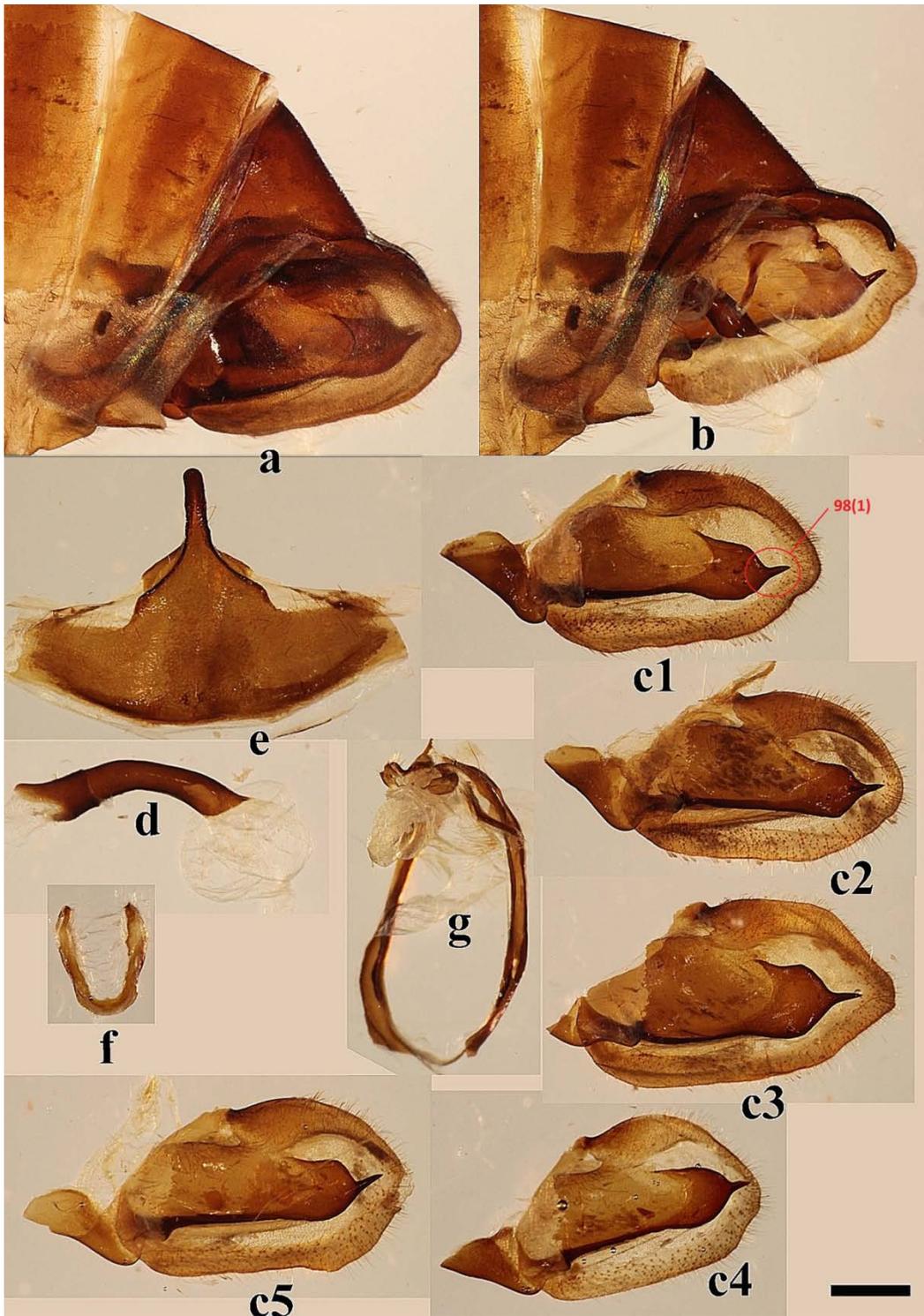


Figure 6-57. *Heraclides isidorus* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. i. isidorus* valve, (c2) *H. i. isidorus* valve, (c3) *H. i. brises* valve, (c4) *H. i. flavescens* valve, (c5) *H. i. tingo* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

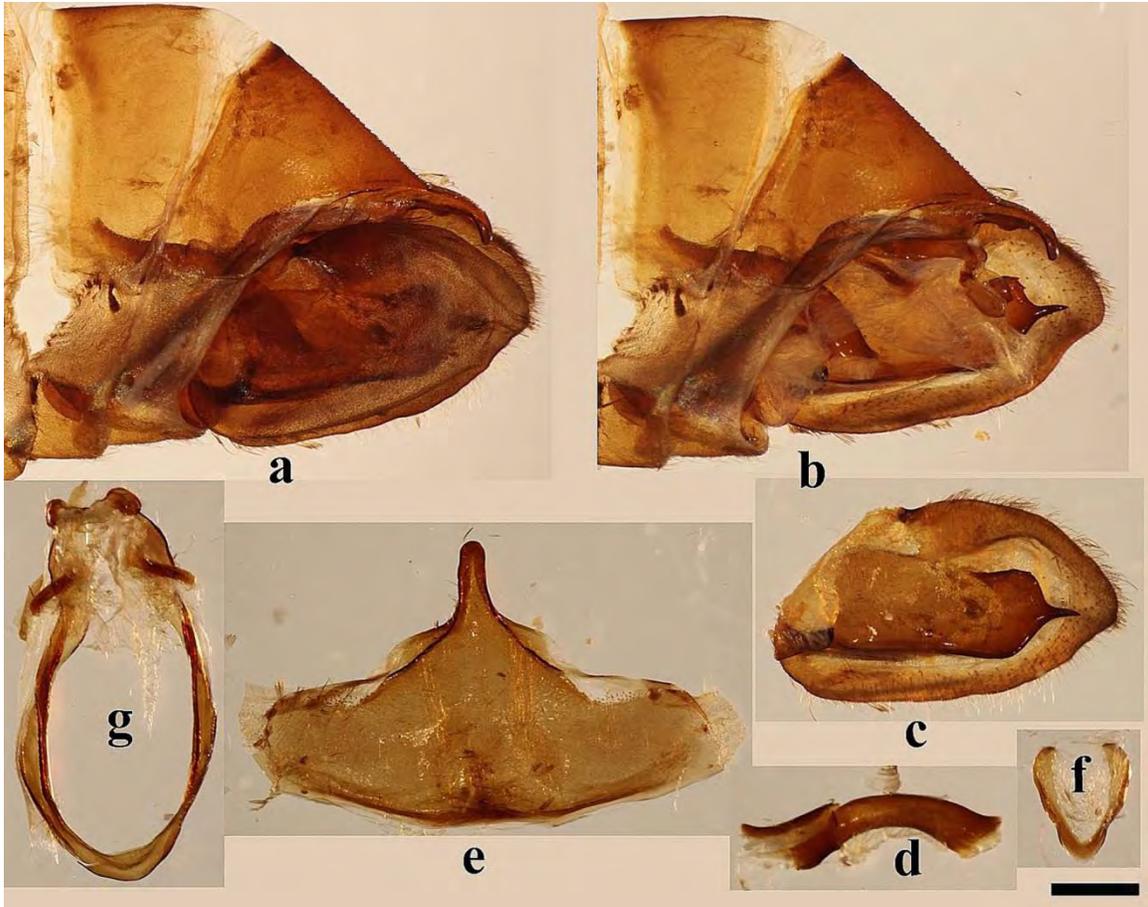


Figure 6-58. *Heraclides chiansiades* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c) valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

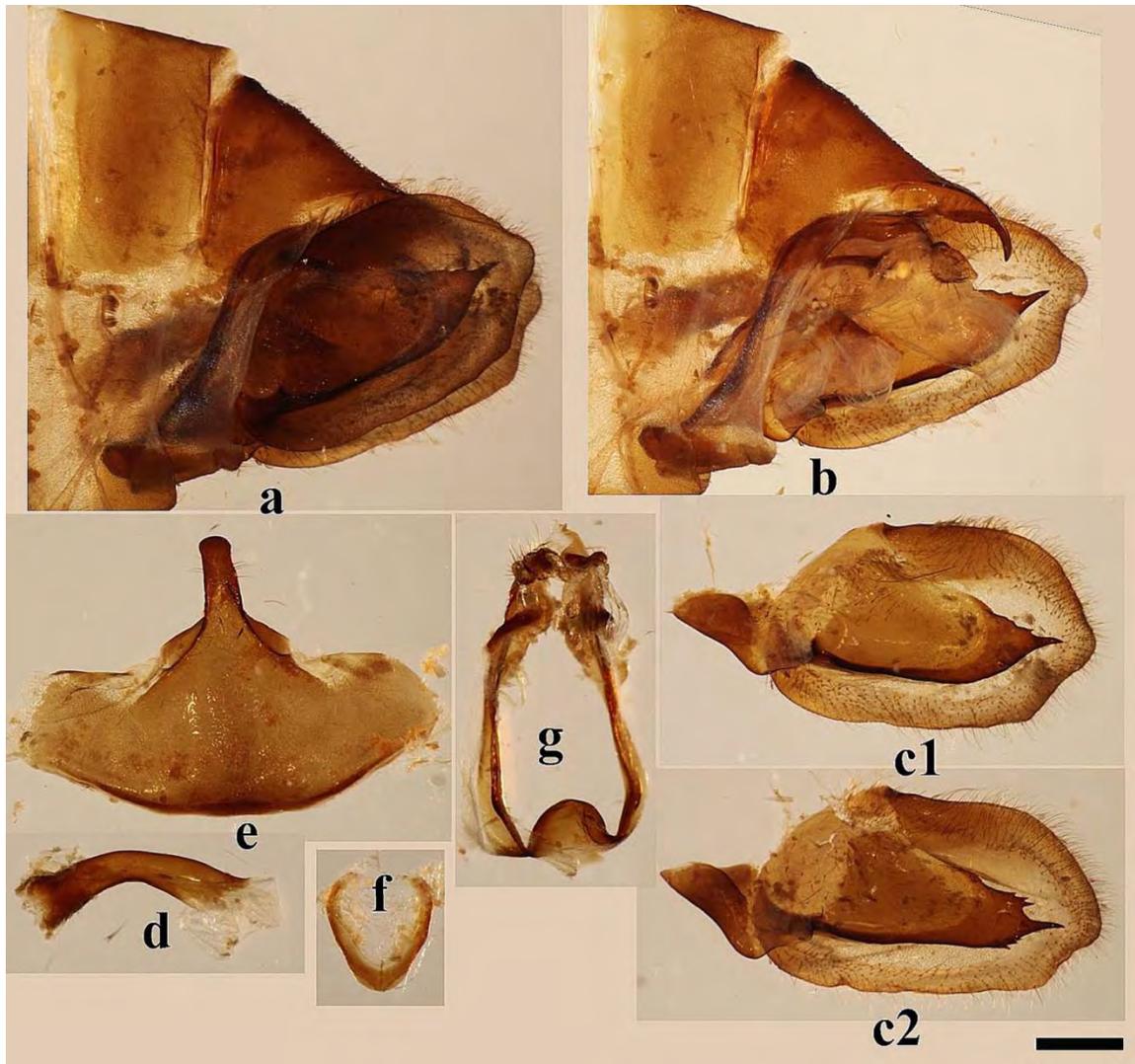


Figure 6-59. *Heraclides rogeri* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. r. rogeri* valve, (c2) *H. r. pharnaces* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

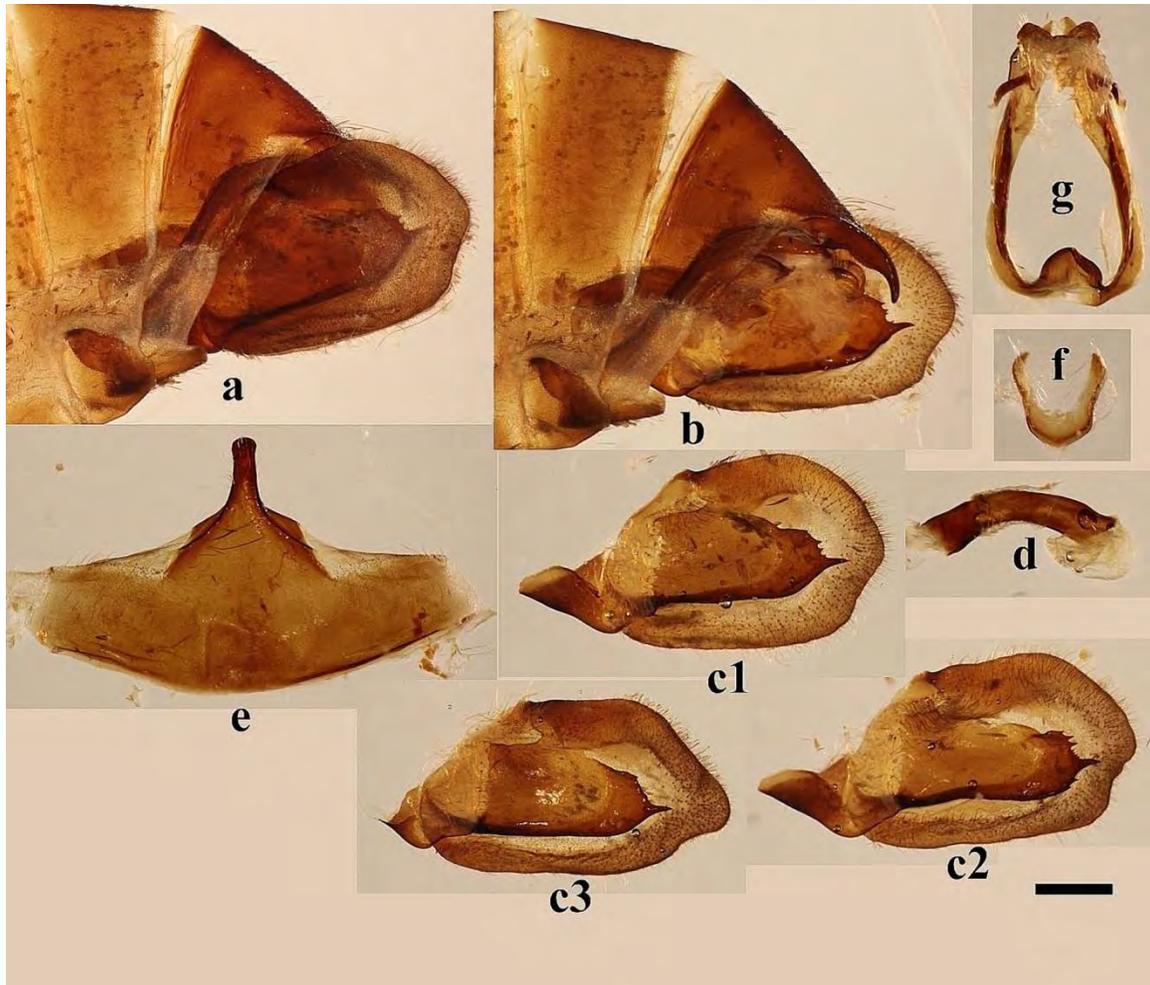


Figure 6-60. *Heraclides erostratus* male genitalia: (a) abdomen, (b) abdomen with left valve removed, (c1) *H. e. erostratus* valve, (c2) *H. e. erostratus* valve, (c3) *H. e. vazquezae* valve, (d) aedeagus, (e) 8th tergite, (f) juxta, (g) uncus, vinculum and saccus. Scale bar approximately 1 mm.

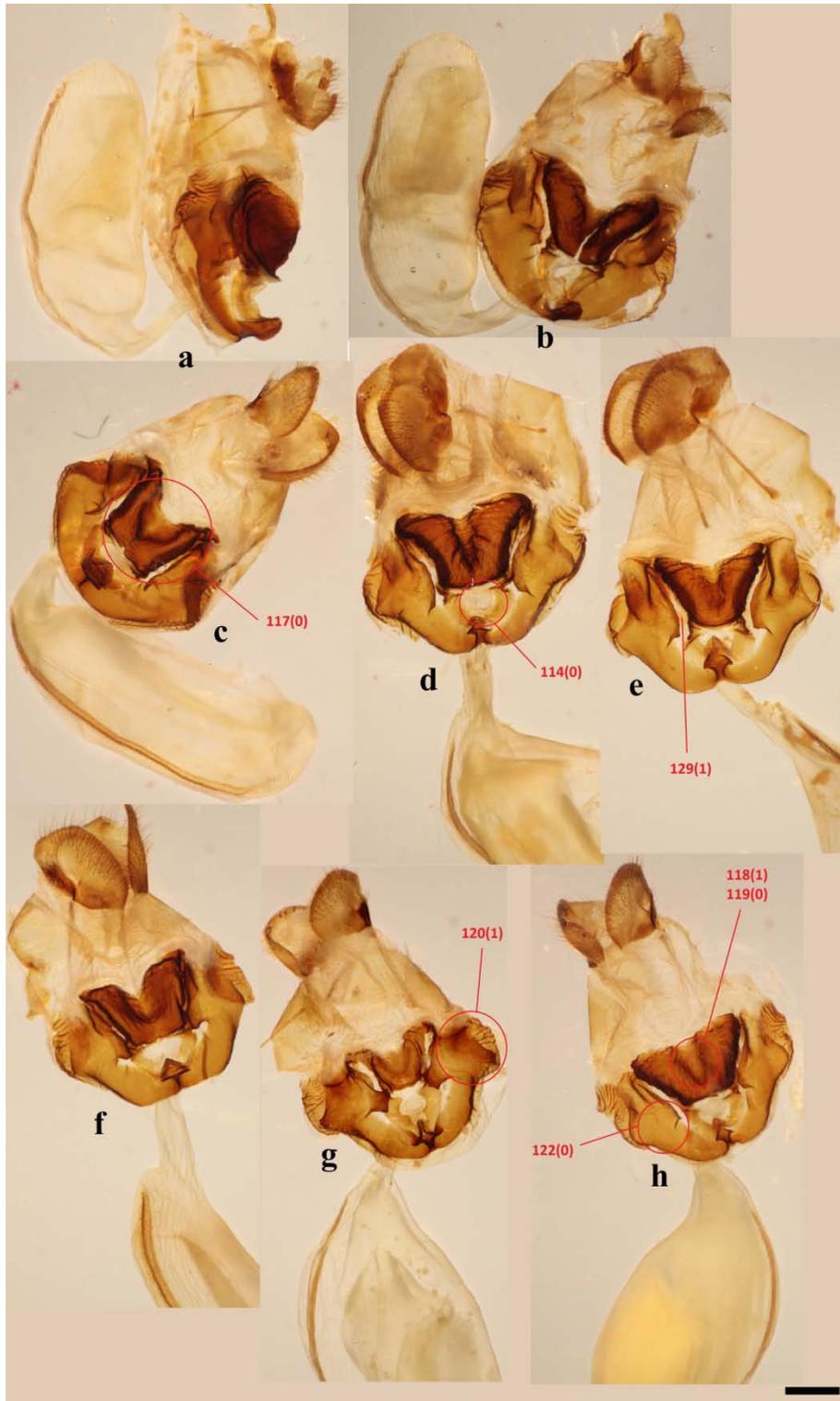


Figure 6-61. *Heraclides* female genitalia showing ostial armature: (a) *H. thoas thoas* (lateral view), (b) *H. t. thoas* (anal view), (c) *H. t. autocles*, (d) *H. t. brasiliensis*, (e) *H. t. cinyras*, (f) *H. t. neacles*, (g) *H. t. oviedo*, (h) *H. t. thoantiades*. Scale bar approximately 1 mm

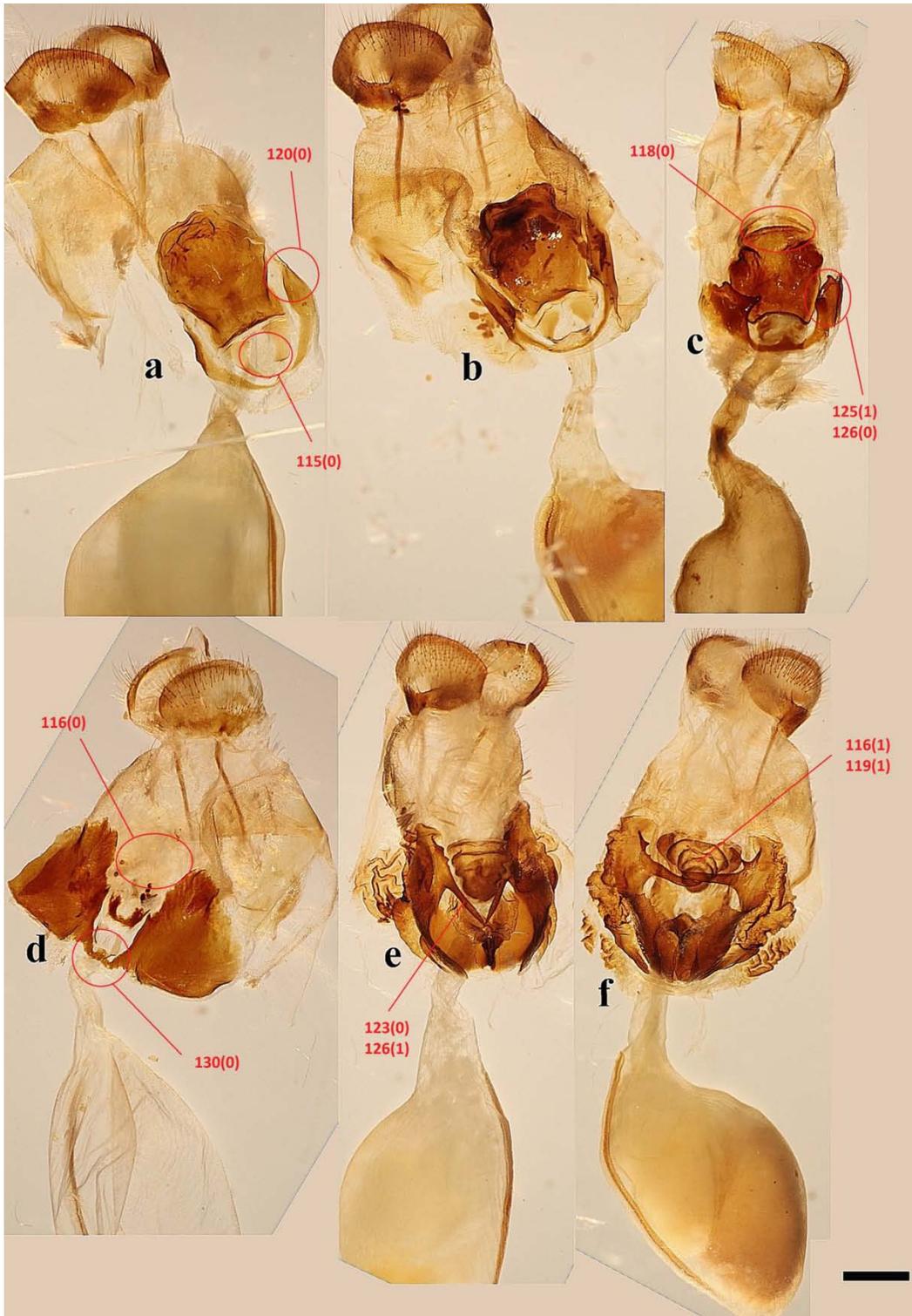


Figure 6-62. *Heraclides* female genitalia showing ostial armature: (a) *H. crespontes* (Florida), (b) *H. crespontes* (Costa Rica), (c) *H. homothoas*, (d) *H. melonius*, (e) *H. paeon paeon*, (f) *H. p. thrason*. Scale bar approximately 1 mm.

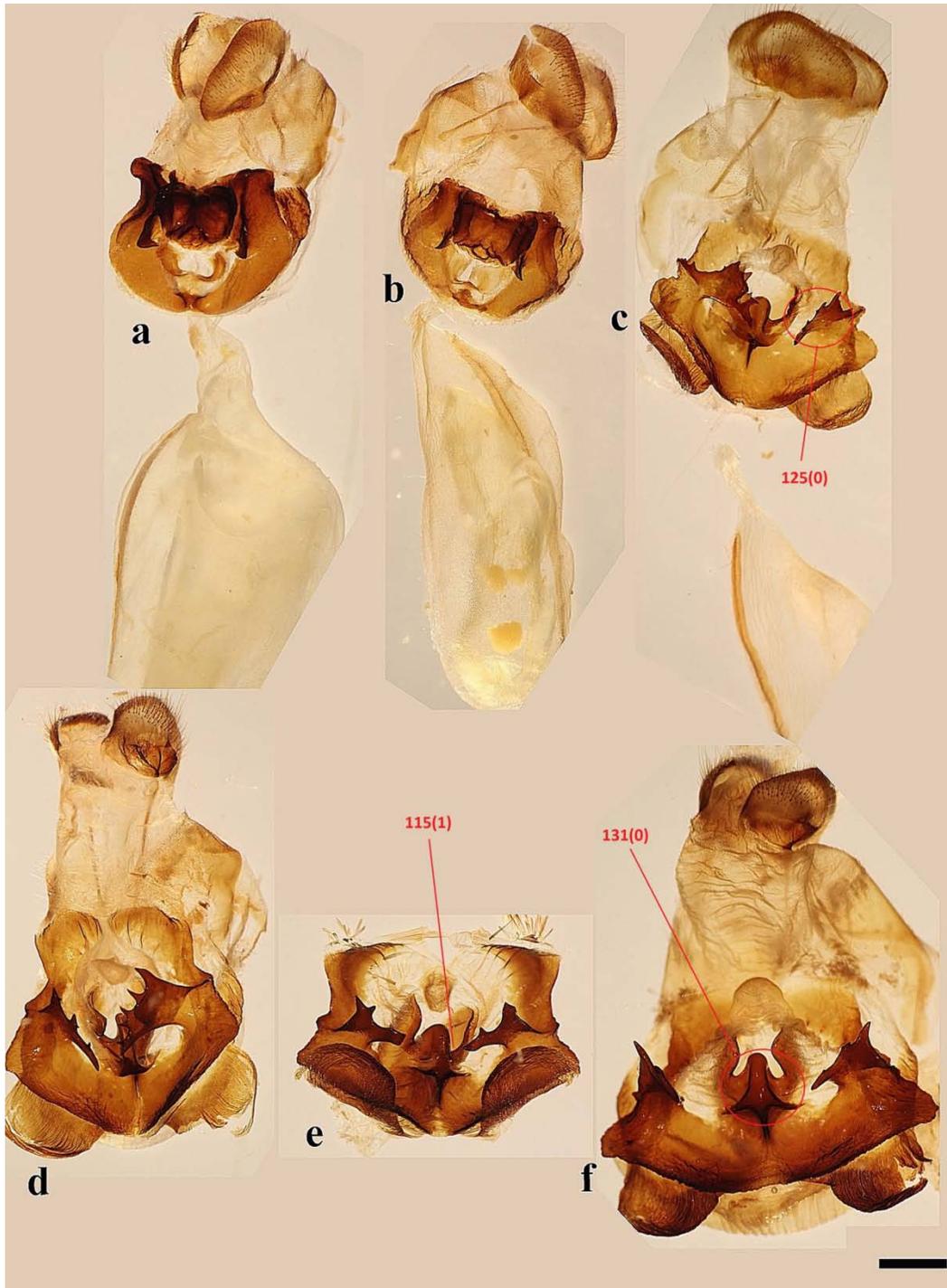


Figure 6-63. *Heraclides* female genitalia showing ostial armature: (a) *H. aristor*, (b) *H. caiguanabus*, (c) *H. thersites*, (d) *H. androgeus androgeus*, (e) *H. a. epidaurus*, (f) *H. a. laodocus*. Scale bar approximately 1 mm.

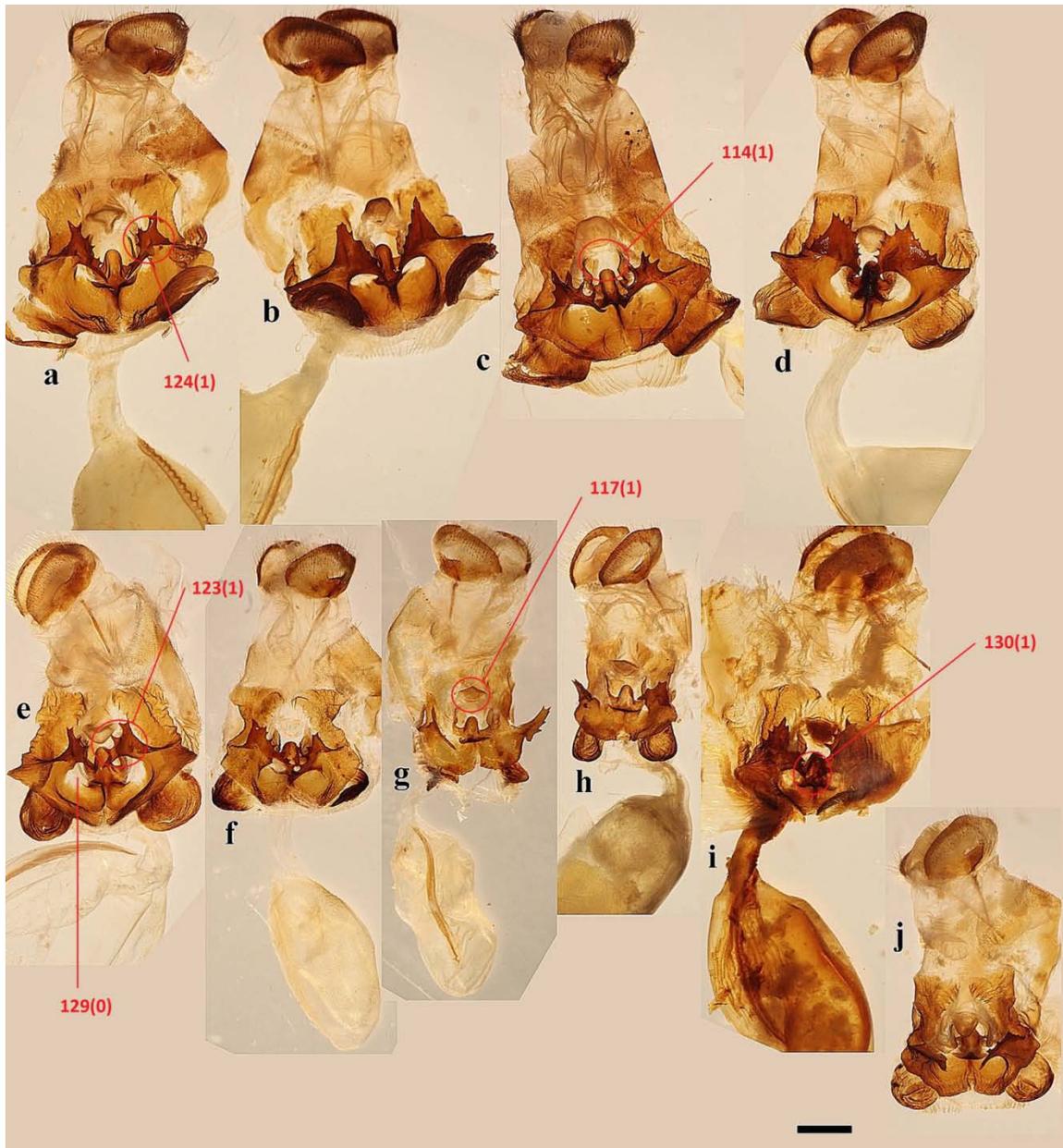


Figure 6-64. *Heraclides* female genitalia showing ostial armature: (a) *H. astyalus astyalus*, (b) *H. a. bajaensis*, (c) *H. a. hippomedon*, (d) *H. a. pallas*, (e) *H. ornythion*, (f) *H. aristodemus aristodemus*, (g) *H. a. bjordalae*, (h) *H. a. majasi*, (i) *H. a. ponceanus*, (j) *H. a. temenes*. Scale bar approximately 1 mm.

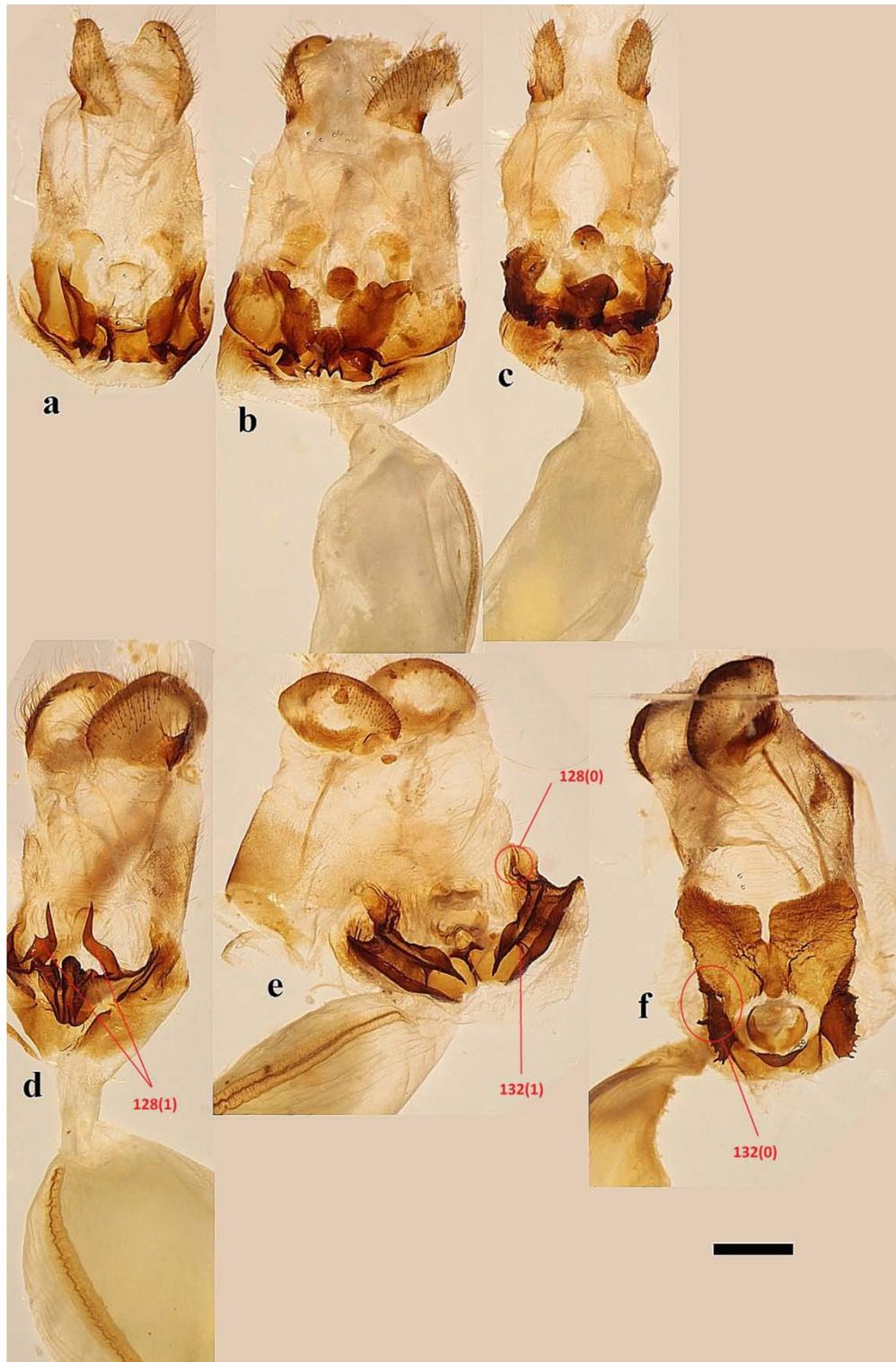


Figure 6-65. *Heraclides* female genitalia showing ostial armature: (a) *H. andraemon andraemon*, (b) *H. a. bonhotei*, (c) *H. a. tailori*, (d) *H. machaonides*, (e) *H. lamarchei*, (f) *H. hectorides*. Scale bar approximately 1 mm.

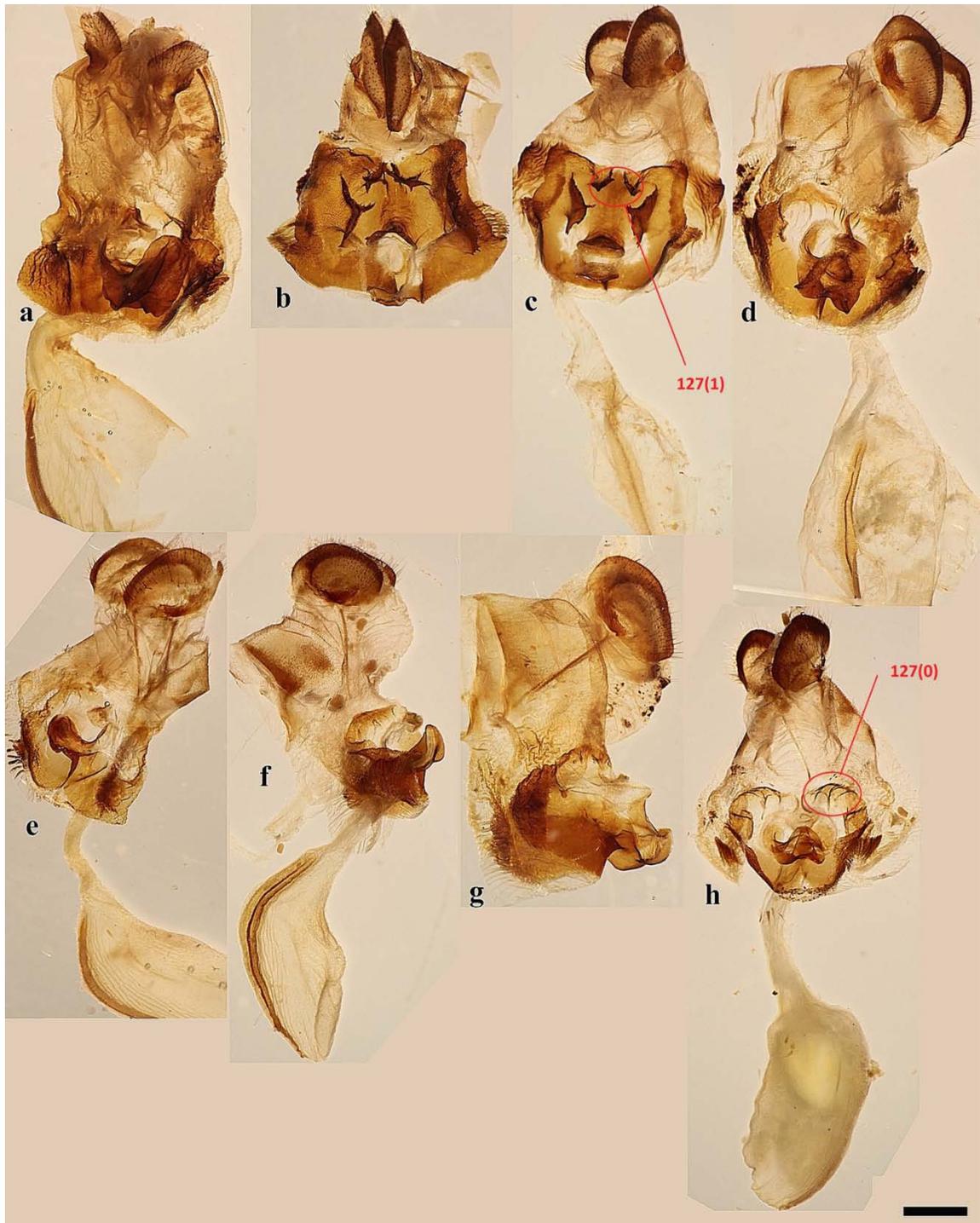


Figure 6-66. *Heraclides* female genitalia showing ostial armature: (a) *H. torquatus torquatus*, (b) *H. garleppi interruptus*, (c) *H. g. lecerfi*, (d) *H. t. torquatus*, (e) *H. t. atsukoeae*, (f) *H. t. leptalea*, (g) *H. t. polybius* (lateral view), (h) *H. t. tolmidis*. Scale bar approximately 1 mm.

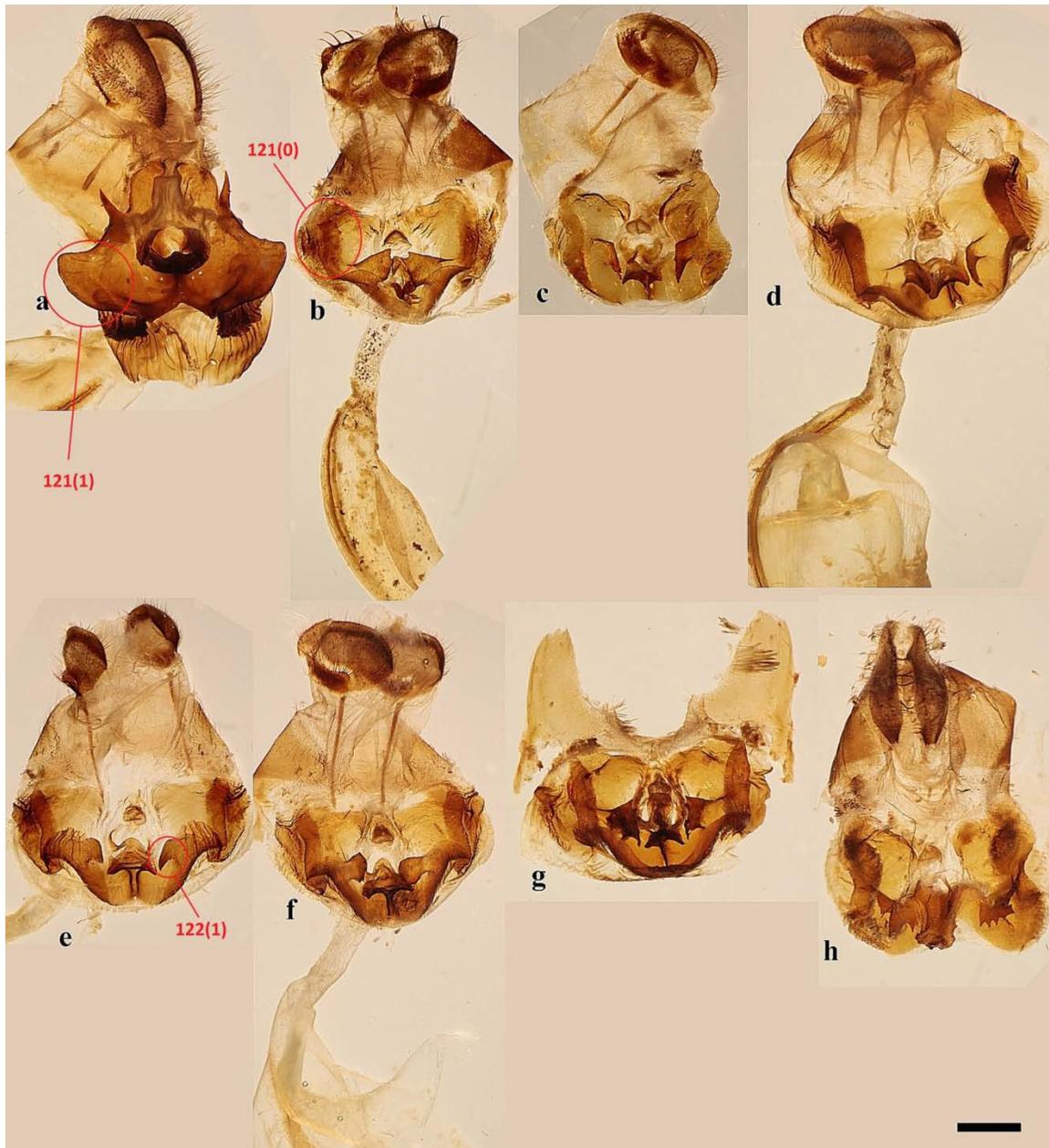


Figure 6-67. *Heraclides* female genitalia showing ostial armature: (a) *H. hyppason*, (b) *H. epenetus*, (c) *H. oxynius*, (d) *H. pelaus pelaus*, (e) *H. p. imerius*, (f) *H. p. puertoricensis*, (g) *H. rogeri rogeri*, (h) *H. r. pharnaces*. Scale bar approximately 1 mm.

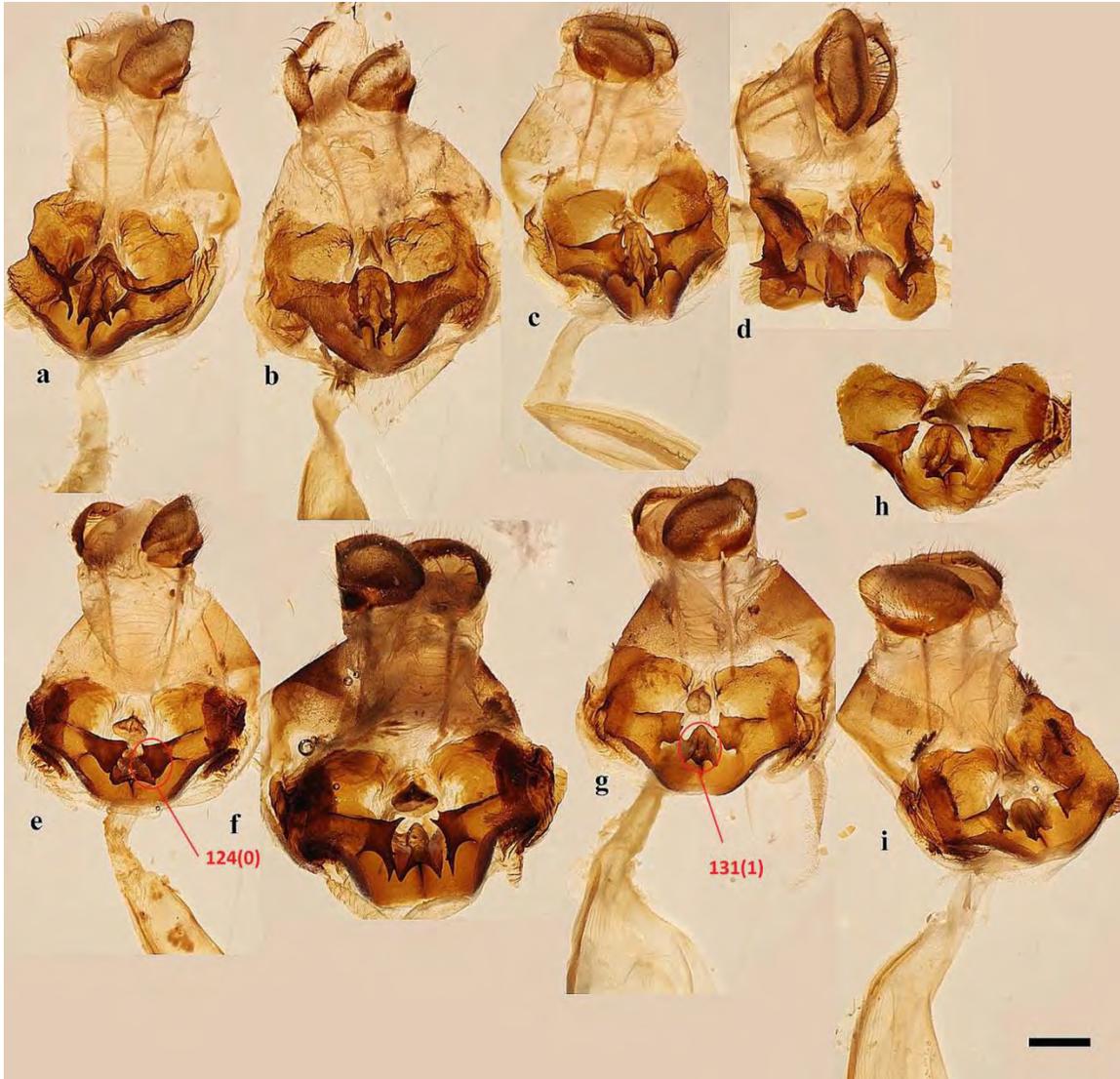


Figure 6-68. *Heraclides* female genitalia showing ostial armature: (a) *H. anchisiades anchisiades*, (b) *H. a. capys*, (c) *H. a. idaeus*, (d) *H. a. philastrius*, (e) *H. isidorus flavescens*, (f) *H. i. isidorus*, (g) *H. erostratus erostratus*, (h) *H. e. erostratus*, (i) *H. e. vazquezae*. Scale bar approximately 1 mm.

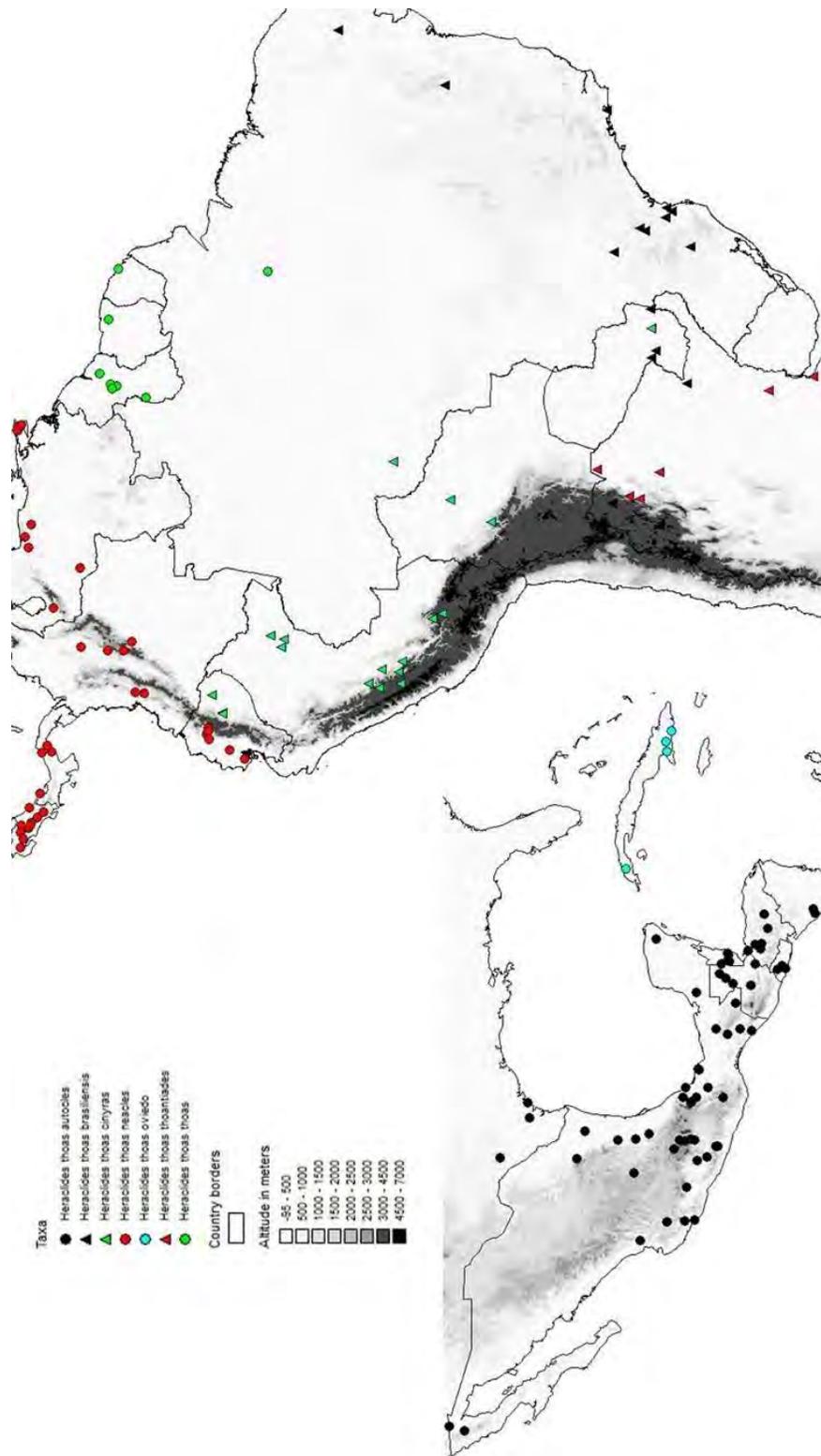


Figure 6-69. Distribution map for *Heraclides thoas*.

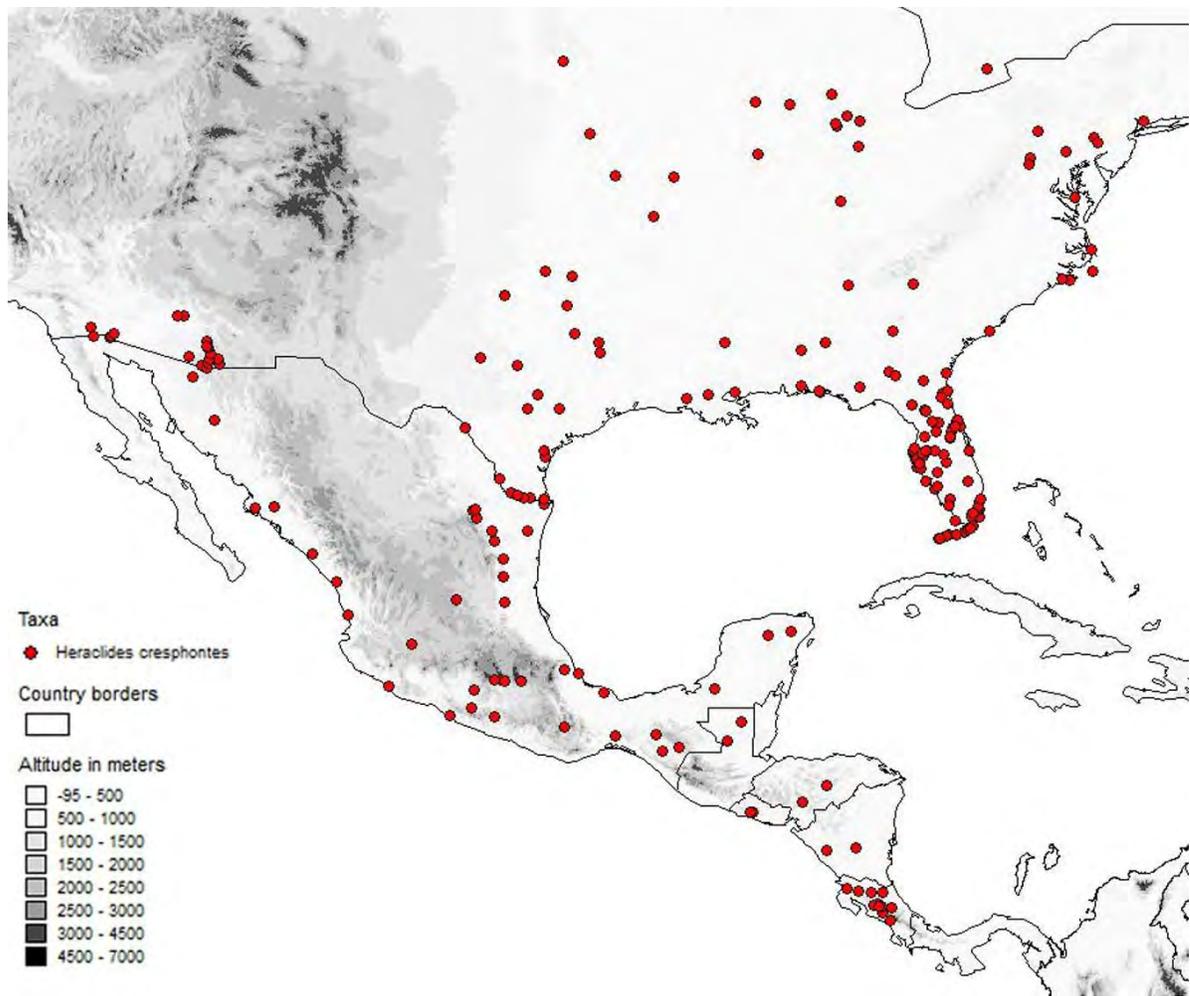


Figure 6-70. Distribution map for *Heraclides crespontes*.



Figure 6-71. Distribution map for *Heraclides homothoas* and *Heraclides melonius*.

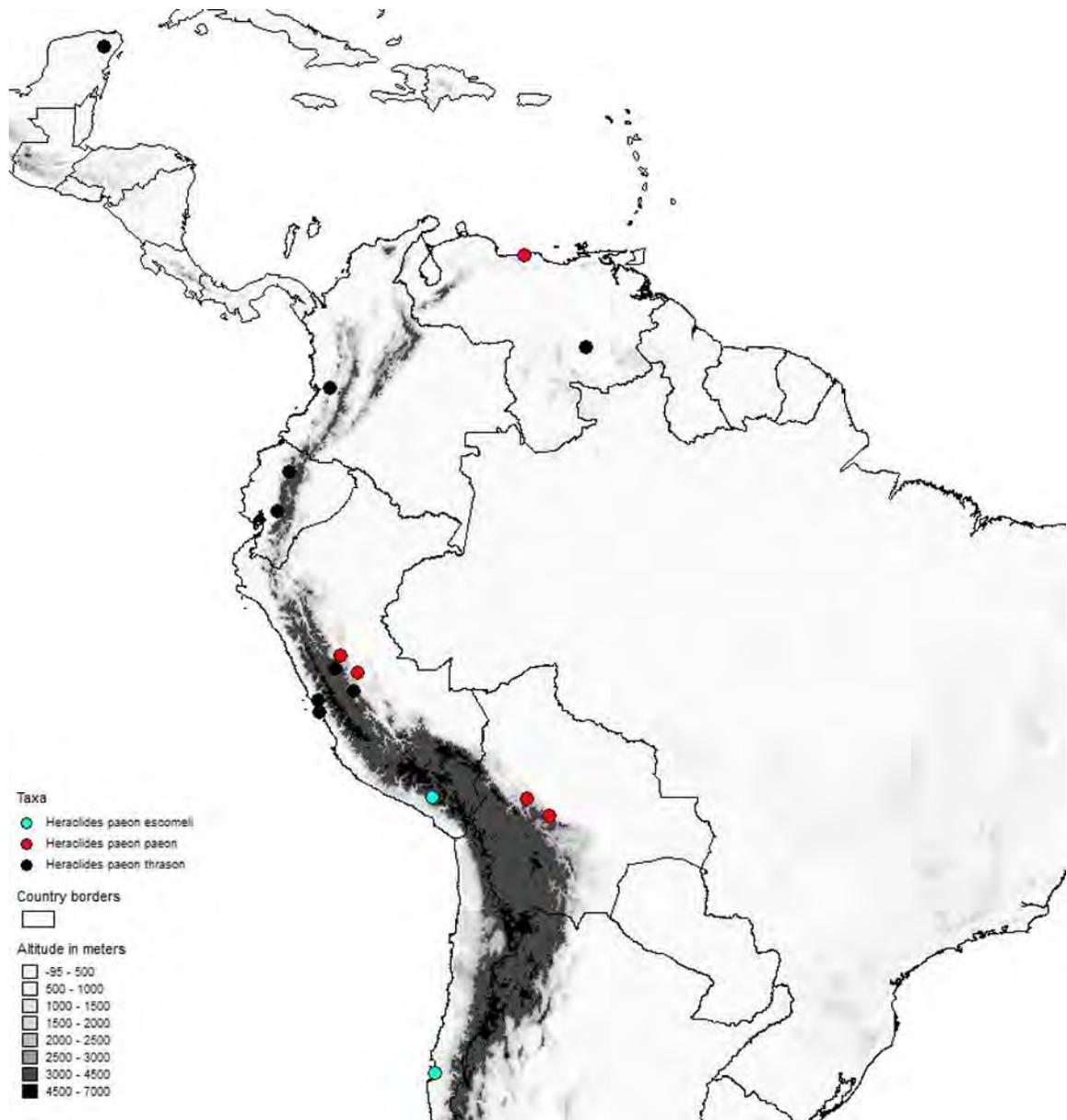


Figure 6-72. Distribution map for *Heraclides paeon*.



Figure 6-73. Distribution map for *Heraclides aristor*, *Heraclides caiguanabus*, and *Heraclides thersites*.



Figure 6-74. Distribution map for *Heraclides androgeus*.

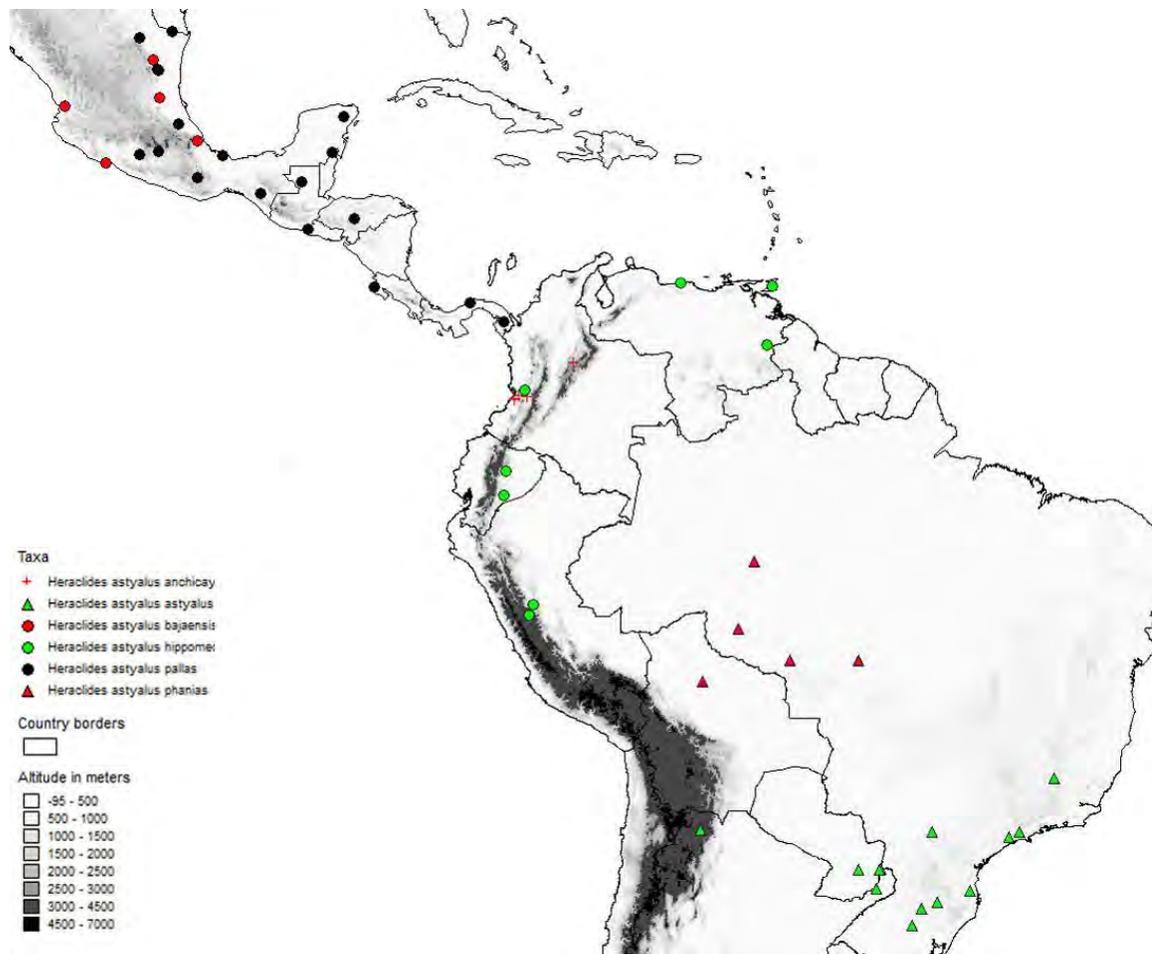


Figure 6-75. Distribution map for *Heraclides astyalus*.

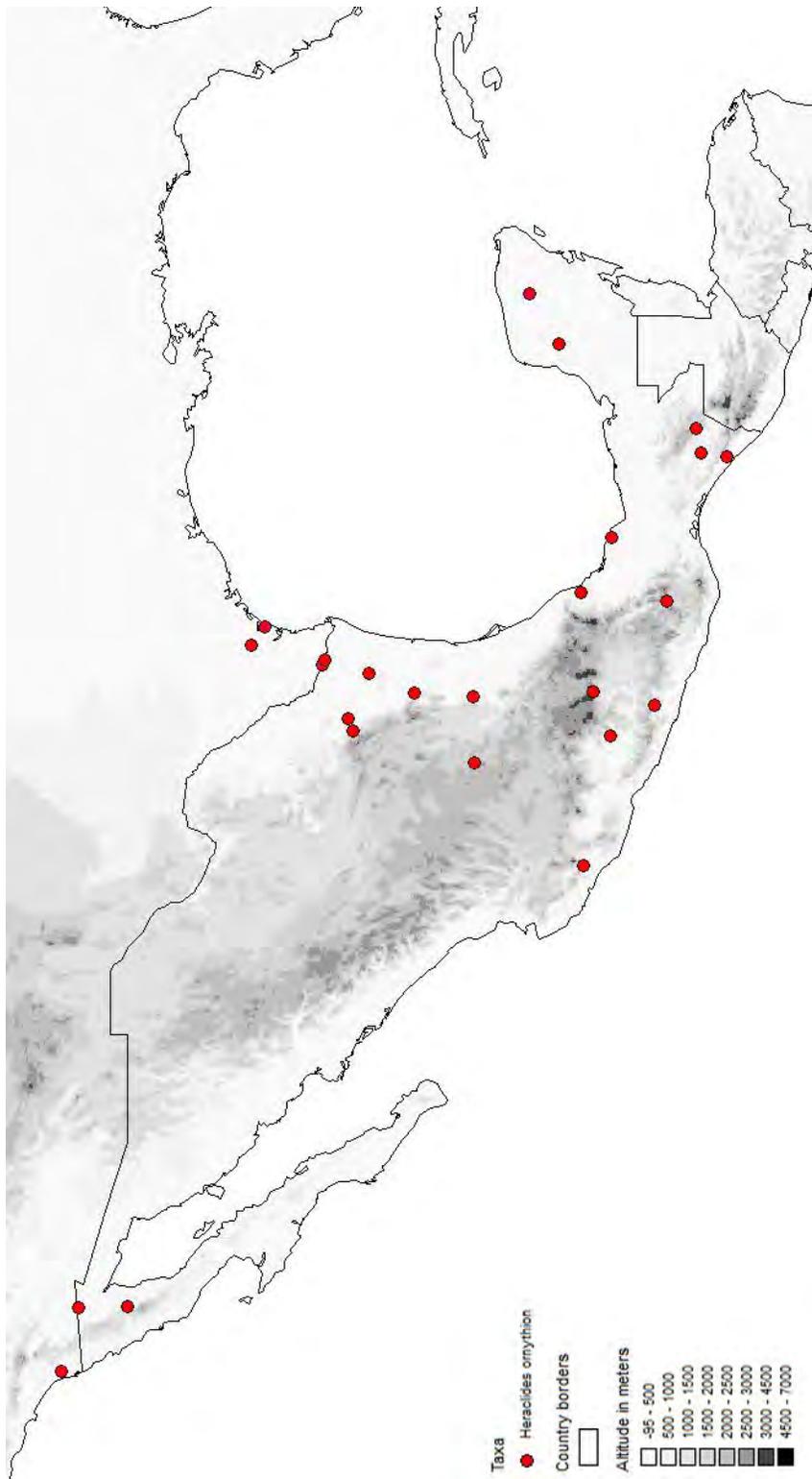


Figure 6-76. Distribution map for *Heraclides ornythion*.

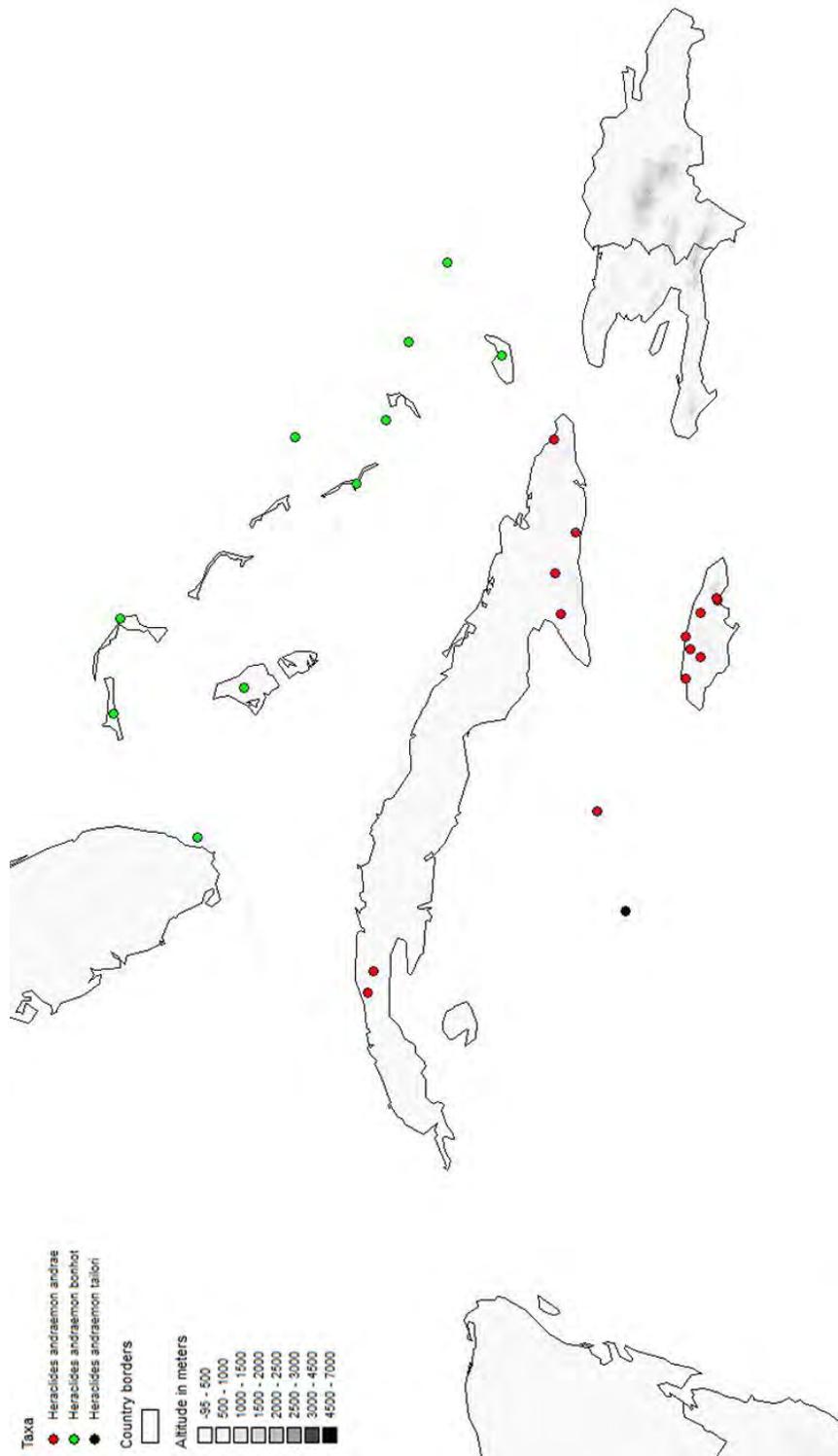


Figure 6-77. Distribution map for *Heraclides andraemon*.

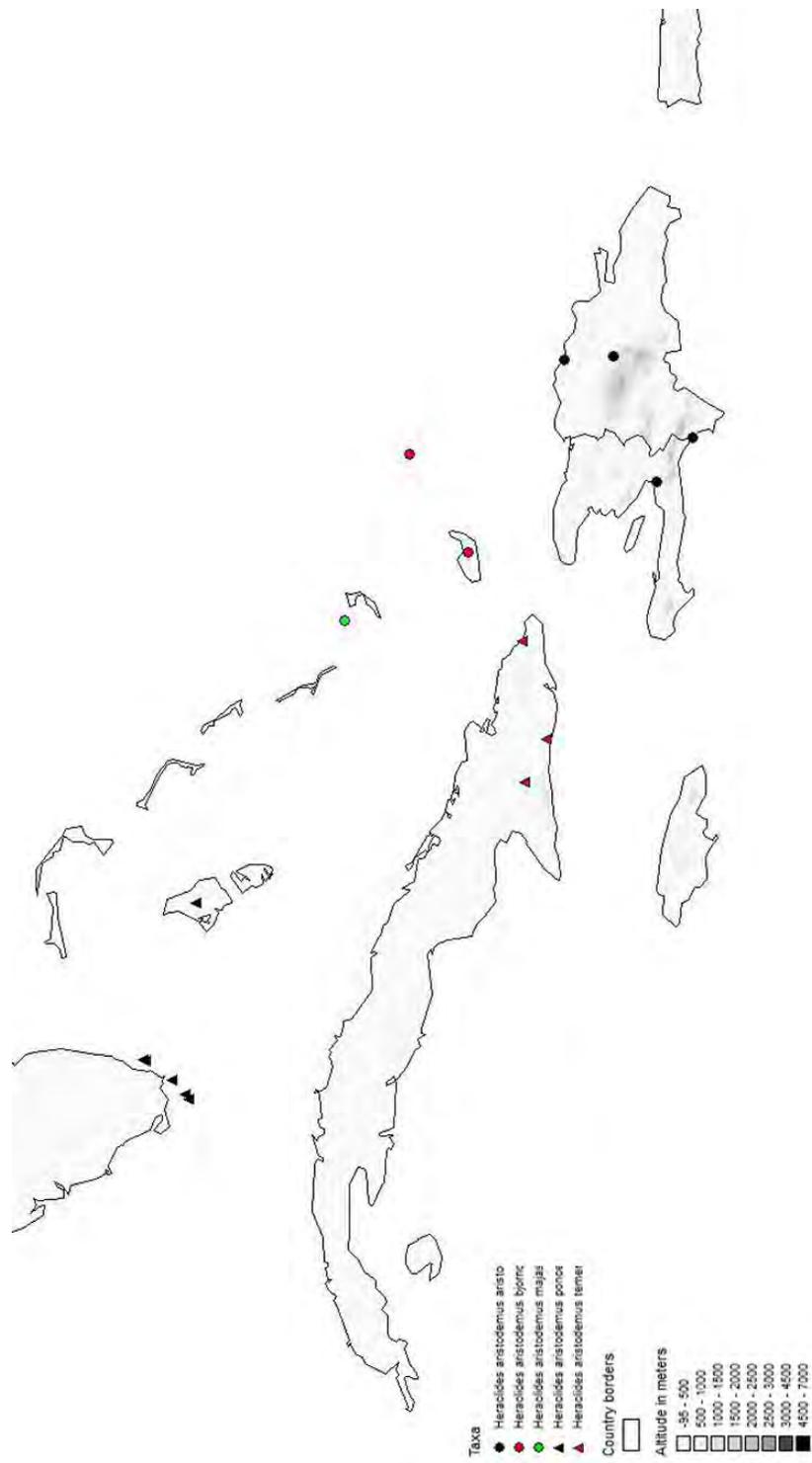


Figure 6-78. Distribution map for *Heraclides aristodemus*.

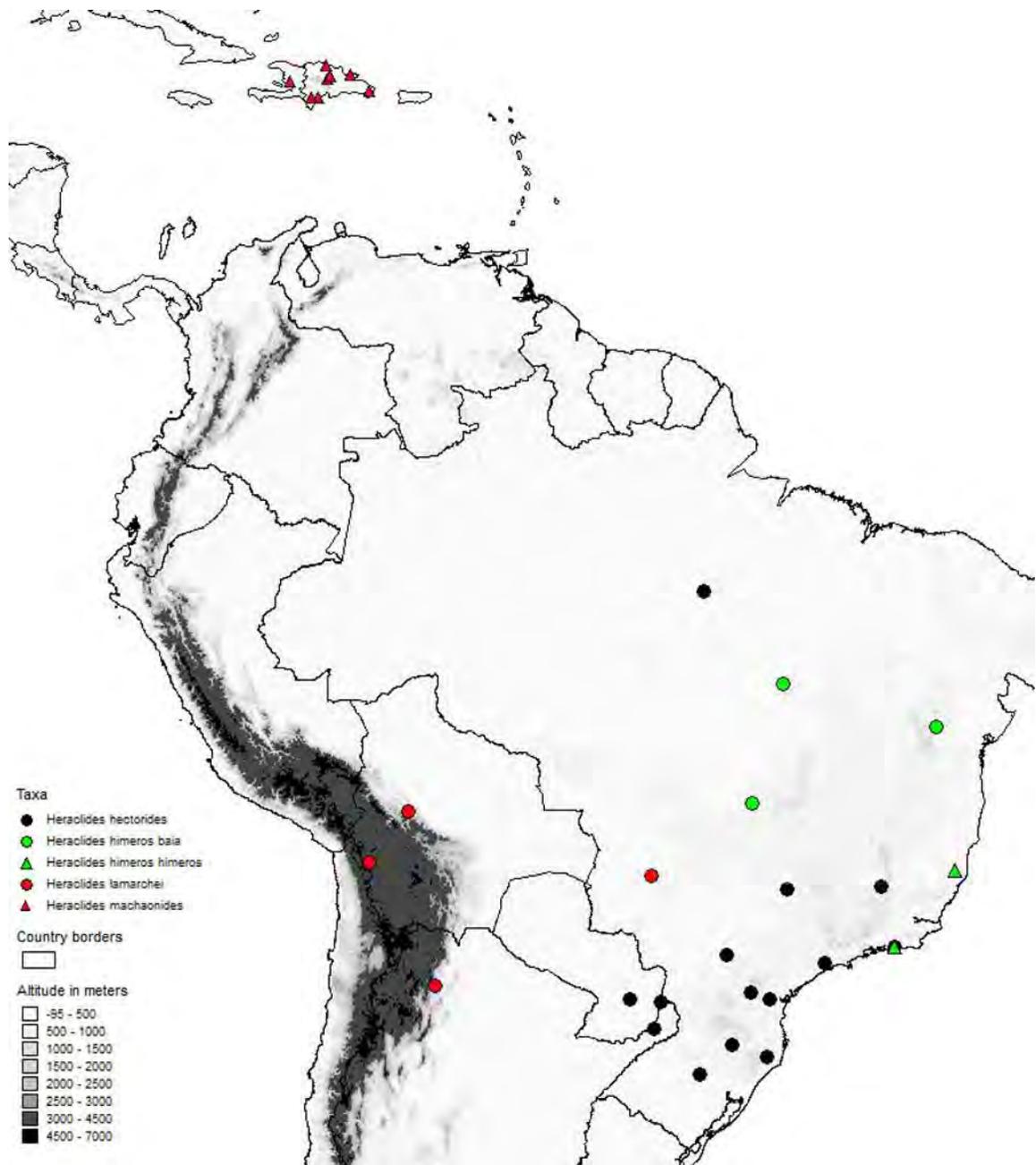


Figure 6-79. Distribution map for *Heraclides machaonides*, *Heraclides lamarchei*, *Heraclides himeros*, and *Heraclides hectorides*.

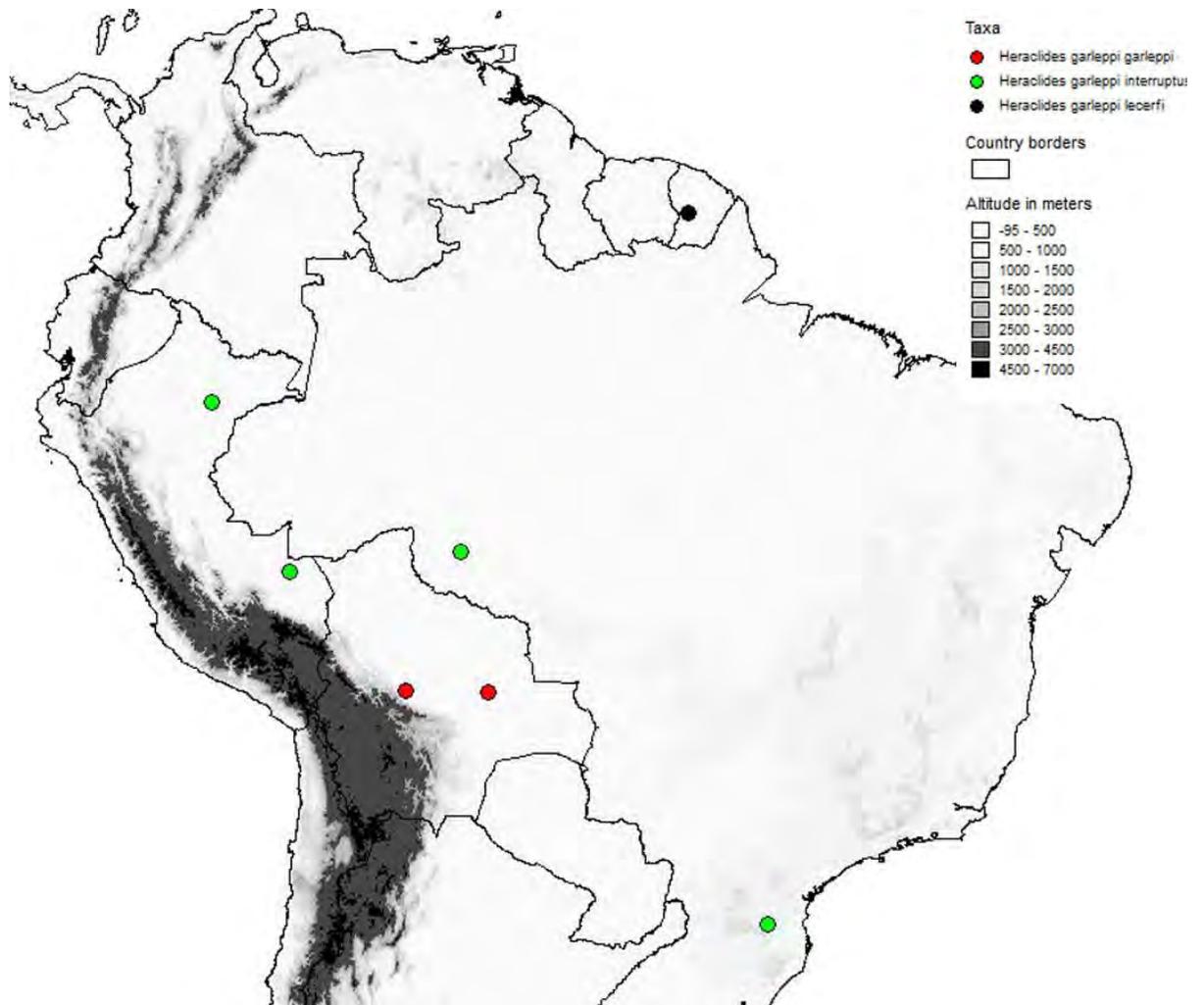


Figure 6-80. Distribution map for *Heraclides garleppi*.

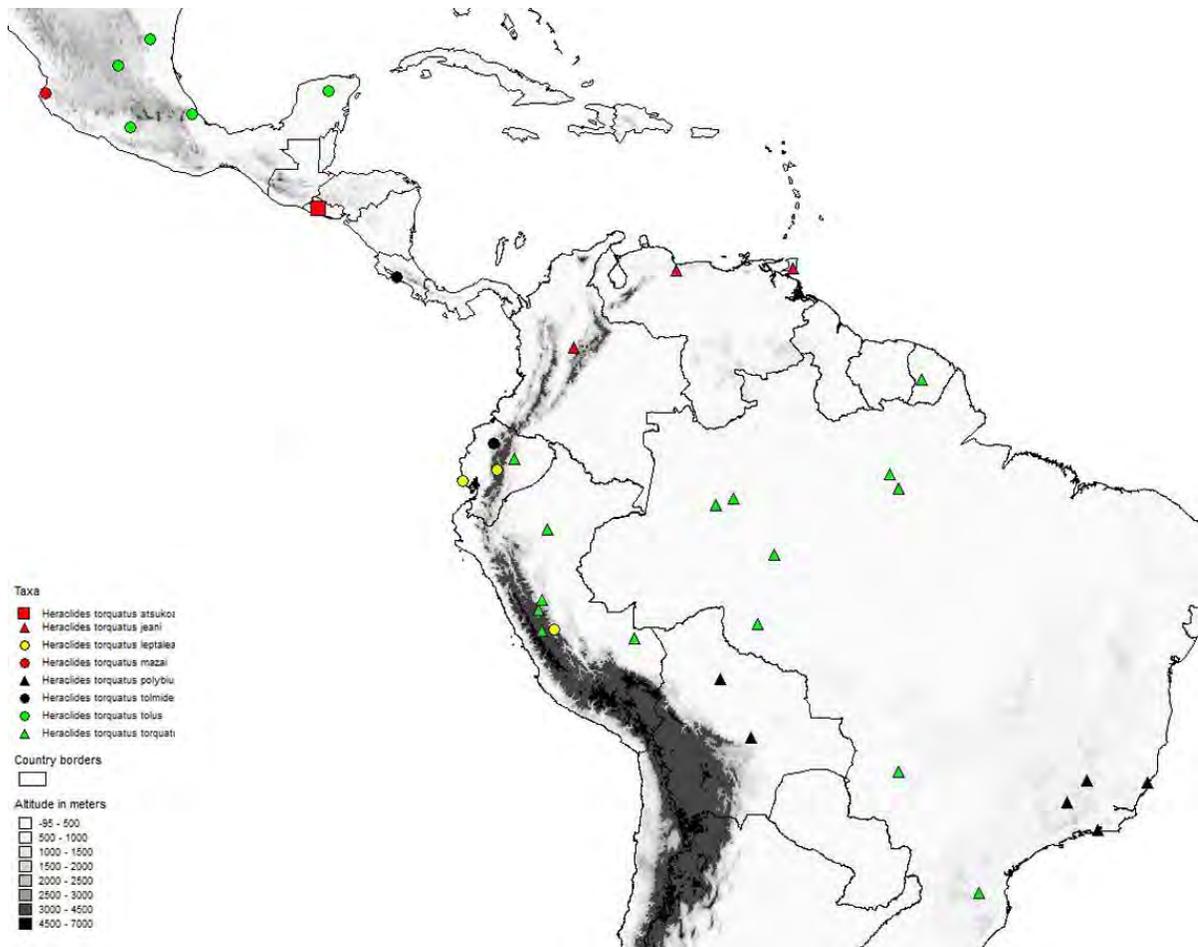


Figure 6-81. Distribution map for *Heraclides torquatus*.

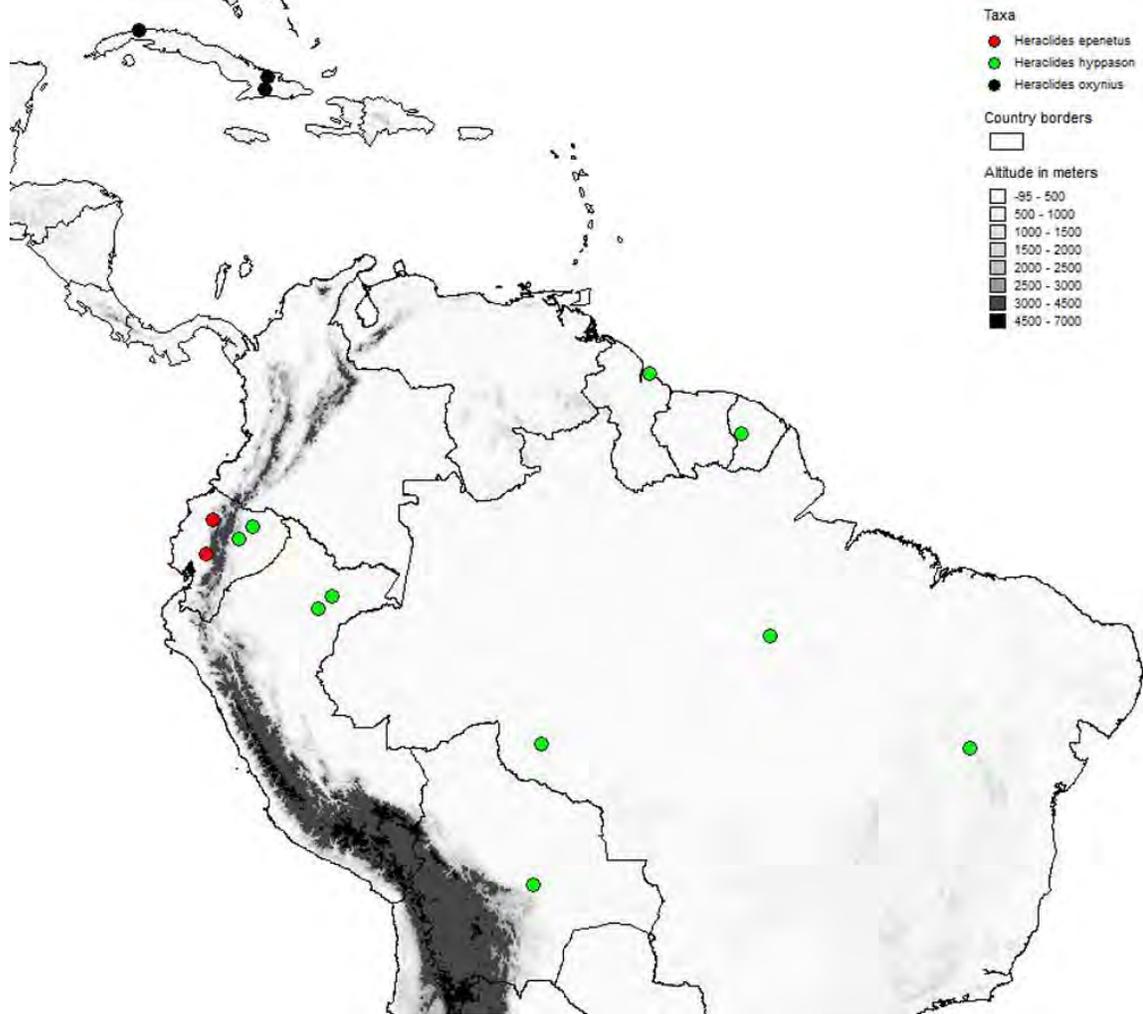


Figure 6-82. Distribution map for *Heraclides epenetus*, *Heraclides hypasson*, and *Heraclides oxynius*.

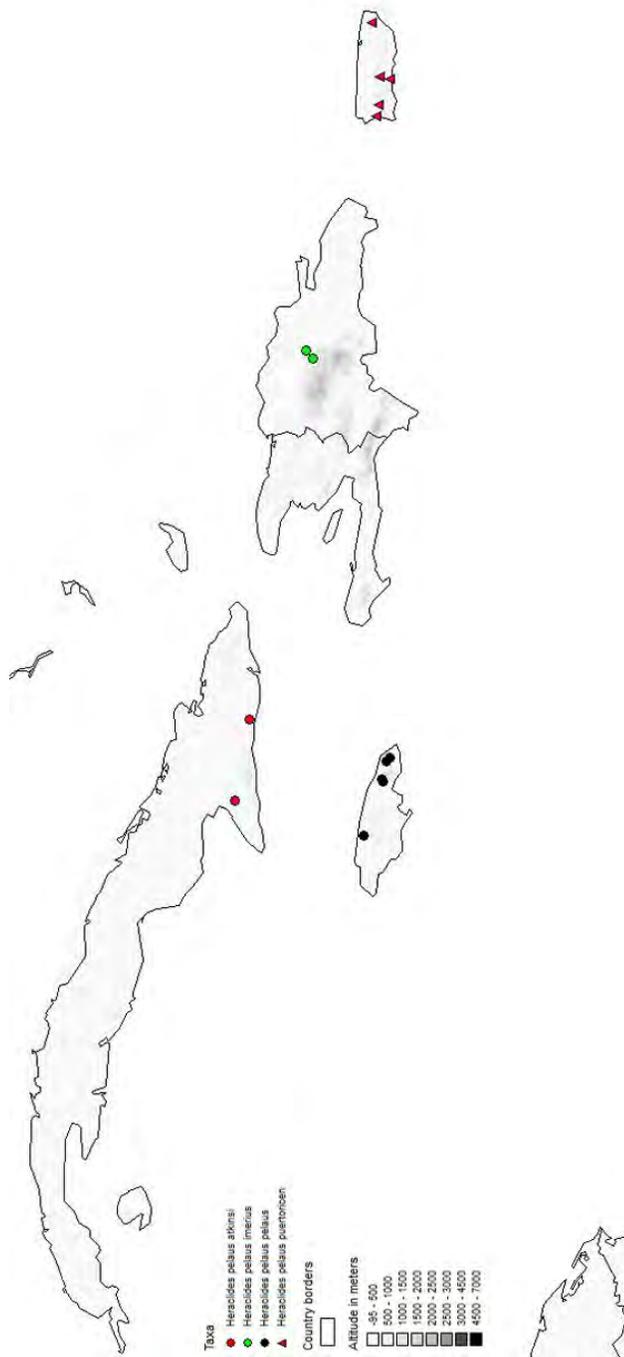


Figure 6-83. Distribution map for *Heraclides pelaus*.

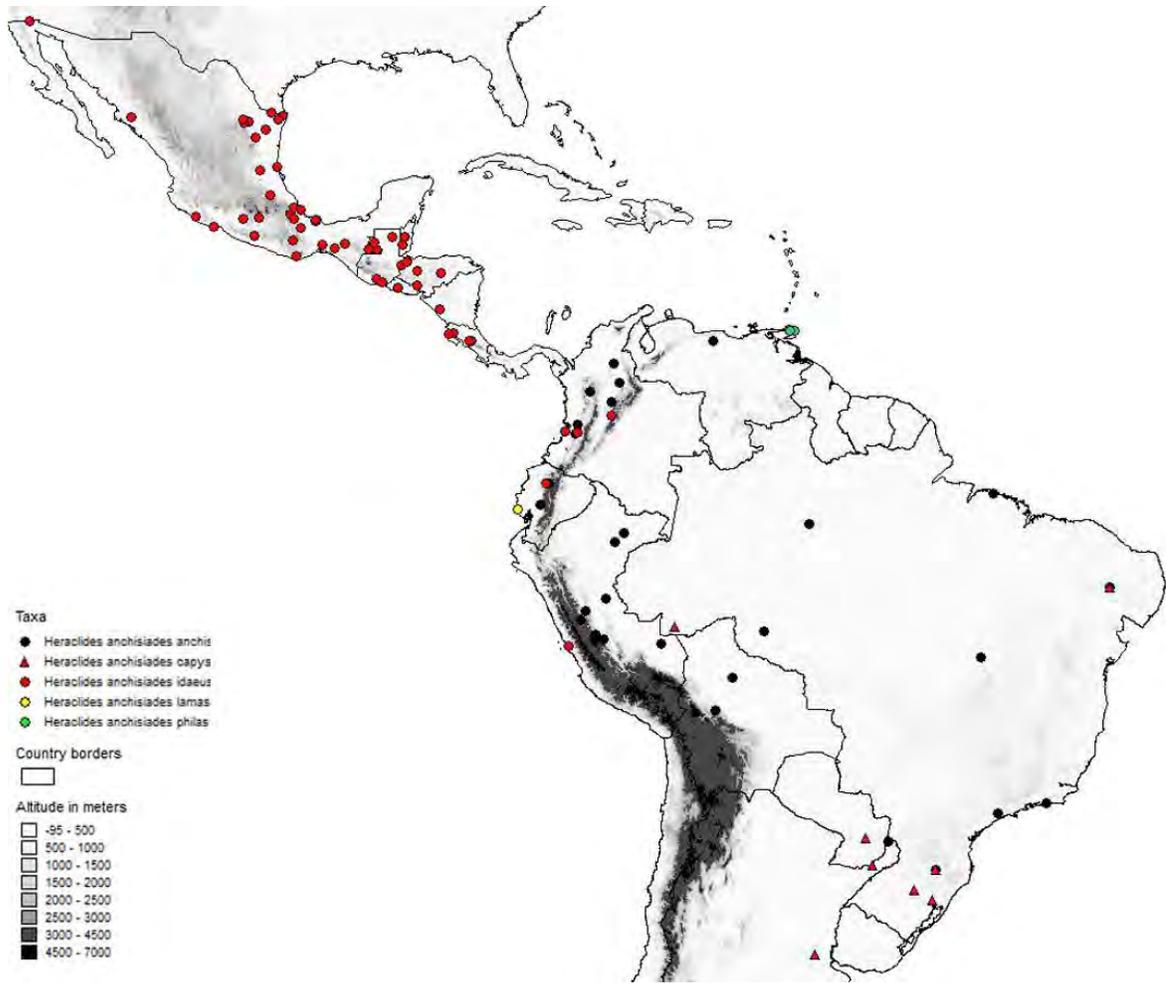


Figure 6-84. Distribution map for *Heraclides anchisiades*.

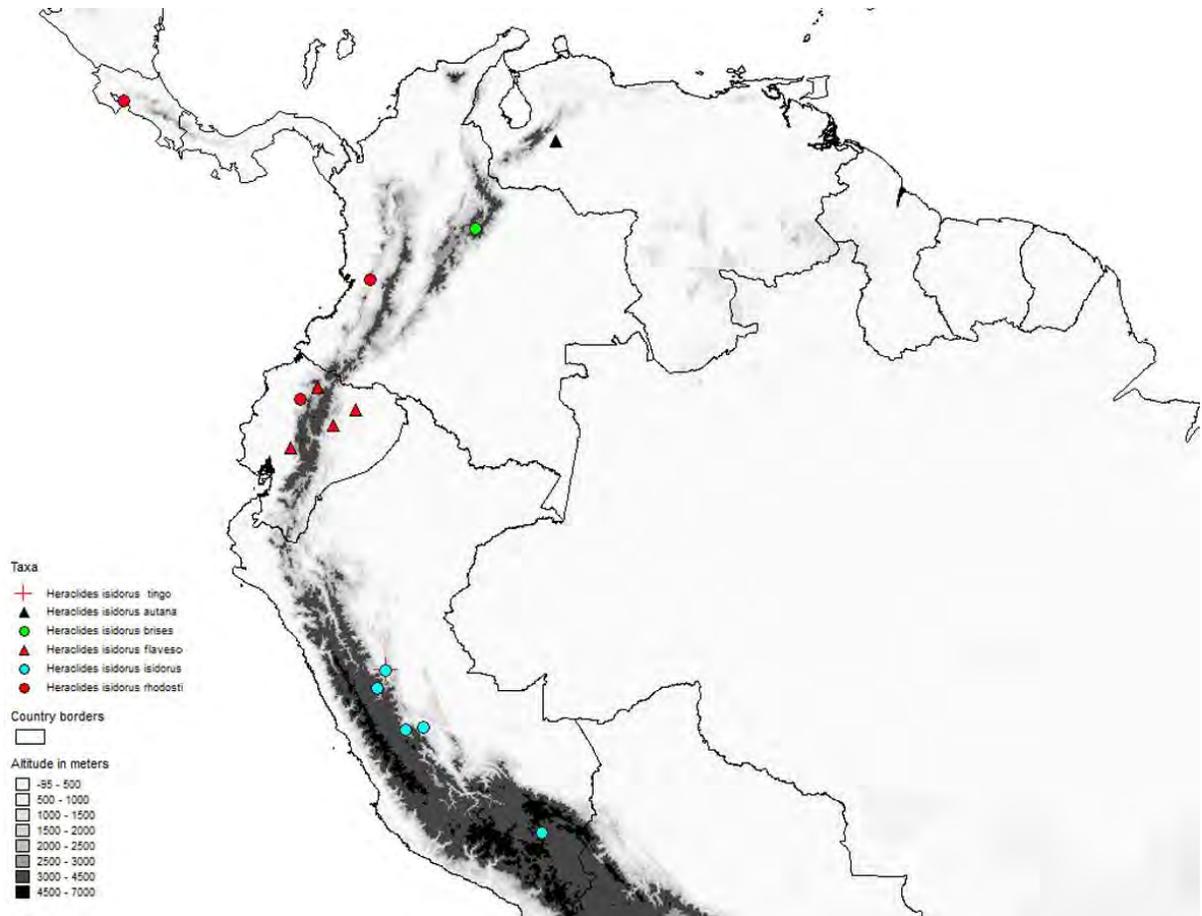


Figure 6-85. Distribution map for *Heraclides isidorus*.

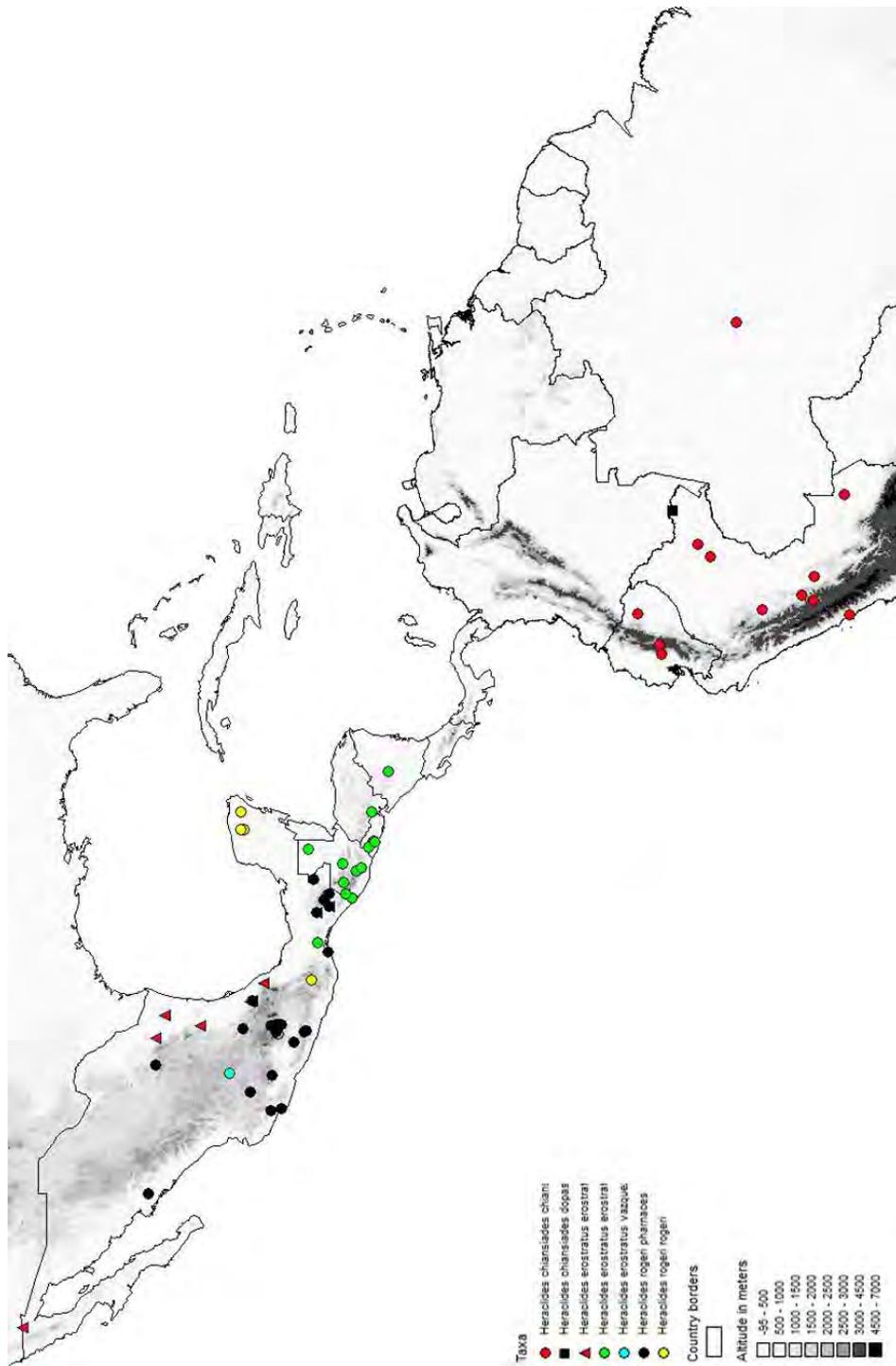


Figure 6-86. Distribution map for *Heraclides chiansiades*, *Heraclides rogeri*, and *Heraclides erostratus*.

APPENDIX

Gazetteer of material examined with associated collecting localities and corresponding latitude and longitude coordinates.

TAXON	COUNTRY	LOCALITY	LATITUDE	LONGITUDE
Heraclides anchisiades anchisiades	Bolivia	Beni	-14.0000005	-65.4999962
Heraclides anchisiades anchisiades	Bolivia	La Paz	-16.5000010	-68.1499977
Heraclides anchisiades anchisiades	Bolivia	Yungas, La Paz	-16.3333330	-66.7499962
Heraclides anchisiades anchisiades	Brazil	Iguazu Falls	-25.6833324	-54.4333324
Heraclides anchisiades anchisiades	Brazil	Manaus - Amazonas	-3.1133332	-60.0252762
Heraclides anchisiades anchisiades	Brazil	Paraiba	-7.6219297	-38.7150265
Heraclides anchisiades anchisiades	Brazil	Parana	-12.6101863	-47.8784179
Heraclides anchisiades anchisiades	Brazil	Rio de Janeiro	-22.9000006	-43.2333317
Heraclides anchisiades anchisiades	Brazil	Rondonia	-10.7634447	-63.2903806
Heraclides anchisiades anchisiades	Brazil	Santa Catarina	-27.6536022	-51.0562440
Heraclides anchisiades anchisiades	Brazil	Santarem - Para	-0.9500003	-46.9833317
Heraclides anchisiades anchisiades	Brazil	Sao Paulo - SP	-23.6606177	-46.6146435
Heraclides anchisiades anchisiades	Colombia	Bolívar	8.3338004	-73.9709472
Heraclides anchisiades anchisiades	Colombia	Calima, Valle del Cauca	3.9341667	-76.4883308
Heraclides anchisiades anchisiades	Colombia	Medellin	6.2761504	-75.6176490
Heraclides anchisiades anchisiades	Colombia	Muzo, Boyaca	5.5352774	-74.1077766
Heraclides anchisiades anchisiades	Colombia	Pance, Cali	3.3283336	-76.6386185
Heraclides anchisiades anchisiades	Colombia	Santander	6.9131274	-73.5339431
Heraclides anchisiades anchisiades	Ecuador	Quito (Villavicencio Ponce)	-0.2396385	-78.5213470
Heraclides anchisiades anchisiades	Ecuador	Balsa Pamba	-1.7666663	-79.1833305
Heraclides anchisiades anchisiades	Ecuador	Quito (Tinalandia)	-0.2167000	-78.5000000
Heraclides anchisiades anchisiades	Peru	Huanuco	-9.9166670	-76.2333336
Heraclides anchisiades anchisiades	Peru	Iquitos (Explorama Lodge)	-3.7480557	-73.2472229
Heraclides anchisiades anchisiades	Peru	Junin	-11.3346391	-75.3002929
Heraclides anchisiades anchisiades	Peru	La Merced (Chanchamayo)	-11.0500011	-75.3166695
Heraclides anchisiades anchisiades	Peru	Loreto	-4.3692612	-73.8805540
Heraclides anchisiades anchisiades	Peru	Madre de Dios	-11.6208192	-70.5285721
Heraclides anchisiades anchisiades	Peru	Perene	-10.9666672	-75.2166634
Heraclides anchisiades anchisiades	Peru	Pucallpa	-8.3825006	-74.5380592
Heraclides anchisiades anchisiades	Peru	Satipo	-11.2666659	-74.6833305
Heraclides anchisiades anchisiades	Peru	Tingo Maria	-9.3000002	-75.9833298
Heraclides anchisiades anchisiades	Venezuela	Aragua	9.8758490	-66.9012451
Heraclides anchisiades capys	Argentina	San Pedro, Buenos Aires Province	-33.6900670	-59.6763610
Heraclides anchisiades capys	Argentina	Santa Ana, Misiones	-27.3699379	-55.5928802

Heraclides anchisiades capys	Brazil	Guanabara - AC	-10.4000006	-69.5833282
Heraclides anchisiades capys	Brazil	Nova Santa Rita	-29.8471622	-51.2766055
Heraclides anchisiades capys	Brazil	Paraiba	-7.6319297	-38.7150265
Heraclides anchisiades capys	Brazil	Rio Grande do Sul	-29.0753751	-52.6245117
Heraclides anchisiades capys	Brazil	Santa Catarina	-27.6636022	-51.0562440
Heraclides anchisiades capys	Paraguay	Caaguazú	-25.4499998	-56.0166683
Heraclides anchisiades idaeus	Belize	British Honduras	17.2499990	-88.7499962
Heraclides anchisiades idaeus	Belize	Chiquibul	16.7006556	-88.9260864
Heraclides anchisiades idaeus	Colombia	Bogota	4.6101977	-74.0819907
Heraclides anchisiades idaeus	Colombia	Buenaventura	3.4808972	-77.3592915
Heraclides anchisiades idaeus	Colombia	Cali, Pance Valle	3.4343724	-76.5191727
Heraclides anchisiades idaeus	Costa Rica	Desamparados	9.8999996	-84.0666695
Heraclides anchisiades idaeus	Costa Rica	Guanacaste	10.4723953	-85.3607331
Heraclides anchisiades idaeus	Costa Rica	Santa Ana, Guanacaste	10.3833342	-85.6333351
Heraclides anchisiades idaeus	Costa Rica	Villa Colon	9.9166670	-84.2499962
Heraclides anchisiades idaeus	Ecuador	Pichincha	-0.1937742	-78.7309531
Heraclides anchisiades idaeus	El Salvador	Cerro Chato	13.8490901	-87.8666649
Heraclides anchisiades idaeus	El Salvador	Santa Tecla	13.6833296	-89.2833328
Heraclides anchisiades idaeus	Guatemala	Escuintla	14.3050003	-90.7849998
Heraclides anchisiades idaeus	Guatemala	Guacamayo (near Honduras)	15.2999997	-89.0666695
Heraclides anchisiades idaeus	Guatemala	Guazacapán	14.0741668	-90.4166718
Heraclides anchisiades idaeus	Guatemala	Tenedores	15.5499997	-88.6333351
Heraclides anchisiades idaeus	Guatemala	Tikal National Park	17.2500000	-89.6500015
Heraclides anchisiades idaeus	Honduras	Lake Yojoa	14.8701372	-87.9428100
Heraclides anchisiades idaeus	Honduras	Spanish Honduras	14.7473973	-86.2530975
Heraclides anchisiades idaeus	Mexico	Acahuzotla	17.3605556	-99.4672241
Heraclides anchisiades idaeus	Mexico	Bonampak	16.7333345	-91.0833282
Heraclides anchisiades idaeus	Mexico	Candelaria Loxicha, Oaxaca	15.9000006	-96.5166702
Heraclides anchisiades idaeus	Mexico	Caracas, Córdoba, Veracruz-Llave	18.8833351	-96.9333305
Heraclides anchisiades idaeus	Mexico	Catarina, Chiapas	16.4719748	-93.7346649
Heraclides anchisiades idaeus	Mexico	Catemaco, Veracruz-Llave	18.4216796	-95.1112067
Heraclides anchisiades idaeus	Mexico	Chiltepec, Oaxaca	17.9499998	-96.1833305
Heraclides anchisiades idaeus	Mexico	Chimalapa, Oaxaca	16.7166662	-94.6833305
Heraclides anchisiades idaeus	Mexico	Coahuayana, Michoacan	18.6999998	-103.6583366
Heraclides anchisiades idaeus	Mexico	Cola de Caballo (Horse Tail Falls), Nuevo Leon	25.3603401	-100.1619644
Heraclides anchisiades idaeus	Mexico	Dos Amates, Veracruz	18.4891663	-95.0597229
Heraclides anchisiades idaeus	Mexico	El Salto falls, Rio Valles (Ciudad Valles), San Luis Potosí	22.0210446	-99.0501594

Heraclides anchisiades idaeus	Mexico	El Vigía (Cerro Vigía), Veracruz	18.5166664	-95.1333351
Heraclides anchisiades idaeus	Mexico	Metepec, Hidalgo	20.2499990	-98.3166695
Heraclides anchisiades idaeus	Mexico	Mexicali	32.6312311	-115.4333305
Heraclides anchisiades idaeus	Mexico	Moctezuma, Valle Hermoso, Tamaulipas	25.6613334	-97.8002929
Heraclides anchisiades idaeus	Mexico	Morelos	18.6808862	-99.1015720
Heraclides anchisiades idaeus	Mexico	Nuevo Leon	25.4736603	-99.8371470
Heraclides anchisiades idaeus	Mexico	Oaxaca	17.0500002	-96.7166634
Heraclides anchisiades idaeus	Mexico	Playa Azul	18.0045389	-102.3440731
Heraclides anchisiades idaeus	Mexico	Presidio, Veracruz-Llave	19.3333330	-96.6666718
Heraclides anchisiades idaeus	Mexico	Raices	24.3761110	-99.4069481
Heraclides anchisiades idaeus	Mexico	Rio Lacanja	16.4000006	-90.7666702
Heraclides anchisiades idaeus	Mexico	San Francisco	18.5333338	-100.2666664
Heraclides anchisiades idaeus	Mexico	San Quintin, Chiapas	16.3833351	-91.3333282
Heraclides anchisiades idaeus	Mexico	Santa Rosa (Loma Larga, Tuxtla Gutiérrez, Cs, Mexico near Comitán)	16.7685492	-93.0677604
Heraclides anchisiades idaeus	Mexico	Santiago, Nuevo Leon	25.4166670	-100.1499977
Heraclides anchisiades idaeus	Mexico	Sarabia	25.6528230	-100.2294731
Heraclides anchisiades idaeus	Mexico	Sinaloa de Leyva	25.8249493	-108.2220917
Heraclides anchisiades idaeus	Mexico	Tampico, Veracruz	22.3000002	-97.8544704
Heraclides anchisiades idaeus	Mexico	Tamulipas	24.9325753	-98.6352230
Heraclides anchisiades idaeus	Mexico	Tezonapa, Oaxaca	18.6002086	-96.6855239
Heraclides anchisiades idaeus	Mexico	Veracruz, Veracruz-Llave	19.1726531	-96.1332893
Heraclides anchisiades idaeus	Mexico	Yaxchilan, Chiapas	16.8851304	-90.9654961
Heraclides anchisiades idaeus	Nicaragua	Managua	12.1499996	-86.2722168
Heraclides anchisiades idaeus	Peru	Santa Rosa, Lima	-11.8037887	-77.1664121
Heraclides anchisiades idaeus	USA	Brownsville, Texas	25.9091729	-97.4945952
Heraclides anchisiades idaeus	USA	Hidalgo, Texas	26.1090531	-98.2624103
Heraclides anchisiades lamasi	Ecuador	Palmar	-2.0234668	-80.7340621
Heraclides anchisiades philastrius	Trinidad & Tobago	Sangre Grande	10.5978456	-61.1272430
Heraclides anchisiades philastrius	Trinidad & Tobago	St Ann's	10.6757904	-61.5186309
Heraclides anchisiades philastrius	Trinidad & Tobago	Tunapuna, Saint George	10.6337837	-61.3831472
Heraclides andraemon andraemon	Cayman	Cayman Brac	19.7166662	-79.8166695
Heraclides andraemon andraemon	Cuba	Baracoa	20.3425182	-74.4968228
Heraclides andraemon andraemon	Cuba	Granma	20.2480250	-77.0004272
Heraclides andraemon andraemon	Cuba	Loma del Gato	20.3166676	-76.4166718
Heraclides andraemon andraemon	Cuba	Rente	22.9166670	-82.1166649
Heraclides andraemon andraemon	Cuba	Santiago de Cuba	20.0247221	-75.8219452

Heraclides andraemon andraemon	Cuba	Wajay	23.0033331	-82.4227791
Heraclides andraemon andraemon	Jamaica	Cross Roads	17.9938357	-76.7879962
Heraclides andraemon andraemon	Jamaica	Kingston	17.9999990	-76.7999992
Heraclides andraemon andraemon	Jamaica	Montego Bay	18.4640274	-77.9284744
Heraclides andraemon andraemon	Jamaica	Runaway Bay	18.4594194	-77.3270988
Heraclides andraemon andraemon	Jamaica	Springfield, St Catherine	18.2511981	-76.9726181
Heraclides andraemon andraemon	Jamaica	St Andrew	18.0175893	-76.7618179
Heraclides andraemon andraemon	Jamaica	Trelawny	18.3838501	-77.4954986
Heraclides andraemon andraemon	Jamaica	Troy, Trelawny	18.2499990	-77.6166649
Heraclides andraemon bonhotei	Bahamas	Crooked Island	22.7476076	-74.2180837
Heraclides andraemon bonhotei	Bahamas	Grand Bahama	26.6333351	-78.4166718
Heraclides andraemon bonhotei	Bahamas	Great Inagua	21.0823848	-73.2999992
Heraclides andraemon bonhotei	Bahamas	Long Island	23.1600898	-75.1341247
Heraclides andraemon bonhotei	Bahamas	Marsh Harbour, Central Abaco	26.5400086	-77.0653152
Heraclides andraemon bonhotei	Bahamas	Mayaguana	22.4126154	-73.1050872
Heraclides andraemon bonhotei	Bahamas	North Andros	24.7667845	-78.0523681
Heraclides andraemon bonhotei	Bahamas	San Salvador Island	24.0333338	-74.4666634
Heraclides andraemon bonhotei	Turks & Caicos	North Caicos	21.8723318	-71.9563293
Heraclides andraemon bonhotei	USA	Elliott Key, Florida	25.4431667	-80.1972694
Heraclides andraemon tailori	Cayman	Grand Cayman	19.3143833	-81.2493896
Heraclides androgeus androgeus	Bolivia	Coroico	-16.1833324	-67.7333336
Heraclides androgeus androgeus	Bolivia	Yungas, La Paz	-16.3333330	-66.7499962
Heraclides androgeus androgeus	Brazil	Manaus - Amazonas	-3.1133332	-60.0252762
Heraclides androgeus androgeus	Brazil	Obidos	-1.9083333	-55.5188885
Heraclides androgeus androgeus	Brazil	Rondonia	-10.7634447	-63.2903806
Heraclides androgeus androgeus	Brazil	Saint Luis, Maranhao	-2.5316960	-44.3001365
Heraclides androgeus androgeus	Ecuador	Misahualli, Napo	-1.0333333	-77.6666718
Heraclides androgeus androgeus	Ecuador	Yasuni National Park	-0.8898568	-76.1599731
Heraclides androgeus androgeus	Ecuador	Quito (Tinalandia)	-0.2167000	-78.5000000
Heraclides androgeus androgeus	Peru	Ayacucho	-13.1506149	-74.2081832
Heraclides androgeus androgeus	Peru	Chuchurras, Pasco	-10.0892058	-75.1835632
Heraclides androgeus androgeus	Peru	Huanuco	-9.9166670	-76.2333336
Heraclides androgeus androgeus	Peru	Iquitos (Explorama Lodge)	-3.7480557	-73.2472229
Heraclides androgeus androgeus	Peru	Loreto	-4.3692612	-73.8805540
Heraclides androgeus androgeus	Peru	Mayo	-9.9367257	-76.2444305
Heraclides androgeus androgeus	Peru	Peru	-9.1939696	-74.9906271
Heraclides androgeus androgeus	Peru	Pucallpa	-8.3825006	-74.5380592
Heraclides androgeus androgeus	Peru	Rio Seco	-11.4705548	-77.0847206
Heraclides androgeus androgeus	Peru	Satipo	-11.2666659	-74.6833305
Heraclides androgeus androgeus	Peru	Tingo Maria	-9.3000002	-75.9833298

Heraclides androgeus epidaurus	Belize	Chiquibul	16.7006556	-88.9260864
Heraclides androgeus epidaurus	Belize	Stann Creek District	16.8333330	-88.4999962
Heraclides androgeus epidaurus	Costa Rica	Puntarenas	9.9829818	-84.8436296
Heraclides androgeus epidaurus	Costa Rica	San Jose	9.9400598	-84.0995256
Heraclides androgeus epidaurus	Cuba	Granma	20.2480250	-77.0004272
Heraclides androgeus epidaurus	Cuba	Holguin	20.8872213	-76.2630577
Heraclides androgeus epidaurus	Cuba	Loma del Gato	20.3166676	-76.4166718
Heraclides androgeus epidaurus	Cuba	Santiago de Cuba	20.0247221	-75.8219452
Heraclides androgeus epidaurus	Dominican Republic	Bayacanes, La Vega	19.2169641	-70.5235069
Heraclides androgeus epidaurus	Dominican Republic	Jarabacoa	19.1166706	-70.6333313
Heraclides androgeus epidaurus	Dominican Republic	La Vega	18.4906797	-69.9976730
Heraclides androgeus epidaurus	Dominican Republic	Puerto Plata	19.7841871	-70.6873547
Heraclides androgeus epidaurus	El Salvador	Santa Tecla	13.6833296	-89.2833328
Heraclides androgeus epidaurus	Guatemala	Peten	16.8348283	-90.2899246
Heraclides androgeus epidaurus	Guatemala	Sayaxche, El Peten	16.5302813	-90.1902008
Heraclides androgeus epidaurus	Haiti	Port au Prince	18.5333309	-72.3333282
Heraclides androgeus epidaurus	Honduras	Cayo	15.6999989	-87.6333351
Heraclides androgeus epidaurus	Mexico	Acahuzotla	17.3605556	-99.4672241
Heraclides androgeus epidaurus	Mexico	Bonampac	16.7060814	-91.0644721
Heraclides androgeus epidaurus	Mexico	Catemaco, Veracruz-Llave	18.4216796	-95.1112067
Heraclides androgeus epidaurus	Mexico	Chiapas	16.1276235	-92.7671813
Heraclides androgeus epidaurus	Mexico	Dos Amates, Veracruz	18.4891663	-95.0597229
Heraclides androgeus epidaurus	Mexico	Mazatlan, Gr	17.4499998	-99.4833336
Heraclides androgeus epidaurus	Mexico	Michoacan	19.1666670	-101.8333321
Heraclides androgeus epidaurus	Mexico	Motzorongo, Veracruz-Llave	18.6424999	-96.7305527
Heraclides androgeus epidaurus	Mexico	Oaxaca	17.0500002	-96.7166634
Heraclides androgeus epidaurus	Mexico	Palenque	17.5091667	-91.9822235
Heraclides androgeus epidaurus	Mexico	Presidio, Veracruz-Llave	19.3333330	-96.6666718
Heraclides androgeus epidaurus	Mexico	Quintana, YUC	20.8666649	-88.6333351
Heraclides androgeus epidaurus	Mexico	Sarabia	25.6528230	-100.2294731
Heraclides androgeus epidaurus	Mexico	X-Can	20.8499994	-87.6833305
Heraclides androgeus epidaurus	Mexico	Yaxchilan, Chiapas	16.8851304	-90.9654961
Heraclides androgeus epidaurus	Panama	Cerro Campana	8.7166700	-79.9000015
Heraclides androgeus epidaurus	Panama	Panama Canal	9.1210802	-79.7442626
Heraclides androgeus epidaurus	Panama	Panama City	9.0247964	-79.4943237
Heraclides androgeus epidaurus	Puerto Rico	Guajataca	18.3668261	-66.9184112
Heraclides androgeus epidaurus	Puerto Rico	Isla Verde	18.4323219	-66.0169411
Heraclides androgeus epidaurus	Trinidad & Tobago	Tobago	11.2322863	-60.7049560

Heraclides androgeus epidaurus	Trinidad & Tobago	Trinidad	10.4175858	-61.2377929
Heraclides androgeus laodocus	Argentina	Iguazu, Misiones	-25.6139951	-54.5682139
Heraclides androgeus laodocus	Argentina	Puerto Peninsula, Misiones	-25.6776697	-54.6324981
Heraclides androgeus laodocus	Brazil	Alto da Serra, Santos	-23.7833338	-46.3166676
Heraclides androgeus laodocus	Brazil	Caviuna, Parana	-23.3000002	-51.3666668
Heraclides androgeus laodocus	Brazil	Rio Claro	-22.4113459	-47.5704574
Heraclides androgeus laodocus	Brazil	Toledo, Parana	-24.7333336	-53.7499962
Heraclides androgeus laodocus	Paraguay	Paraguay	-23.4486172	-58.4525756
Heraclides aristodemus aristodemus	Dominican Republic	Jarabacoa	19.1166706	-70.6333313
Heraclides aristodemus aristodemus	Dominican Republic	Pedernales	18.0376670	-71.7391777
Heraclides aristodemus aristodemus	Dominican Republic	Puerto Plata	19.7841871	-70.6873547
Heraclides aristodemus aristodemus	Haiti	Port au Prince	18.5333309	-72.3333282
Heraclides aristodemus bjoerdalae	Bahamas	Great Inagua	21.0823848	-73.2999992
Heraclides aristodemus bjoerdalae	Turks & Caicos	North Caicos	21.8723318	-71.9563293
Heraclides aristodemus majasi	Bahamas	Crooked Island	22.7476076	-74.2180837
Heraclides aristodemus ponceanus	Bahamas	North Andros	24.7667845	-78.0523681
Heraclides aristodemus ponceanus	USA	Biscayne National Park, FL	25.4823313	-80.1823425
Heraclides aristodemus ponceanus	USA	Elliott Key, Florida	25.4431667	-80.1972694
Heraclides aristodemus ponceanus	USA	Key Largo, Florida	25.0865135	-80.4472771
Heraclides aristodemus ponceanus	USA	Lower Matecumbe Key, Florida	24.8626356	-80.7172890
Heraclides aristodemus ponceanus	USA	Matecumbe Key, Florida	24.9132176	-80.6410217
Heraclides aristodemus temenes	Cuba	Baracoa	20.3425182	-74.4968228
Heraclides aristodemus temenes	Cuba	Loma del Gato	20.3166676	-76.4166718
Heraclides aristodemus temenes	Cuba	Santiago de Cuba	20.0247221	-75.8219452
Heraclides aristor	Dominican Republic	Monte Cristi	19.8330764	-71.6166649
Heraclides astyalus anchicayaensis	Colombia	Aguaclara	3.3833339	-77.1333351
Heraclides astyalus anchicayaensis	Colombia	Anchicaya	3.6186109	-76.9133339
Heraclides astyalus anchicayaensis	Colombia	Bella Vista	3.5616670	-76.3522224
Heraclides astyalus anchicayaensis	Colombia	Cajambre	3.4383340	-77.1744423
Heraclides astyalus anchicayaensis	Colombia	Calima, Valle del Cauca	3.9341667	-76.4883308
Heraclides astyalus anchicayaensis	Colombia	Villa de Leyva	5.6324003	-73.5351485
Heraclides astyalus astyalus	Argentina	Jujuy	-23.1969843	-65.6855545
Heraclides astyalus astyalus	Argentina	Misiones	-26.8343187	-54.8257730
Heraclides astyalus astyalus	Argentina	Puerto Peninsula, Misiones	-25.6776697	-54.6324981
Heraclides astyalus astyalus	Brazil	Blumenau	-26.9183964	-49.0652847
Heraclides astyalus astyalus	Brazil	Caviuna, Parana	-23.3000002	-51.3666668
Heraclides astyalus astyalus	Brazil	Iguazu	-25.5632000	-54.5469319

Heraclides astyalus astyalus	Brazil	Jacarei	-23.3047389	-45.9692001
Heraclides astyalus astyalus	Brazil	Nova Lima	-19.9833336	-43.8500023
Heraclides astyalus astyalus	Brazil	Rio Grande do Sul	-29.0753751	-52.6245117
Heraclides astyalus astyalus	Brazil	Santa Catarina	-27.6536022	-51.0562440
Heraclides astyalus astyalus	Brazil	Sao Paulo - SP	-23.6606177	-46.6146435
Heraclides astyalus astyalus	Brazil	Tapejara	-28.0604682	-52.0127105
Heraclides astyalus astyalus	Paraguay	Paso Yobai	-25.6390502	-55.9416961
Heraclides astyalus bajaensis	Mexico	El Salto falls, Rio Valles (Ciudad Valles), San Luis Potosí	22.0210446	-99.0501594
Heraclides astyalus bajaensis	Mexico	Playa Azul	18.0045389	-102.3440731
Heraclides astyalus bajaensis	Mexico	Presidio, Veracruz-Llave	19.3333330	-96.6666718
Heraclides astyalus bajaensis	Mexico	Raices	24.3761110	-99.4069481
Heraclides astyalus bajaensis	Mexico	Tepic	21.5164375	-104.8940811
Heraclides astyalus hippomedon	Colombia	Calima, Valle del Cauca	3.9441667	-76.4883308
Heraclides astyalus hippomedon	Ecuador	Misahualli, Napo	-1.0305993	-77.6676750
Heraclides astyalus hippomedon	Ecuador	Morona Santiago	-2.5142121	-77.8193931
Heraclides astyalus hippomedon	Peru	Huanuco	-9.9166670	-76.2333336
Heraclides astyalus hippomedon	Peru	Tingo Maria	-9.3000002	-75.9833298
Heraclides astyalus hippomedon	Trinidad & Tobago	Trinidad	10.4175858	-61.2377929
Heraclides astyalus hippomedon	Venezuela	El Dorado, Bolivar	6.7331443	-61.5979385
Heraclides astyalus hippomedon	Venezuela	Macuto	10.5851680	-66.8828058
Heraclides astyalus pallas	Costa Rica	Santa Rosa	10.3025902	-85.8047676
Heraclides astyalus pallas	El Salvador	Ahuachapan	13.9213886	-89.8449974
Heraclides astyalus pallas	Guatemala	Peten	16.8348283	-90.2899246
Heraclides astyalus pallas	Honduras	Honduras	14.5197800	-87.0446777
Heraclides astyalus pallas	Mexico	Bacalar, Quintana Roo	18.6666670	-88.3833351
Heraclides astyalus pallas	Mexico	Canon del Novillo, TAMPS	23.7140105	-99.1200685
Heraclides astyalus pallas	Mexico	Catemaco, Veracruz-Llave	18.4216796	-95.1112067
Heraclides astyalus pallas	Mexico	Chiapas	16.1276235	-92.7671813
Heraclides astyalus pallas	Mexico	Ciudad Victoria	23.7364807	-99.1463165
Heraclides astyalus pallas	Mexico	Morelos	18.6808862	-99.1015720
Heraclides astyalus pallas	Mexico	Oaxaca	17.0500002	-96.7166634
Heraclides astyalus pallas	Mexico	Rio San Marcos	20.3924225	-97.8746223
Heraclides astyalus pallas	Mexico	San Francisco	18.5333338	-100.2666664
Heraclides astyalus pallas	Mexico	Tierra Blanca, Guadalupe	25.7049207	-100.2449655
Heraclides astyalus pallas	Mexico	X-Can	20.8499994	-87.6833305
Heraclides astyalus pallas	Panama	Colon	9.3635934	-79.8909233
Heraclides astyalus pallas	Panama	Darien	8.1522962	-77.8299175
Heraclides astyalus pallas	USA	Hidalgo, Texas	26.1090531	-98.2624103

Heraclides astyalus pallas	USA	Santa Ana, Hidalgo, Texas	26.1203016	-98.2586288
Heraclides astyalus phanias	Bolivia	Beni	-14.0000005	-65.4999962
Heraclides astyalus phanias	Brazil	Mato Grosso	-12.6955497	-55.9287605
Heraclides astyalus phanias	Brazil	Rio Madeira, Manicore	-6.6468750	-62.3137664
Heraclides astyalus phanias	Brazil	Rondonia	-10.7634447	-63.2903806
Heraclides astyalus phanias	Brazil	Vilhena, Rondonia	-12.7334517	-60.1477432
Heraclides caiguanabus	Cuba	Baracoa	20.3425182	-74.4968228
Heraclides caiguanabus	Cuba	Oriente	20.3000002	-76.0833282
Heraclides chiansiades chiansiades	Brazil	Manicore	-5.8122225	-61.2975006
Heraclides chiansiades chiansiades	Ecuador	Riobamba	-1.6722593	-78.6524963
Heraclides chiansiades chiansiades	Ecuador	Balsa Pamba	-1.7666663	-79.1833305
Heraclides chiansiades chiansiades	Ecuador	Rio Coca	-0.4833332	-76.9666634
Heraclides chiansiades chiansiades	Peru	Cahuapanas	-10.0094452	-74.9922218
Heraclides chiansiades chiansiades	Peru	Huanuco	-9.9166670	-76.2333336
Heraclides chiansiades chiansiades	Peru	Iquitos (Explorama Lodge)	-3.7480557	-73.2472229
Heraclides chiansiades chiansiades	Peru	Juanjui	-7.1833329	-76.7499962
Heraclides chiansiades chiansiades	Peru	Loreto	-4.3692612	-73.8805540
Heraclides chiansiades chiansiades	Peru	Madre de Dios	-11.6208192	-70.5285721
Heraclides chiansiades chiansiades	Peru	Rio Seco	-11.9090098	-77.0127868
Heraclides chiansiades chiansiades	Peru	Tingo Maria	-9.3000002	-75.9833298
Heraclides chiansiades dopassosi	Colombia	Rio Putumayo	-2.3627638	-71.3898468
Heraclides crespontes	Canada	Hamilton, Ontario, Canada	43.2451706	-79.8500824
Heraclides crespontes	Costa Rica	Alajuela, Costa Rica	10.0166702	-84.2166672
Heraclides crespontes	Costa Rica	Desamprados	9.8999996	-84.0666695
Heraclides crespontes	Costa Rica	Liberia	10.6333303	-85.4333267
Heraclides crespontes	Costa Rica	Puerto Viejo	10.4597908	-84.0042114
Heraclides crespontes	Costa Rica	Puntarenas	10.4662055	-84.4628906
Heraclides crespontes	Costa Rica	Rio Grande	9.9634403	-84.3701934
Heraclides crespontes	Costa Rica	Rio Piedras	10.5499997	-84.9833336
Heraclides crespontes	Costa Rica	Rodeo	9.6725919	-84.0177726
Heraclides crespontes	Costa Rica	San Isidro	9.3691277	-83.7068939
Heraclides crespontes	Costa Rica	San Jose	9.9333334	-84.0833359
Heraclides crespontes	Costa Rica	Santa Ana, San Jose	9.9333334	-84.1833344
Heraclides crespontes	Costa Rica	Turrialba	9.8999996	-83.6833267
Heraclides crespontes	El Salvador	Los Andes	13.6666665	-89.1833305
Heraclides crespontes	El Salvador	Santa Tecla	13.6833296	-89.2833328
Heraclides crespontes	Guatemala	Sayaxche, El Peten	16.5302813	-90.1902008
Heraclides crespontes	Guatemala	Tikal National Park	17.2500000	-89.6500015
Heraclides crespontes	Honduras	Spanish Honduras	14.7473973	-86.2530975
Heraclides crespontes	Honduras	Tegucigalpa	14.0999994	-87.2166634
Heraclides crespontes	Mexico	Atlixco	18.9069443	-98.4375000

Heraclides crespontes	Mexico	Catemaco, Veracruz-Llave	18.4216796	-95.1112067
Heraclides crespontes	Mexico	Chiapas	16.1276235	-92.7671813
Heraclides crespontes	Mexico	Chimalapa, Oaxaca	16.7166662	-94.6833305
Heraclides crespontes	Mexico	Ciudad Victoria	23.7364807	-99.1463165
Heraclides crespontes	Mexico	Coahuayana, Michoacan	18.6999998	-103.6583366
Heraclides crespontes	Mexico	Cola de Caballo (Horse Tail Falls), Nuevo Leon	25.3603401	-100.1619644
Heraclides crespontes	Mexico	Comitan	16.2499990	-92.1333351
Heraclides crespontes	Mexico	Cuernavaca	18.9186115	-99.2341690
Heraclides crespontes	Mexico	El Salto falls, Rio Valles (Ciudad Valles), San Luis Potosí	22.0210446	-99.0501594
Heraclides crespontes	Mexico	Elota	23.9691620	-106.7111511
Heraclides crespontes	Mexico	Escarcega	18.5999994	-90.7333336
Heraclides crespontes	Mexico	Escuinapa	22.8341923	-105.7785873
Heraclides crespontes	Mexico	Gomez Farias, Tamaulipas	23.0355064	-99.1468048
Heraclides crespontes	Mexico	Iguala	17.8499994	-100.3666649
Heraclides crespontes	Mexico	La Salada	31.0166664	-111.4833336
Heraclides crespontes	Mexico	Linares	24.8600750	-99.5669403
Heraclides crespontes	Mexico	Los Mochis	25.7935543	-108.9926529
Heraclides crespontes	Mexico	Malinalco	18.9483337	-99.4947205
Heraclides crespontes	Mexico	Mazatlan, Gr	17.4499998	-99.4833336
Heraclides crespontes	Mexico	Mexicali	32.6312311	-115.4333305
Heraclides crespontes	Mexico	Monterrey	25.6666670	-100.3166695
Heraclides crespontes	Mexico	Oaxaca	17.0500002	-96.7166634
Heraclides crespontes	Mexico	Ocotlan, Jalisco	20.3499994	-102.7666664
Heraclides crespontes	Mexico	Petatlan, Guerrero	17.5389691	-101.2668228
Heraclides crespontes	Mexico	Piste, YUC	20.6984653	-88.5882797
Heraclides crespontes	Mexico	Presidio, Veracruz-Llave	19.3333330	-96.6666718
Heraclides crespontes	Mexico	San Blas	21.5397663	-105.2854843
Heraclides crespontes	Mexico	San Fernando, Tamulipas	24.8478718	-98.1585693
Heraclides crespontes	Mexico	San Francisco	18.5333338	-100.2666664
Heraclides crespontes	Mexico	San Luis Potosi	22.1500006	-100.9833336
Heraclides crespontes	Mexico	Santa Rosa (Loma Larga, Tuxtla Gutiérrez, Cs, Mexico near Comitán)	16.7685492	-93.0677604
Heraclides crespontes	Mexico	Sinaloa de Leyva	25.8249493	-108.2220917
Heraclides crespontes	Mexico	Sonora	29.3007710	-110.6323242
Heraclides crespontes	Mexico	Tierra Blanca, Guadalupe	25.7049207	-100.2449655

Heraclides crespontes	Mexico	Veracruz, Veracruz-Llave	19.1726531	-96.1332893
Heraclides crespontes	Mexico	Villagran, Tamaulipas	24.4738894	-99.4880562
Heraclides crespontes	Mexico	X-Can (Nuevo X-Can)	20.8499994	-87.6833305
Heraclides crespontes	Mexico	Yautepec	18.8770519	-99.0657806
Heraclides crespontes	Nicaragua	Managua	12.1499996	-86.2722168
Heraclides crespontes	Nicaragua	Santo Domingo	12.2666664	-85.0833282
Heraclides crespontes	USA	Alachua County, Florida	29.6816754	-82.3539696
Heraclides crespontes	USA	Albion, Indiana	41.3956032	-85.4244270
Heraclides crespontes	USA	Arcadia, Florida	27.2164268	-81.8590012
Heraclides crespontes	USA	Atascosa Mountains, Arizona	31.4325943	-111.1467552
Heraclides crespontes	USA	Atwood Park, Winnebago, Illinois	41.9308586	-89.0820427
Heraclides crespontes	USA	Austin, Texas	30.2672081	-97.7432785
Heraclides crespontes	USA	Avon Park, Florida	27.5949116	-81.5034943
Heraclides crespontes	USA	Baboquivari Canyon, Arizona	31.7834158	-111.6239967
Heraclides crespontes	USA	Ballinger City Lake, Texas	31.7480219	-100.0325775
Heraclides crespontes	USA	Barton Springs, Texas	30.2638197	-97.7713966
Heraclides crespontes	USA	Bedford, New York	41.2042637	-73.6437454
Heraclides crespontes	USA	Big Pine Key, Florida	24.6946396	-81.3724433
Heraclides crespontes	USA	Boone County, Missouri	38.9460694	-92.3387756
Heraclides crespontes	USA	Brawley, California	32.9786549	-115.5302658
Heraclides crespontes	USA	Brickell Hammock, Florida	25.7533824	-80.2044945
Heraclides crespontes	USA	Brownsville, Texas	25.9091729	-97.4945952
Heraclides crespontes	USA	Brunswick, Georgia	31.1499466	-81.4871362
Heraclides crespontes	USA	Bullitt County, Kentucky	37.9641648	-85.6835746
Heraclides crespontes	USA	Cameron County, Texas	26.1265753	-97.5063441
Heraclides crespontes	USA	Camp Owaissa Bauer, Homestead, Florida	25.5238539	-80.4700469
Heraclides crespontes	USA	Canal Point, Florida	26.8637799	-80.6255631
Heraclides crespontes	USA	Cape Coral, Florida	26.5628538	-81.9495354
Heraclides crespontes	USA	Cape Haze, Florida	26.8524073	-82.2966957
Heraclides crespontes	USA	Cape Sable, Florida	25.2728977	-81.1214638
Heraclides crespontes	USA	Carteret County, North Carolina	34.8507499	-76.5980456
Heraclides crespontes	USA	Chicago, Illinois	41.8337408	-87.7320794
Heraclides crespontes	USA	Chinsegut Hill, Florida	28.6191587	-82.3645363
Heraclides crespontes	USA	Chinsegut Hill, Florida	28.6191587	-82.3645363

Heraclides crespontes	USA	Clearwater, Florida	27.9658966	-82.7963299
Heraclides crespontes	USA	Clemson, South Carolina	34.6810074	-82.8353653
Heraclides crespontes	USA	Clinton, Mississippi	32.3415356	-90.3217583
Heraclides crespontes	USA	Collier County, Florida	26.1601353	-81.3607445
Heraclides crespontes	USA	Corpus Christi, Nueces, Texas	27.8141918	-97.4619408
Heraclides crespontes	USA	Crandon Park, Florida	25.7120476	-80.1543756
Heraclides crespontes	USA	Davidson, Oklahoma	34.2430284	-99.0756340
Heraclides crespontes	USA	Daytona Beach, Florida	29.2093449	-81.0967148
Heraclides crespontes	USA	Destin, Florida (Hole in the Doughnut)	30.3954897	-86.4957428
Heraclides crespontes	USA	Donna, Texas	26.1703520	-98.0519524
Heraclides crespontes	USA	Dunedin, Florida	28.0196953	-82.7717209
Heraclides crespontes	USA	Elliott Key, Florida	25.4431667	-80.1972694
Heraclides crespontes	USA	Fair Grove, Greene, Missouri	37.3836228	-93.1526596
Heraclides crespontes	USA	Florida City, Florida	25.4477430	-80.4812310
Heraclides crespontes	USA	Fort Lauderdale, Florida	26.1411172	-80.1482717
Heraclides crespontes	USA	Fort Myers, Florida	26.6256316	-81.8259309
Heraclides crespontes	USA	Gadsden, Yuma, Arizona	32.5544987	-114.7631055
Heraclides crespontes	USA	Gainesville (Kanapaha Botanical Gardens)	29.6516457	-82.3248215
Heraclides crespontes	USA	Gainesville, Florida	29.6516457	-82.3248215
Heraclides crespontes	USA	Gold Canon, Arizona	32.3943124	-110.9486103
Heraclides crespontes	USA	Goldthwaite, Texas	31.4547104	-98.5693691
Heraclides crespontes	USA	Hancock, Maryland	39.6986670	-78.1775093
Heraclides crespontes	USA	Harlan, Indiana	41.1961613	-84.9196892
Heraclides crespontes	USA	Hatteras, North Carolina	35.2142952	-75.6887924
Heraclides crespontes	USA	Havelock, Raven County, North Carolina	34.8790219	-76.9013329
Heraclides crespontes	USA	Hidalgo, Texas	28.9474894	-100.6237391
Heraclides crespontes	USA	Hillsborough County, Florida	27.8764614	-82.4000705
Heraclides crespontes	USA	Hollywood, Florida	26.0112009	-80.1546514
Heraclides crespontes	USA	Honeymoon Island, Florida	28.0665273	-82.8293609
Heraclides crespontes	USA	Huachuca Mountains, Arizona	31.5127773	-110.4081421
Heraclides crespontes	USA	Isle of Palms, South Carolina	32.8083156	-79.7672773
Heraclides crespontes	USA	Jacksonville, Florida	30.3261913	-81.6596985
Heraclides crespontes	USA	Jacksonville, Texas	31.9637794	-95.2705040
Heraclides crespontes	USA	Key Largo, Florida	25.0865135	-80.4472771

Heraclides crespontes	USA	Key West, Florida	24.5549302	-81.7811965
Heraclides crespontes	USA	Kingsley Plantation, Florida	30.4389430	-81.4375734
Heraclides crespontes	USA	Kitty Hawk, North Carolina	36.0710811	-75.7124756
Heraclides crespontes	USA	Lake Helen, Florida	28.9808178	-81.2333946
Heraclides crespontes	USA	Lake Texoma, Oklahoma	33.8389683	-96.5708963
Heraclides crespontes	USA	Lake Thonotosassa, Thonotosassa, Hillsborough, Florida	28.0608511	-82.2805613
Heraclides crespontes	USA	Lake Wales, Florida	27.9014139	-81.5859108
Heraclides crespontes	USA	Laketon Bog, Indiana	40.9742107	-85.8358192
Heraclides crespontes	USA	Las Palmas, Texas	26.9525375	-99.2750359
Heraclides crespontes	USA	Leesburg, Florida	28.8125668	-81.8822021
Heraclides crespontes	USA	Lignumvitae Key, Florida	24.8992049	-80.6986999
Heraclides crespontes	USA	Little River, Oklahoma	34.9970303	-96.3650093
Heraclides crespontes	USA	Long Key, Florida	24.8217594	-80.8117708
Heraclides crespontes	USA	Longboat Key, Manatee, Florida	27.4195676	-82.6594166
Heraclides crespontes	USA	Lower Sugarloaf Key, Florida	24.6501133	-81.5153091
Heraclides crespontes	USA	Macon County, Georgia	32.8407364	-83.6324005
Heraclides crespontes	USA	Macon County, Illinois	39.8543163	-88.9823876
Heraclides crespontes	USA	Madero, Texas	26.1707176	-98.3314018
Heraclides crespontes	USA	Marathon, Florida	24.7110498	-81.0852097
Heraclides crespontes	USA	Matecumbe Key, Florida	24.9116608	-80.6420516
Heraclides crespontes	USA	Matheson Hammock County Park, Florida	25.6721641	-80.2649116
Heraclides crespontes	USA	Melbourne, Brevard, Florida	28.0828481	-80.6080780
Heraclides crespontes	USA	Mesa, Arizona	33.4222450	-111.8225937
Heraclides crespontes	USA	Miami, Florida	25.8163980	-80.2353593
Heraclides crespontes	USA	Monkey Jungle, Florida	25.5664968	-80.4317169
Heraclides crespontes	USA	Montgomery County, Alabama	32.3676376	-86.3002701
Heraclides crespontes	USA	Moultrie, Colquitt, Georgia	31.1799078	-83.7890663
Heraclides crespontes	USA	Mustang Peak, Mustang Mountain, Arizona	31.6934233	-110.4764671
Heraclides crespontes	USA	New Braunfels, Texas	29.7120501	-98.1381255
Heraclides crespontes	USA	New Smyrna Beach, Florida	29.0295669	-80.9548447
Heraclides crespontes	USA	Nogales, Arizona	31.3671779	-110.9342422

Heraclides crespontes	USA	Norman, Oklahoma	35.2230644	-97.4393158
Heraclides crespontes	USA	Ocala National Forest, Florida	29.1679554	-81.7919998
Heraclides crespontes	USA	Oneco, Florida	27.4475412	-82.5462112
Heraclides crespontes	USA	Orange Park, Florida	30.1681706	-81.7071092
Heraclides crespontes	USA	Orlando, Florida	28.5484810	-81.3649902
Heraclides crespontes	USA	Ormond Beach, Florida	29.2858133	-81.0627186
Heraclides crespontes	USA	Palmetto, Florida	27.5211511	-82.5720429
Heraclides crespontes	USA	Phoenix, Arizona	33.4483414	-112.0740051
Heraclides crespontes	USA	Pigeon Mountain, Georgia	34.6486893	-85.3916283
Heraclides crespontes	USA	Pine Key, Florida	27.6832204	-82.7123875
Heraclides crespontes	USA	Plantation Key, Florida	24.9777903	-80.5572286
Heraclides crespontes	USA	Potomac River, Maryland	38.1345565	-76.3604736
Heraclides crespontes	USA	Prairie Village, Kansas	38.9894750	-94.6447433
Heraclides crespontes	USA	Prairieville, Louisiana	30.3029718	-90.9720421
Heraclides crespontes	USA	Quemado, Texas	28.9474894	-100.6237391
Heraclides crespontes	USA	Rio Grande City, Texas	26.3800710	-98.8199997
Heraclides crespontes	USA	Rock Bridge, Virginia	31.0496340	-83.4993248
Heraclides crespontes	USA	Saint John, Louisiana	30.1588106	-91.8087273
Heraclides crespontes	USA	Saint Johns County, Florida	29.9377908	-81.4346961
Heraclides crespontes	USA	Saint Petersburg, Florida	27.7708597	-82.6793778
Heraclides crespontes	USA	Saint Tammany Road, Louisiana	30.3940830	-89.8950691
Heraclides crespontes	USA	Sanford, Florida	28.7951717	-81.2679901
Heraclides crespontes	USA	Santa Cruz County, Arizona	31.5738555	-110.8547973
Heraclides crespontes	USA	Santa Fe River, Florida	29.8874540	-82.8792915
Heraclides crespontes	USA	Santa Rita Mountains, Arizona	31.7202873	-110.8083420
Heraclides crespontes	USA	Sarasota, Florida	27.3371301	-82.5226091
Heraclides crespontes	USA	Shalimar, Florida	30.4427377	-86.5808145
Heraclides crespontes	USA	Silver Lake, Indiana	41.0723632	-85.8948898
Heraclides crespontes	USA	Silver Springs, Florida	29.2166538	-82.0576096
Heraclides crespontes	USA	Simpson Park, Florida	28.0694647	-81.9598045
Heraclides crespontes	USA	Sinton, Texas	28.0362930	-97.5092773
Heraclides crespontes	USA	Sioux Falls, South Dakota	43.5434172	-96.7263601
Heraclides crespontes	USA	Sleepy Creek Mountain, West Virginia	39.4581977	-78.1975936
Heraclides crespontes	USA	Snake Bite Trail, Everglades, Florida	25.8577560	-81.3760757

Heraclides crespontes	USA	Somerton, Arizona	32.5966850	-114.7118268
Heraclides crespontes	USA	Spring Creek, Pennsylvania	40.5337086	-75.5993538
Heraclides crespontes	USA	State College, Pennsylvania	40.7933617	-77.8600235
Heraclides crespontes	USA	Stock Island, Florida	24.5667314	-81.7363812
Heraclides crespontes	USA	Sullivan City, Texas	26.2756424	-98.5661025
Heraclides crespontes	USA	Sumneytown, Montgomery, Pennsylvania	40.3289871	-75.4510040
Heraclides crespontes	USA	Sunny Brown Trail, Cravens Hammock, Georgia	30.8693876	-82.4279060
Heraclides crespontes	USA	Sunrise, Florida	26.1339741	-80.1297661
Heraclides crespontes	USA	Sycamore Canyon, Arizona	31.9326426	-110.7983207
Heraclides crespontes	USA	Tampa, Florida	27.9487393	-82.4575653
Heraclides crespontes	USA	Tarpon Springs, Florida	28.1451912	-82.7498037
Heraclides crespontes	USA	Terra Ceia, Manatee, Florida	27.5780678	-82.5777919
Heraclides crespontes	USA	Terrell, Kaufman, Texas	32.7359657	-96.2752571
Heraclides crespontes	USA	Thonotosassa, Hillsborough, Florida	28.0614061	-82.3023148
Heraclides crespontes	USA	Torrey State Park, Florida	30.5690832	-84.9477005
Heraclides crespontes	USA	Tucson, Arizona	32.1770556	-110.8838155
Heraclides crespontes	USA	Tuscon, Arizona	32.1942086	-110.9069824
Heraclides crespontes	USA	Tyler, Texas	32.3512592	-95.3010597
Heraclides crespontes	USA	U.S. 29, Escambia, Florida	30.6381203	-87.2598266
Heraclides crespontes	USA	Van Buren County, Michigan	42.2443693	-86.0637550
Heraclides crespontes	USA	Volusia County, Florida	29.0163198	-81.1508715
Heraclides crespontes	USA	Waubonsie State Park, Webster City, Freemont County, Iowa	40.6774979	-95.6919441
Heraclides crespontes	USA	Welder Wildlife Refuge, Texas	29.7512632	-96.9069671
Heraclides crespontes	USA	Wilcox County, Alabama	32.0498849	-87.2623100
Heraclides crespontes	USA	Winchester, Indiana	40.1722450	-84.9785690
Heraclides crespontes	USA	Winter Park, Florida	28.6007786	-81.3391953
Heraclides crespontes	USA	York, Pennsylvania	39.9625969	-76.7277374
Heraclides crespontes	USA	Yuma County, Arizona	32.7054846	-114.6207340
Heraclides epenetus	Ecuador	Balsa Pamba	-1.7666663	-79.1833305
Heraclides epenetus	Ecuador	Pichincha	-0.1187895	-78.8632965
Heraclides erostratus erostratus	Mexico	Chiapas	16.1276235	-92.7671813

<i>Heraclides erostratus erostratus</i>	Mexico	Gomez Farias, Tamaulipas	23.0355064	-99.1468048
<i>Heraclides erostratus erostratus</i>	Mexico	Mexicali	32.6312311	-115.4333305
<i>Heraclides erostratus erostratus</i>	Mexico	Naolinco (Veracruz- Llave)	19.6548741	-96.8592453
<i>Heraclides erostratus erostratus</i>	Mexico	Necaxa, Pu	20.2473808	-97.8538513
<i>Heraclides erostratus erostratus</i>	Mexico	Nuevo Leon	25.4736603	-99.8371470
<i>Heraclides erostratus erostratus</i>	Mexico	Rio San Marcos	20.3924225	-97.8746223
<i>Heraclides erostratus erostratus</i>	Mexico	Santa Rosa (Loma Larga, Tuxtla Gutiérrez, Cs, Mexico near Comitán)	16.7685492	-93.0677604
<i>Heraclides erostratus erostratus</i>	Mexico	Tamulipas	24.9325753	-98.6352230
<i>Heraclides erostratus erostratus</i>	El Salvador	Cerro El Picacho, San Salvador	13.7455549	-89.2561150
<i>Heraclides erostratus erostratus</i>	El Salvador	San Salvador	13.6999998	-89.1999969
<i>Heraclides erostratus erostratus</i>	El Salvador	Santa Ana	13.9941669	-89.5597191
<i>Heraclides erostratus erostratus</i>	El Salvador	Santa Tecla	13.6833296	-89.2833328
<i>Heraclides erostratus erostratus</i>	Guatemala	Chimaltenango	14.6686110	-90.8166695
<i>Heraclides erostratus erostratus</i>	Guatemala	Huehuetenango	15.3197203	-91.4708328
<i>Heraclides erostratus erostratus</i>	Guatemala	Palin	14.4055567	-90.6983299
<i>Heraclides erostratus erostratus</i>	Guatemala	Parque Nacional Tikal, Petén	17.2499990	-89.6499977
<i>Heraclides erostratus erostratus</i>	Guatemala	San Cristobal Verapaz	15.3679567	-90.4761886
<i>Heraclides erostratus erostratus</i>	Guatemala	Tacana	15.2444398	-92.0685195
<i>Heraclides erostratus erostratus</i>	Honduras	El Boqueron	13.8166676	-87.6663274
<i>Heraclides erostratus erostratus</i>	Mexico	Chiapas	16.1376235	-92.7671813
<i>Heraclides erostratus erostratus</i>	Mexico	Chimalapa, Oaxaca	16.7166662	-94.6833305
<i>Heraclides erostratus erostratus</i>	Mexico	Pacayal	14.8799258	-92.2678184
<i>Heraclides erostratus erostratus</i>	Mexico	Santa Rosa (Loma Larga, Tuxtla Gutiérrez, Cs, Mexico near Comitán)	16.7785492	-93.0677604
<i>Heraclides erostratus erostratus</i>	Nicaragua	Matagalpa	12.9407228	-85.5006601
<i>Heraclides erostratus vazquezae</i>	Mexico	Acahizotla	17.3605556	-99.4672241
<i>Heraclides erostratus vazquezae</i>	Mexico	Colima, Cl	19.2430592	-103.7305603
<i>Heraclides erostratus vazquezae</i>	Mexico	Comitan	16.2499990	-92.1333351
<i>Heraclides erostratus vazquezae</i>	Mexico	Cuarenta	21.4999990	-101.7666664
<i>Heraclides erostratus vazquezae</i>	Mexico	San Jeronimo	18.8333330	-99.6000023
<i>Heraclides erostratus vazquezae</i>	Mexico	Santa Rosa (Loma Larga, Tuxtla Gutiérrez, Cs, Mexico near Comitán)	16.7885492	-93.0677604
<i>Heraclides garleppi garleppi</i>	Bolivia	Chapare region	-16.6641687	-65.6173556
<i>Heraclides garleppi garleppi</i>	Bolivia	Santa Cruz	-16.7512904	-62.1036529

Heraclides garleppi interruptus	Brazil	Fazenda, Rancho Grande	-26.5999994	-50.2499962
Heraclides garleppi interruptus	Brazil	Rondonia	-10.7634447	-63.2903806
Heraclides garleppi interruptus	Peru	Loreto	-4.3692612	-73.8805540
Heraclides garleppi interruptus	Peru	Madre de Dios	-11.6208192	-70.5285721
Heraclides garleppi lecerfi	French Guiana	Bas-Maroni	3.6499996	-53.6166668
Heraclides hectorides	Argentina	Misiones	-26.8343187	-54.8257730
Heraclides hectorides	Brazil	Brusque	-28.2500010	-49.3833332
Heraclides hectorides	Brazil	Caviuna, Parana	-23.3000002	-51.3666668
Heraclides hectorides	Brazil	Curitiba	-25.4166670	-49.2499962
Heraclides hectorides	Brazil	Iguazu	-25.5632000	-54.5469319
Heraclides hectorides	Brazil	Nova Lima	-19.9833336	-43.8500023
Heraclides hectorides	Brazil	Para	-5.6815836	-52.4487304
Heraclides hectorides	Brazil	Ponta Grossa	-25.0958594	-50.1628875
Heraclides hectorides	Brazil	Rio de Janeiro	-22.9000006	-43.2333317
Heraclides hectorides	Brazil	Rio Grande do Sul	-29.0753751	-52.6245117
Heraclides hectorides	Brazil	Rio Sapucaí, Minas Gerais	-20.1333351	-48.4500008
Heraclides hectorides	Brazil	Santa Catarina	-27.6536022	-51.0562440
Heraclides hectorides	Brazil	Sao Paulo - SP	-23.6606177	-46.6146435
Heraclides hectorides	Paraguay	Caaguazu	-25.4499998	-56.0166683
Heraclides himeros baia	Brazil	Bahia	-12.2755988	-41.2207031
Heraclides himeros baia	Brazil	Boias	-15.9333324	-50.1333332
Heraclides himeros baia	Brazil	Tocantins	-10.1770774	-48.5897827
Heraclides himeros himeros	Brazil	Espirito Santo	-19.1892716	-40.3067779
Heraclides himeros himeros	Brazil	Rio de Janeiro	-22.9000006	-43.2333317
Heraclides homothoas	Brazil	Santarem - Para	-0.9500003	-46.9833317
Heraclides homothoas	Colombia	Muzo, Boyaca	5.5352774	-74.1077766
Heraclides homothoas	Costa Rica	Hacienda el Rodeo	9.9166670	-84.2666702
Heraclides homothoas	Costa Rica	Rodrigues, San Jose	9.9400598	-84.0995256
Heraclides homothoas	Trinidad & Tobago	Petit Valley	10.7022223	-61.5333328
Heraclides homothoas	Trinidad & Tobago	Sangre Grande	10.5978456	-61.1272430
Heraclides homothoas	Trinidad & Tobago	St Ann's	10.6757904	-61.5186309
Heraclides hyppason	Bolivia	Buena Vista, Santa Cruz	-17.4499998	-63.6666660
Heraclides hyppason	Brazil	Para	-5.6815836	-52.4487304
Heraclides hyppason	Brazil	Rondonia	-10.7634447	-63.2903806
Heraclides hyppason	Brazil	Utinga	-10.9833336	-42.9500008
Heraclides hyppason	Ecuador	Misahualli, Napo	-1.0333333	-77.6666718
Heraclides hyppason	Ecuador	Rio Coca	-0.4833332	-76.9666634
Heraclides hyppason	Guayana	Georgetown	6.7950073	-58.1666603

Heraclides hyppason	Guyana	Saint Laurent du Maroni	3.9517953	-53.7981091
Heraclides hyppason	Peru	Iquitos (Explorama Lodge)	-3.7480557	-73.2472229
Heraclides hyppason	Peru	Loreto	-4.3692612	-73.8805540
Heraclides isidorus tingo	Peru	Tingo Maria	-9.3000002	-75.9833298
Heraclides isidorus autana	Venezuela	Barinas	8.6291676	-70.2072258
Heraclides isidorus brises	Colombia	Boyaca	5.6392192	-72.9080200
Heraclides isidorus flavescens	Ecuador	Balsa Pamba	-1.7666663	-79.1833305
Heraclides isidorus flavescens	Ecuador	Napo	-1.0268233	-77.7159118
Heraclides isidorus flavescens	Ecuador	Rio Coca	-0.4833332	-76.9666634
Heraclides isidorus flavescens	Ecuador	Rio Jatunyacu	0.2499998	-78.2666702
Heraclides isidorus isidorus	Peru	Huanuco	-9.9166670	-76.2333336
Heraclides isidorus isidorus	Peru	Junin	-11.3346391	-75.3002929
Heraclides isidorus isidorus	Peru	San Antonio	-14.8166666	-70.6833305
Heraclides isidorus isidorus	Peru	Satipo	-11.2666659	-74.6833305
Heraclides isidorus isidorus	Peru	Tingo Maria	-9.3100002	-75.9833298
Heraclides isidorus isidorus	Colombia	Calima, Valle del Cauca	3.9341667	-76.4883308
Heraclides isidorus isidorus	Costa Rica	Puntarenas	9.9829818	-84.8436296
Heraclides isidorus isidorus	Ecuador	Pichincha	-0.1187895	-78.8632965
Heraclides lamarchei	Argentina	Salta	-24.7833309	-65.4166718
Heraclides lamarchei	Bolivia	Las Yungas	-16.3333330	-66.7499962
Heraclides lamarchei	Bolivia	Puente Villa (Villa Tunari)	-18.7833338	-68.6000023
Heraclides lamarchei	Brazil	Rio Negro	-19.4606167	-54.9767095
Heraclides machaonides	Dominican Republic	Barahona	18.2000008	-71.0999985
Heraclides machaonides	Dominican Republic	Jarabacoa	19.1166706	-70.6333313
Heraclides machaonides	Dominican Republic	La Altagracia	18.5401659	-68.6212845
Heraclides machaonides	Dominican Republic	La Vega	19.2166691	-70.5166702
Heraclides machaonides	Dominican Republic	Las Terrenas	19.2879174	-69.5316047
Heraclides machaonides	Dominican Republic	Pico Isabel de Torres	19.7626546	-70.7001670
Heraclides machaonides	Dominican Republic	Sierra de Baoruco	18.1666670	-71.4166718
Heraclides machaonides	Haiti	Haiti	18.9999990	-72.4166718
Heraclides melonius	Jamaica	Blue Mountain	18.1243180	-76.6794204
Heraclides melonius	Jamaica	Mona	18.0061048	-76.7666702
Heraclides ornythion	Mexico	Acahuizotla	17.3605556	-99.4672241
Heraclides ornythion	Mexico	Baja California	31.3161013	-115.4113769
Heraclides ornythion	Mexico	Chiapas	16.1276235	-92.7671813
Heraclides ornythion	Mexico	Chichen Itza, Yucatan	20.6751901	-88.5662841
Heraclides ornythion	Mexico	Ciudad Victoria	23.7364807	-99.1463165

Heraclides ornythion	Mexico	Cola de Caballo (Horse Tail Falls), Nuevo Leon	25.3603401	-100.1619644
Heraclides ornythion	Mexico	Colima, Cl	19.2430592	-103.7305603
Heraclides ornythion	Mexico	Comitan	16.2499990	-92.1333351
Heraclides ornythion	Mexico	Mapastepec	15.4416666	-92.8916702
Heraclides ornythion	Mexico	Mexicali	32.6312311	-115.4333305
Heraclides ornythion	Mexico	Micos	22.1833324	-99.2499962
Heraclides ornythion	Mexico	Montebello	19.9000006	-89.8833351
Heraclides ornythion	Mexico	Nuevo Leon	25.4736603	-99.8371470
Heraclides ornythion	Mexico	Oaxaca	17.0500002	-96.7166634
Heraclides ornythion	Mexico	Puente Nacional	19.3269444	-96.4833298
Heraclides ornythion	Mexico	San Francisco	18.5333338	-100.2666664
Heraclides ornythion	Mexico	San Luis Potosi	22.1500006	-100.9833336
Heraclides ornythion	Mexico	Sontecomapan	18.5041676	-95.0355530
Heraclides ornythion	Mexico	Tamulipas	24.9325753	-98.6352230
Heraclides ornythion	Mexico	Tepoztlan	18.9833345	-99.1000023
Heraclides ornythion	USA	Bensten Rio Grande Valley State Park, Texas	26.1730021	-98.3832550
Heraclides ornythion	USA	Corpus Christi, Texas	27.7049800	-97.4014589
Heraclides ornythion	USA	Del Dios, California	33.0728207	-117.1191978
Heraclides ornythion	USA	Hidalgo, Texas	26.1090531	-98.2624103
Heraclides ornythion	USA	Lake Corpus Cristi, Texas	28.0419579	-97.8686066
Heraclides oxynius	Cuba	Havana	23.1317561	-82.3641701
Heraclides oxynius	Cuba	Holguin	20.8872213	-76.2630577
Heraclides oxynius	Cuba	Loma del Gato	20.3166676	-76.4166718
Heraclides paeon escomeli	Chile	Coquimbo	-29.9333324	-71.3166695
Heraclides paeon escomeli	Peru	Arequipa	-16.3201394	-71.4770507
Heraclides paeon escomeli	Peru	Lima	-12.0500002	-77.0500031
Heraclides paeon paeon	Bolivia	Cochabamba	-17.2377247	-65.6479456
Heraclides paeon paeon	Bolivia	Yungas, La Paz	-16.3333330	-66.7499962
Heraclides paeon paeon	Peru	Chuchurras, Pasco	-10.0999994	-75.1499977
Heraclides paeon paeon	Peru	Tingo Maria	-9.3000002	-75.9833298
Heraclides paeon paeon	Venezuela	Caracas	10.4999995	-66.9166718
Heraclides paeon thrason	Colombia	Calima, Valle del Cauca	3.9341667	-76.4883308
Heraclides paeon thrason	Ecuador	Bucay	-2.1666668	-79.0999985
Heraclides paeon thrason	Ecuador	Quito (Tinalandia)	-0.2167000	-78.5000000
Heraclides paeon thrason	Mexico	X-Can	20.8499994	-87.6833305
Heraclides paeon thrason	Peru	Huanuco	-9.9166670	-76.2333336
Heraclides paeon thrason	Peru	La Merced (Chanchamayo)	-11.0500011	-75.3166695
Heraclides paeon thrason	Peru	Lima	-12.0500002	-77.0500031
Heraclides paeon thrason	Peru	Rio Seco	-11.4705548	-77.0847206
Heraclides paeon thrason	Venezuela	Bolivar	6.0023888	-63.8261415

Heraclides pelaus atkinsi	Cuba	Granma	20.2480250	-77.0004272
Heraclides pelaus atkinsi	Cuba	Santiago de Cuba	20.0247221	-75.8219452
Heraclides pelaus imerius	Dominican Republic	Guayacanes (near La Vega)	19.2166691	-70.5166702
Heraclides pelaus imerius	Dominican Republic	Jarabacoa	19.1166706	-70.6333313
Heraclides pelaus pelaus	Jamaica	Barron Hall	18.1204025	-76.7144393
Heraclides pelaus pelaus	Jamaica	Blue Mountain	18.1243180	-76.6794204
Heraclides pelaus pelaus	Jamaica	Cuna Cuna Pass	18.0133449	-76.3858795
Heraclides pelaus pelaus	Jamaica	Moore Town	18.0727569	-76.4236450
Heraclides pelaus pelaus	Jamaica	Trelawny	18.3838501	-77.4954986
Heraclides pelaus puertoricensis	Puerto Rico	El Yunque (Caribbean National Forest)	18.2833338	-65.7999992
Heraclides pelaus puertoricensis	Puerto Rico	Maricao forest reserve	18.1827793	-66.9802742
Heraclides pelaus puertoricensis	Puerto Rico	Mayaguez	18.2065233	-67.1422576
Heraclides pelaus puertoricensis	Puerto Rico	Ponce	18.0130548	-66.6144485
Heraclides pelaus puertoricensis	Puerto Rico	Toro Negro	18.1615109	-66.5666770
Heraclides rogeri pharnaces	Mexico	Acahuzotla	17.3833351	-99.4500008
Heraclides rogeri pharnaces	Mexico	Cerro Toquian Grande, Chiapas	15.1833334	-92.2168476
Heraclides rogeri pharnaces	Mexico	Chiapas	16.1276235	-92.7671813
Heraclides rogeri pharnaces	Mexico	Coahuayana, Michoacan	18.6999998	-103.6583366
Heraclides rogeri pharnaces	Mexico	Colima, Cl	19.2430592	-103.7305603
Heraclides rogeri pharnaces	Mexico	Guerrero	18.0038981	-100.0763806
Heraclides rogeri pharnaces	Mexico	Jiutepec, Morelos	18.8734198	-99.1233176
Heraclides rogeri pharnaces	Mexico	Lacanja, Cs	16.9499998	-91.2833366
Heraclides rogeri pharnaces	Mexico	Malinalco	18.9483337	-99.4947205
Heraclides rogeri pharnaces	Mexico	Mazatlan, Gr	17.4499998	-99.4833336
Heraclides rogeri pharnaces	Mexico	Michoacan	19.1666670	-101.8333321
Heraclides rogeri pharnaces	Mexico	Morelos	18.6808862	-99.1015720
Heraclides rogeri pharnaces	Mexico	Necaxa, Pu	20.2486692	-97.8511047
Heraclides rogeri pharnaces	Mexico	Ocotlan, Jalisco	20.3499994	-102.7666664
Heraclides rogeri pharnaces	Mexico	Pinola	16.4000006	-92.3833351
Heraclides rogeri pharnaces	Mexico	Puebla, COAH	25.4333324	-101.2999992
Heraclides rogeri pharnaces	Mexico	San Martin, Salina Cruz	16.1825008	-95.1958313
Heraclides rogeri pharnaces	Mexico	San Miguel, Ciudad de México	19.2499990	-99.1666718
Heraclides rogeri pharnaces	Mexico	Santa Rosa (Loma Larga, Tuxtla Gutiérrez, Cs, Mexico near Comitán)	16.7685492	-93.0677604
Heraclides rogeri pharnaces	Mexico	Sinaloa de Leyva	25.8249493	-108.2220917
Heraclides rogeri pharnaces	Mexico	Tepoztlan, Morelos	18.9824672	-99.1000023
Heraclides rogeri pharnaces	Mexico	Zapaluta	16.1166649	-92.0499992

Heraclides rogeri pharnaces	Mexico	Zimapan, Hg	20.7499990	-99.3500023
Heraclides rogeri rogeri	Mexico	Oaxaca	17.0500002	-96.7166634
Heraclides rogeri rogeri	Mexico	Piste, YUC	20.6984653	-88.5882797
Heraclides rogeri rogeri	Mexico	Quintana, YUC	20.8666649	-88.6333351
Heraclides rogeri rogeri	Mexico	X-Can	20.8499994	-87.6833305
Heraclides thersites	Jamaica	Barron Hall	18.1204025	-76.7144393
Heraclides thersites	Jamaica	Blue Mountain	18.1243180	-76.6794204
Heraclides thersites	Jamaica	Jackson Town	18.4159420	-77.4833336
Heraclides thersites	Jamaica	Kingston	17.9999990	-76.7999992
Heraclides thersites	Jamaica	Mona	18.0061048	-76.7666702
Heraclides thoas autocles	Belize	Chaa Creek	16.8295177	-88.9054870
Heraclides thoas autocles	Belize	Chiquibul	16.7006556	-88.9260864
Heraclides thoas autocles	Belize	Cockscomb	16.7782463	-88.5992431
Heraclides thoas autocles	Belize	San Ignacio	17.1509603	-89.0771484
Heraclides thoas autocles	Belize	Stann Creek District	16.8333330	-88.4999962
Heraclides thoas autocles	El Salvador	La Libertad	13.5097754	-89.3221866
Heraclides thoas autocles	El Salvador	Lima, San Juan	13.9833341	-89.3833351
Heraclides thoas autocles	El Salvador	San Salvador	13.6999998	-89.1999969
Heraclides thoas autocles	Guatemala	Alta Verapaz	15.5019874	-90.3333663
Heraclides thoas autocles	Guatemala	Flores	16.9044278	-89.9000930
Heraclides thoas autocles	Guatemala	Laguna Tinta	15.6530224	-88.3366667
Heraclides thoas autocles	Guatemala	Quirigua	15.2666702	-89.0833282
Heraclides thoas autocles	Guatemala	Sayaxche, El Peten	16.5302813	-90.1902008
Heraclides thoas autocles	Guatemala	Tikal National Park	17.2500000	-89.6500015
Heraclides thoas autocles	Honduras	El Jaral, Cortes	14.9472726	-88.0081272
Heraclides thoas autocles	Honduras	Honduras	14.5197800	-87.0446777
Heraclides thoas autocles	Honduras	Lake Yojoa	14.8701372	-87.9428100
Heraclides thoas autocles	Honduras	Potrerrillos, Cortes	15.2391398	-87.9630661
Heraclides thoas autocles	Honduras	Santa Barbara	14.9285719	-88.2309436
Heraclides thoas autocles	Honduras	Spanish Honduras	14.7473973	-86.2530975
Heraclides thoas autocles	Mexico	Acahuzotla	17.3605556	-99.4672241
Heraclides thoas autocles	Mexico	Catemaco, Veracruz-Llave	18.4216796	-95.1112067
Heraclides thoas autocles	Mexico	Chiapas	16.1276235	-92.7671813
Heraclides thoas autocles	Mexico	Chiltepec	17.9542394	-96.1540603
Heraclides thoas autocles	Mexico	Chiricahua	16.7952150	-93.1173920
Heraclides thoas autocles	Mexico	Coahuayana, Michoacan	18.6999998	-103.6583366
Heraclides thoas autocles	Mexico	Cola de Caballo (Horse Tail Falls), Nuevo Leon	25.3603401	-100.1619644
Heraclides thoas autocles	Mexico	Colima, Cl	19.2430592	-103.7305603
Heraclides thoas autocles	Mexico	Cordoba	18.8833351	-96.9333305
Heraclides thoas autocles	Mexico	Cosolapa	18.6016729	-96.6824340
Heraclides thoas autocles	Mexico	Cuatlalpan	19.2346093	-99.1829180

Heraclides thoas autocles	Mexico	Dos Amates, Veracruz	18.4891663	-95.0597229
Heraclides thoas autocles	Mexico	El Salto falls, Rio Valles (Ciudad Valles), San Luis Potosí	22.0210446	-99.0501594
Heraclides thoas autocles	Mexico	Escarcega	18.5999994	-90.7333336
Heraclides thoas autocles	Mexico	Fortin de las Flores	18.9000006	-96.9999962
Heraclides thoas autocles	Mexico	Gomez Farias, Tamaulipas	23.0355064	-99.1468048
Heraclides thoas autocles	Mexico	Guerrero	18.0038981	-100.0763806
Heraclides thoas autocles	Mexico	Mapastepec	15.4416666	-92.8916702
Heraclides thoas autocles	Mexico	Mazatlan, Gr	17.4499998	-99.4833336
Heraclides thoas autocles	Mexico	Mexico City	32.6312311	-115.4333305
Heraclides thoas autocles	Mexico	Michoacan	19.1666670	-101.8333321
Heraclides thoas autocles	Mexico	Morelos	18.6808862	-99.1015720
Heraclides thoas autocles	Mexico	Nayarit	21.7591808	-104.8493957
Heraclides thoas autocles	Mexico	Nismalaya Creek, Jalisco	20.2621971	-103.7658691
Heraclides thoas autocles	Mexico	Oaxaca	17.0500002	-96.7166634
Heraclides thoas autocles	Mexico	Presidio, Veracruz-Llave	19.3333330	-96.6666718
Heraclides thoas autocles	Mexico	San Francisco	18.5333338	-100.2666664
Heraclides thoas autocles	Mexico	San Luis Potosi	22.1500006	-100.9833336
Heraclides thoas autocles	Mexico	San Quintin, Chiapas	16.3833351	-91.3333282
Heraclides thoas autocles	Mexico	Santa Rosa, Morelos	19.5672288	-99.1096035
Heraclides thoas autocles	Mexico	Sierra de Juarez	31.7499990	-115.6666679
Heraclides thoas autocles	Mexico	Tamazunchale	21.2545017	-98.7918090
Heraclides thoas autocles	Mexico	Tamulipas	24.9325753	-98.6352230
Heraclides thoas autocles	Mexico	Tapijulapa, Tabasco	17.4666662	-92.7813974
Heraclides thoas autocles	Mexico	Textepec	19.8563881	-99.6352806
Heraclides thoas autocles	Mexico	Tezonapa	18.5959785	-96.6701602
Heraclides thoas autocles	Mexico	Veracruz, Veracruz- Llave	19.1726531	-96.1332893
Heraclides thoas autocles	Mexico	X-Can	20.8499994	-87.6833305
Heraclides thoas autocles	Mexico	X-Can (Nuevo X-Can)	20.8499994	-87.6833305
Heraclides thoas autocles	Mexico	Yautepec	18.8770519	-99.0657806
Heraclides thoas autocles	Nicaragua	Granada	11.9335318	-85.9683609
Heraclides thoas autocles	Nicaragua	Jinotepe	11.8499994	-86.2000008
Heraclides thoas autocles	USA	Goose Island State Park, Texas	28.1384535	-96.9873046
Heraclides thoas autocles	USA	Lake Corpus Cristi, Texas	28.0419579	-97.8686066
Heraclides thoas autocles	USA	Texas	29.7262223	-100.1513671
Heraclides thoas brasiliensis	Argentina	Caa Guazu	-27.4666662	-58.8333340
Heraclides thoas brasiliensis	Argentina	Jujuy	-23.1969843	-65.6855545
Heraclides thoas brasiliensis	Argentina	Las Piedras	-25.4259120	-57.4052810

Heraclides thoas brasiliensis	Brazil	Casa Grande	-13.6666665	-41.8166676
Heraclides thoas brasiliensis	Brazil	Castro, Parana	-24.7833338	-49.9999962
Heraclides thoas brasiliensis	Brazil	Caviuna, Parana	-23.3000002	-51.3666668
Heraclides thoas brasiliensis	Brazil	Joinville	-26.3000002	-48.8333340
Heraclides thoas brasiliensis	Brazil	Massaranduba	-26.6118578	-49.0306091
Heraclides thoas brasiliensis	Brazil	Paraiba	-7.6219297	-38.7150265
Heraclides thoas brasiliensis	Brazil	Ponta Grossa, Parana	-25.0833330	-50.1499977
Heraclides thoas brasiliensis	Brazil	Rio de Janeiro	-22.9000006	-43.2333317
Heraclides thoas brasiliensis	Brazil	Santa Catarina	-27.6536022	-51.0562440
Heraclides thoas brasiliensis	Brazil	Sao Bento do Sul	-26.2497215	-49.3824978
Heraclides thoas brasiliensis	Paraguay	Itaipu	-25.3663640	-54.6027374
Heraclides thoas brasiliensis	Paraguay	Sapucai	-25.6768055	-56.9555282
Heraclides thoas cinyras	Bolivia	Beni	-14.0000005	-65.4999962
Heraclides thoas cinyras	Bolivia	Yungas, La Paz	-16.3333330	-66.7499962
Heraclides thoas cinyras	Brazil	Rondonia	-10.7634447	-63.2903806
Heraclides thoas cinyras	Ecuador	Limoncocha	-0.4013410	-76.6286087
Heraclides thoas cinyras	Ecuador	Misahualli, Napo	-1.0333333	-77.6666718
Heraclides thoas cinyras	Ecuador	Napo	-1.0268233	-77.7159118
Heraclides thoas cinyras	Paraguay	Somerfield	-25.4333324	-55.7166672
Heraclides thoas cinyras	Peru	Cerro Pilcopata	-12.9818095	-72.2749328
Heraclides thoas cinyras	Peru	Chuchurras, Pasco	-10.0892058	-75.1835632
Heraclides thoas cinyras	Peru	Cuzca	-13.5183334	-71.9780540
Heraclides thoas cinyras	Peru	Huanuco	-9.9166670	-76.2333336
Heraclides thoas cinyras	Peru	Iquitos (Explorama Lodge)	-3.7480557	-73.2472229
Heraclides thoas cinyras	Peru	Junin	-11.1588893	-75.9930534
Heraclides thoas cinyras	Peru	La Merced (Chanchamayo)	-11.0500011	-75.3166695
Heraclides thoas cinyras	Peru	Loreto	-4.3692612	-73.8805540
Heraclides thoas cinyras	Peru	Rio Maranon	-4.5000005	-73.4500008
Heraclides thoas cinyras	Peru	Satipo	-11.2666659	-74.6833305
Heraclides thoas cinyras	Peru	Tingo Maria	-9.3000002	-75.9833298
Heraclides thoas neacles	Brazil	Para	-3.6057762	-52.4795815
Heraclides thoas neacles	Colombia	Bogota	4.6101977	-74.0819907
Heraclides thoas neacles	Colombia	Cali, Pance Valle	3.4343724	-76.5191727
Heraclides thoas neacles	Colombia	Calima, Valle del Cauca	3.9341667	-76.4883308
Heraclides thoas neacles	Colombia	Casabe	7.0262756	-73.8957595
Heraclides thoas neacles	Colombia	Muzo, Boyaca	5.5352774	-74.1077766
Heraclides thoas neacles	Colombia	Villavicencio	4.1471472	-73.6132431
Heraclides thoas neacles	Costa Rica	Alajuela	10.0166702	-84.2166672
Heraclides thoas neacles	Costa Rica	Buenos Aires	9.1666670	-83.3333359
Heraclides thoas neacles	Costa Rica	Cartago	9.8579221	-83.9225006
Heraclides thoas neacles	Costa Rica	Guanacaste	10.4723953	-85.3607331

Heraclides thoas neacles	Costa Rica	Limon	9.9901526	-83.0611038
Heraclides thoas neacles	Costa Rica	Magsasay	10.4098194	-84.0546798
Heraclides thoas neacles	Costa Rica	Puntarenas	10.4662055	-84.4628906
Heraclides thoas neacles	Costa Rica	Rio Blanco	9.5100160	-83.6124801
Heraclides thoas neacles	Costa Rica	San Jose	9.9400598	-84.0995256
Heraclides thoas neacles	Costa Rica	Santa Elena	10.3142437	-84.8240661
Heraclides thoas neacles	Ecuador	Guayas	-2.2619091	-80.2688598
Heraclides thoas neacles	Ecuador	Palenque (river)	-1.4332230	-79.7552490
Heraclides thoas neacles	Ecuador	Reserva Endesa (Pichincha)	-0.1937742	-78.7309531
Heraclides thoas neacles	Ecuador	Santo Domingo de Los Colorados	-0.2540580	-79.1757202
Heraclides thoas neacles	Ecuador	Pichincha	-0.1187895	-78.8632965
Heraclides thoas neacles	Ecuador	Quito (Tinalandia)	-0.2167000	-78.5000000
Heraclides thoas neacles	Panama	Bocas del Toro Province	9.3468013	-82.2548527
Heraclides thoas neacles	Panama	Cerro Campana	8.7166700	-79.9000015
Heraclides thoas neacles	Panama	Gatun, Canal Zone	9.2668795	-79.9166718
Heraclides thoas neacles	Panama	Tocumen (near airport)	8.9817528	-79.5097947
Heraclides thoas neacles	Suriname	Zanderij	5.4499998	-55.2000008
Heraclides thoas neacles	Trinidad & Tobago	Arima	10.6423879	-61.2776184
Heraclides thoas neacles	Trinidad & Tobago	Fondes Amandes	10.6861647	-61.5158843
Heraclides thoas neacles	Trinidad & Tobago	Port of Spain	10.6520390	-61.5148190
Heraclides thoas neacles	Trinidad & Tobago	St Ann's	10.6757904	-61.5186309
Heraclides thoas neacles	Trinidad & Tobago	Trinidad	10.4175858	-61.2377929
Heraclides thoas neacles	Venezuela	Apure	7.0935764	-69.3757591
Heraclides thoas neacles	Venezuela	Aragua	9.8758490	-66.9012451
Heraclides thoas neacles	Venezuela	Carabobo	10.0337668	-68.2086181
Heraclides thoas neacles	Venezuela	Maracay	10.2469449	-67.5958366
Heraclides thoas neacles	Venezuela	Merida, El Vigia	8.6166663	-71.6666718
Heraclides thoas oviedo	Cuba	Granma	20.2480250	-77.0004272
Heraclides thoas oviedo	Cuba	Loma del Gato	20.3166676	-76.4166718
Heraclides thoas oviedo	Cuba	Pinar L Rio	22.5810465	-83.6595153
Heraclides thoas oviedo	Cuba	Santiago de Cuba	20.0247221	-75.8219452
Heraclides thoas thoantiades	Argentina	Belgrano	-25.8759054	-63.8947677
Heraclides thoas thoantiades	Argentina	Buenos Aires	-34.6284992	-58.4470319
Heraclides thoas thoantiades	Argentina	Cerro San Bernardo	-24.7833309	-65.4166718
Heraclides thoas thoantiades	Argentina	Entre Rios	-32.1033247	-59.2771320
Heraclides thoas thoantiades	Argentina	Piquirenda	-22.3333330	-63.7833328
Heraclides thoas thoantiades	Argentina	Salta	-24.7833309	-65.4166718

Heraclides thoas thoantiades	Argentina	San Pedro de Jujuy, Jujuy	-24.1833305	-65.3000031
Heraclides thoas thoas	French Guiana	Montagne du Mahury	4.9105967	-52.3105825
Heraclides thoas thoas	Guyana	Guyana	4.9999995	-58.9999962
Heraclides thoas thoas	Guyana	Mckenzie	5.9999995	-58.2833328
Heraclides thoas thoas	Guyana	Moco Moco River Valley	3.3358975	-59.6664047
Heraclides thoas thoas	Guyana	Potaro River, Essequibo	5.3666663	-58.8999977
Heraclides thoas thoas	Guyana	Tumatumari	5.2591703	-59.1476440
Heraclides torquatus atsukoae	El Salvador	San Salvador	13.6999998	-89.1999969
Heraclides torquatus jeani	Colombia	Muzo, Boyaca	5.5352774	-74.1077766
Heraclides torquatus jeani	Trinidad	Cat's Hill	10.1986191	-61.2074947
Heraclides torquatus jeani	Venezuela	Carabobo	10.1108380	-68.0754089
Heraclides torquatus leptalea	Ecuador	Rio Verde	-2.3166661	-80.7000008
Heraclides torquatus leptalea	Ecuador	Riobamba	-1.6722593	-78.6524963
Heraclides torquatus leptalea	Ecuador	Pichincha	-0.1187895	-78.8632965
Heraclides torquatus leptalea	Peru	La Merced (Chanchamayo)	-11.0500011	-75.3166695
Heraclides torquatus mazai	Mexico	Mismaloya, Puerto Vallarta, Jalisco	20.5552547	-105.2690049
Heraclides torquatus polybius	Bolivia	Beni	-14.0000005	-65.4999962
Heraclides torquatus polybius	Bolivia	Buena Vista, Santa Cruz	-17.4499998	-63.6666660
Heraclides torquatus polybius	Brazil	Nova Lima	-19.9833336	-43.8500023
Heraclides torquatus polybius	Brazil	Rio de Janeiro	-22.9000006	-43.2333317
Heraclides torquatus polybius	Brazil	Rio Solimoes, Lavras	-21.2611637	-45.0228631
Heraclides torquatus polybius	Brazil	Santa Crezda, Serra	-20.1166706	-40.2999992
Heraclides torquatus tolmides	Costa Rica	Carara National Park	9.7280072	-84.5947265
Heraclides torquatus tolmides	Ecuador	Pichincha	-0.1287895	-78.8632965
Heraclides torquatus tolus	Mexico	Canon del Novillo, TAMPS	23.7140105	-99.1200685
Heraclides torquatus tolus	Mexico	Piste, YUC	20.6984653	-88.5882797
Heraclides torquatus tolus	Mexico	Presidio, Veracruz-Llave	19.3333330	-96.6666718
Heraclides torquatus tolus	Mexico	San Francisco	18.5333338	-100.2666664
Heraclides torquatus tolus	Mexico	San Luis Potosi	22.1500006	-100.9833336
Heraclides torquatus torquatus	Brazil	Amazonas	-3.7217452	-65.7312011
Heraclides torquatus torquatus	Brazil	Fazenda, Rancho Grande	-26.5999994	-50.2499962
Heraclides torquatus torquatus	Brazil	Misahualli, Rio Napo	-1.0326589	-77.6651000
Heraclides torquatus torquatus	Brazil	Obidos	-1.9083333	-55.5188885
Heraclides torquatus torquatus	Brazil	Rio Madeira, Manicore	-6.6468750	-62.3137664
Heraclides torquatus torquatus	Brazil	Rio Negro	-19.4606167	-54.9767095
Heraclides torquatus torquatus	Brazil	Rio Tapajos	-2.7846239	-55.0009918

Heraclides torquatus torquatus	Brazil	Rondonia	-10.7634447	-63.2903806
Heraclides torquatus torquatus	Brazil	Teffe, Amazonas	-3.3666661	-64.7000008
Heraclides torquatus torquatus	French Guiana	Bas-Maroni	3.6499996	-53.6166668
Heraclides torquatus torquatus	Peru	Huallaga Valley	-5.1388179	-75.6779479
Heraclides torquatus torquatus	Peru	Huanuco	-9.9166670	-76.2333336
Heraclides torquatus torquatus	Peru	Junin	-11.1588893	-75.9930534
Heraclides torquatus torquatus	Peru	Madre de Dios	-11.6208192	-70.5285721
Heraclides torquatus torquatus	Peru	Tingo Maria	-9.3000002	-75.9833298

LIST OF REFERENCES

- Adams JK (2002) What's in a name: Determining what is, and what is not, a new species/subspecies. *News of the Lepidopterists' Society* **24(1)**, 12-15.
- Aubert J, Legal L, Descimon H, Michel F (1999) Molecular phylogeny of swallowtail butterflies of the tribe Papilionini (Papilionidae, Lepidoptera). *Molecular Phylogenetics and Evolution* **12(2)**, 156-167.
- Bates DM (1935(a)) The butterflies of Cuba. *Bulletin of the Museum of comparative Zoology* **78(2)**, 63-258.
- Beccaloni GW, Vilorio AL, Hall SK, Robinson GS (2008) Catalogue of the Hostplants of the Neotropical Butterflies/ Catálogo de las Plantas Huésped de las Mariposas Neotropicales. m3m : Monografías Tercer Milenio **8**, S.E.A. The Natural History Museum. London.
- Beldade P, Brakefield PM (2002) The genetics and evo-devo of butterfly wing patterns. *Nature Reviews Genetics* **3**, 442-452.
- Bessey CE (1908) The Taxonomic Aspect of the Species Question. *The American Naturalist* **42(496)**, 218-224.
- Boisduval J (1836) *Suites à Buffon. Histoire naturelle des Insectes. Spécies général des Lépidoptères*. Paris, Librairie Encyclopédique de Roret 1.
- Brown FM, Heinemann B (1972) *Jamaica and its butterflies*. London, E. W. Classey Ltd.
- Brown JW, Real HG, Faulkner DK (1992) *Butterflies of Baja California. Faunal survey, natural history, conservation biology*. Beverly Hills, The Lepidoptera Research Foundation, Inc.
- Beutelspacher CR (1977) Reconsideración taxonómica de *Papilio tolus* G. y S. (Lep: Papilionidae) y descripción de una nueva subespecie. *Revista de la Sociedad mexicana de Historia natural* **35**, 149-157.
- Beutelspacher CR (1986) Una nueva subespecie mexicana de *Papilio erostratus* Westwood (Insecta, Lepidoptera, Papilionidae). *Anales del Instituto de Biología. Universidad nacional autónoma de México (Zoología)* **56(1)**, 241-244.
- Black SH, Vaughan DM (2005) *Species Profile: Heraclides aristodemus ponceanus*. In Shepherd, MD, Vaughan, DM, Black SH *Red List of Pollinator Insects of North America*. CD-ROM Version 1.
- Burma BH (1949(a)) The species concept: A semantic review. *Evolution* **3(4)**, 369-370.
- Burma BH (1949(b)) Postscriptum. *Evolution* **3(4)**, 372-373.

- Burmeister HCC (1878-[81]) *Description physique de la République Argentine d'après des observations personnelles et étrangères. 5. Lépidoptères. Première partie. Contenant les diurnes, crépusculaires et bombycoïdes*. Buenos Aires, P. E. Coni; Paris, F. Savy; Halle, E. Anton. vi + 526 pp.
- Butler AG, Druce H (1874) List of the butterflies of Costa Rica, with descriptions of new species. *Proceedings of the zoological Society of London* **1874(3)**, 330-370.
- Caterino MS, Reed RD, Kuo MM, Sperling FAH (2001) A partitioned likelihood analysis of swallowtail butterfly phylogeny (Lepidoptera: Papilionidae). *Systematic Biology* **50(1)**, 106-127.
- Caterino MS, Sperling FAH (1999) *Papilio* phylogeny based on mitochondrial cytochrome oxidase I and II genes. *Molecular Phylogenetics and Evolution* **11(1)**, 122-137.
- Chumpitazi ME (2003) Life history of *Priamides anchisiades idaeus*, Fabricius 1793. *News of the Lepidopterists' Society* **45(2)**, 41 & 46.
- Civeyrel LA, Thomas L, Ferguson K, Chase WM (1998) Critical reexamination of palynological characters used to delimit Asclepiadaceae in comparison to the molecular phylogeny obtained from plastid matK sequences. *Molecular Phylogenetics and Evolution* **9**, 517-527.
- Clench HK (1979) *Papilio aristodemus* (Papilionidae in the Bahamas). *Journal of the Lepidopterists' Society* **32(4)**, 273-276.
- Cockerell T (1893) Brief notes on two Jamaican Papilionidae. *Psyche* (Cambridge) **6(205)**, 450.
- Cockerell T (1927) A new subspecies of *Papilio paeon* (Lepidoptera). *Proceedings of the entomological Society of Washington* **29(2)**, 48.
- Collins NM, Morris MG (1985) *Threatened swallowtail butterflies of the world*. The IUCN Red Data Book. Gland, International Union for Conservation of Nature and Natural Resources.
- Cramer P (1775-1780) *De uitlandische Kapellen voorkomende in de drie Waereld-Deelen Asia, Africa en America. Papillons exotiques des trois parties du monde l'Asie, l'Afrique et l'Amérique*. Amsteldam, SJ Baalde; Utrecht, Barthelemy Wild and J Van Schoonhoven & Comp.
- D'Almeida RF (1966) *Catálogo dos Papilionidae americanos*. São Paulo, Sociedade Brasileira de Entomologia.
- Daniels JC, Emmel TC (2004) Florida golf courses help to save endangered butterfly. *USGA Turfgrass and Environmental Research Online* **3(11)**, 1-7.
- DeVries PJ (1987) *The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae*. Princeton, Princeton University Press.

- de Queiroz K (2005) Ernst Mayr and the modern concept of species. *Proceedings of the National Academy of Sciences* **102**, 6600–6607.
- Donnelly TW (1988) Geologic constraints on Caribbean biogeography, in: Liebherr JK (ed) *Zoogeography of Caribbean Insects*, Cornell University Press, Ithaca, New York, 15-37.
- Doubleday E (1846) Descriptions of new or imperfectly described diurnal Lepidoptera. *Annals and Magazine of natural History* **18(121)**, 371-376.
- Ehrlich PR (1958) The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). *University of Kansas Science Bulletin* **39(8)**, 305-370.
- Einem GE (2004) Oviposition and early stages of pink-spotted swallowtail, *Papilio rogeri*, in Mexico. *News of the Lepidopterists' Society* **46(2)**, 41, 52, & 58.
- Erixon P, Sventenblad B, Britton T, Oxelman B (2003) Reliability of bayesian posterior probabilities and bootstrap frequencies in phylogenies. *Systematic Biology* **52(5)**, 665-673.
- Esper EJC (1784-93) *Die ausländische oder die ausserhalb Europa zur Zeit in den übrigen Welttheilen vorgefundene Schmetterlinge in Abbildungen nach der Natur mit Beschreibungen*. Erlangen, Wolfgang Walther 1.
- Esper EJC (1794) *Magazin der neuesten ausländischen Insecten*. Erlangen, Wolfgang Walther 1.
- Esper EJC (1796-1801) *Die ausländische oder die ausserhalb Europa zur Zeit in den übrigen Welttheilen vorgefundene Schmetterlinge in Abbildungen nach der Natur mit Beschreibungen*. Erlangen, Wolfgang Walther 4.
- Fabricius JC (1775) *Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Flensburgi et Lipsiae, Korte.
- Fabricius JC (1793) *Entomologia systematica emendata et aucta. Secundum classes, ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus*. Hafniae, Christian Gottlieb Proft, Fil. et Soc. 3(1).
- Farris JS (1969) A successive approximations approach to character weighting. *Systematic Biology* **18**, 374–385.
- Felder C, Felder R (1859-60) Lepidopterologische Fragmente. *Wiener entomologische Monatschrift* 3(6).
- Felder C, Felder R ([1865]-74) *Reise der österreichischen Fregatte Novara um die 162 Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair. Zoologischer Theil. Zweiter Band. Zweite Abtheilung: Lepidoptera*. Wien, Carl Gerold's Sohn.

- Ford EB (1944) Studies on the chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 4. The classification of the Papilionidae. *Transactions of the royal entomological Society of London* **94(2)**, 201-223.
- Fruhstorfer H (1915) Neue papilionidenrassen aus dem neotropischen Faunengebiet. *Entomologische Rundschau* **32(12)**, 70.
- Geyer C (1827) In: Hübner, J., *Sammlung exotischer Schmetterlinge*. Augsburg, Jacob Hübner. 2.
- Ghiselin MT (1975) A radical solution to the species problem. *Systematic Zoology* **23(4)**, 536-544.
- Gray GR ([1853]) *Catalogue of lepidopterous insects in the collection of the British Museum. Part I. Papilionidae*. London.
- Godart JB (1819) Pp. 13-328. In: Latreille, P. A. & J. B. Godart, *Encyclopédie Méthodique. Histoire naturelle. Entomologie, ou histoire naturelle des crustacés, des arachnides et des insectes*. Paris, veuve Agasse 9.
- Godman FD, Salvin O (1889b-91) *Biologia Centrali-Americana. Insecta. Lepidoptera-Rhopalocera*. London, Dulau & Co., Bernard Quaritch. 2.
- Goose PH (1881) The prehensores of male butterflies of the genera *Ornithoptera* and *Papilio*. *Proceedings of the Royal Society, London* **33**, 23-27.
- Gundlach JC (1866) *Descripción de una nueva especie de mariposa diurnal cubana del género Papilio*, pp. 279-280, 1 pl. In: Poey, F. (Ed.), *Repertorio físico-natural de la Isla de Cuba*. La Habana, Imprenta del Gobierno y Capitanía General por S. M. 1(10).
- Gundlach JC (1891) Apuntes para la fauna puerto-riqueña. *Anales de la Sociedad española de Historia natural* **20(1)**, 109-128.
- Hancock DL (1983) Classification of the Papilionidae (Lepidoptera): a phylogenetic approach. *Smithersia* **2**, 1-48.
- Häuser C, de Jong R, Lamas G, Robbins RK, Smith CR, Vane-Wright RI (2003) Papilionidae – revised GloBIS/GART species checklist (2nd draft). <http://www.insectsonline.de/frames/papilio.htm>
- Hewitson WC (1961) *Illustrations of new species of exotic butterflies, selected chiefly from the collections of W. Wilson Saunders and William C. Hewitson*. London, John Van Voorst. 1(9).
- Honey M, Scoble M (2001) Linnaeus's butterflies (Lepidoptera: Papilionoidea and Hesperioidea). *Zoological Journal of the Linnean Society* **132(3)**, 277-399.

- Hopffer CH (1865) Neue Arten der Gattung *Papilio* im Berliner Museum. *Stettiner entomologische Zeitung* **27(1/3)**, 22-32.
- Hübner J (1809) *Sammlung exotischer Smetterlinge*. Augsburg, Jacob Hübner. Volume 1.
- Hübner J (1819) *Sammlung exotischer Smetterlinge*. Augsburg, Jacob Hübner. Volume 1.
- Hübner J (1823-1825) *Sammlung exotischer Smetterlinge*. Augsburg, Jacob Hübner. Volume 2.
- Igarashi S (1984) The classification of the Papilionidae mainly based on the morphology of their immature stages. *Tyô to Ga* **34(2)**, 41-96.
- Jiang ST, Hong GY, Yu M, Li N, Yang Y, Liu YQ, Wei ZJ (2009) Characterization of the complete mitochondrial genome of the giant silkworm moth, *Eriogyna pyretorum* (Lepidoptera: Saturniidae). *International Journal of Biological Sciences* **5**, 351-365.
- Jordan K, Stichel H (1907) Lepidopterologische Miscellen. III. Zum Heimatnachweis von *Zerynthia cerisyi* God. *Entomologische Zeitschrift*, Frankfurt am Main **21**, 82-83.
- Kristensen NP (1976) Remarks on the family-level phylogeny of butterflies (Insecta, Lepidoptera, Rhopalocera). *Zeitschrift für zoologische Systematik und Evolutionsforschung* **14(1)**, 25- 33.
- Kunte K (2009) The Diversity and Evolution of Batesian Mimicry in *Papilio* Swallowtail Butterflies. *Evolution* **63(10)**, 2707-2716.
- Lamas G (2004) Atlas of Neotropical Lepidoptera. Checklist: Part 4A. Hesperioidea - Papilionoidea. Scientific Publishers, Gainesville.
- Le Cerf FL (1924) Lépidoptères nouveaux de la collection du Muséum (Rhopalocères). *Bulletin du Muséum national d'Histoire Naturelle* (Paris) **30(2)**, 137-139.
- Le Crom JF, Constantino LM, Salazar JA (2002) *Mariposas de Colombia. Tomo I: Papilionidae*. Bogotá, 301 Carlec Ltda.
- Linnaeus C (1771) *Regni animalis*, Appendix. Insecta, pp. 529-543. In: *Mantissa plantarum altera generum editionis VI & specierum editionis II*. Holmiae, Laurentius Salvius.
- Mallet J (1995) A species definition for the Modern Synthesis. *Trends in Ecology and Evolution* **10**, 294-299.
- Mallet J (2007) *Species, concepts of*. In Levin, S.A. (ed.) *Encyclopedia of Biodiversity*. Elsevier, Oxford. Online update, pp. 1-15.
- Mallet J (2008) Hybridization, ecological races, and the nature of species: empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 2971–2986.

- Mayden RL (1997) *A hierarchy of species concepts: the denouement in the saga of the species problem*. In: Claridge, MF, Dawah HA, Wilson, MR (Eds.), *Species: The units of biodiversity*, London: Chapman and Hall, 381-424.
- Mayr E (1949) The species concept: Semantics versus semantics. *Evolution* **3(4)**, 371-372.
- Mayr E (1969) *Principles of systematic zoology*. McGraw-Hill, New York.
- Mayr E (1996) What is a species, and what is not? *Philosophy of Science* **63(2)**, 262-277.
- Ménétriés E (1855-57) *Enumeratio corporum animalium Musei Imperialis Academiae Scientiarum Petropolitanae. Classis insectorum. Ordo lepidopterorum*. Petropoli, Eggers et Soc.; Lipsiae, Leop. Voss 1.
- McAsulane H (2009) *Papilio cresphontes* Cramer (Insecta: Lepidoptera: Papilionidae). <http://entnemdept.ufl.edu/creatures/citrus/giantswallowtail.htm>. Retrieved January 1st 2010.
- Miller JS (1987) Phylogenetic studies in the Papilioninae (Lepidoptera: Papilionidae). *Bulletin of the American Museum of Natural History* **186(4)**, 365-512.
- Miller LD (1969) Nomenclature of wing veins and cells. *Journal of Research on the Lepidoptera* **8(2)**, 37-48.
- Miller LD (1987) A new subspecies of *Heraclides aristodemus* from Crooked Island, Bahamas, with a discussion of the distribution of the species. *Bulletin of the Allyn Museum* **113**, 1-8.
- Miller LD, Miller JY (2001) The biogeography of West Indian butterflies (Lepidoptera): An application of a vicariance/dispersalist model, in: Woods CA (ed), *Biogeography of the West Indies, Patterns and Perspectives*, second edition, CRC Press LLC, USA, 127-152.
- Minno MC, Emmel TC (1993) *Butterflies of the Florida Keys*. Gainesville, Scientific Publishers.
- Möhn E (1999) *Papilionidae V. Neue und wenig bekannte papilioniden aus der neotropischen Region (Papilionidae, Lepidoptera)*. In: Bauer, E. & T. Frankenbach (Eds.), *Butterflies of the World*. Keltern, Goecke & Evers. **8**, 1-5.
- Moreau E (1923(a)) Un *Papilio* nouveau de la Guyane française. *Bulletin de la Société entomologique de France* **10**, 144.
- Moreau E (1923(b)) Rectification (Lep.). *Bulletin de la Société entomologique de France* **17**, 215.
- Munroe E (1961) The Classification of the Papilionidae (Lepidoptera). *The Canadian Entomologist supplement* **17**, 1-51.
- Nazari VE, Zakharov V, Sperling FAH (2007) Phylogeny, historical biogeography, and taxonomic ranking of Parnassiinae (Lepidoptera, Papilionidae based on morphology and seven genes. *Molecular Phylogenetics and Evolution* **42(1)**, 131-156.

- Nijhout HF (1991) The Development and Evolution of Butterfly Wing Patterns. Smithsonian Series in Comparative Evolutionary Biology. Smithsonian Institution Press.
- Nijhout HF (2001) Elements of butterfly wing patterns. *Journal of Experimental Zoology* **291**, 213-225.
- Nijhout HF (2003) Polymorphic mimicry in *Papilio dardanus*: mosaic dominance, big effects, and origins. *Evolution and Development* **5(6)**, 579-592.
- Oberthür C (1879) Catalogue raisonné des Papilionidae de la collection de Ch. Oberthür à Rennes. *Études d'Entomologie* **4**: i-xviii, 19-117.
- Okano K (1985) Descriptions of four new butterflies on Amathusiidae, Nymphalidae and Papilionidae (Lepidoptera). *Tokurana* **10(2)**, 1-17.
- Pelham JP (2008) A Catalogue of the Butterflies of the United States and Canada. *The Journal of Research on the Lepidoptera* **40**, 658 p.
- Penz CM, de Araújo AM (1991) Interaction between *Papilio hectorides* (Papilionidae) and four host plants (Piperaceae, Rutaceae) in a southern Brazilian population. *Journal of Research on the Lepidoptera* **29(1/2)**, 161-171.
- Poey F (1852) XIV [sic]. *Centuria de lepidópteros y catálogo de las mariposas de la Isla de Cuba. Obras ya publicadas por el autor de estas memorias*, pp. 194-200. In: *Memorias sobre la Historia Natural de la Isla de Cuba, acompañadas de sumarios latinos y extractos en francés*. La Habana, Imprenta de Barcina 1.
- Racheli T, Racheli L (1995) Two new subspecies of *Heracles isidorus* (Doubleday, 1846) (Lepidoptera: Papilionidae). *Lambillionea* **4(2)**, 620-624.
- Reed RD, Sperling FAH (1999) Interaction of process partitions in phylogenetic analysis: An example from the swallowtail butterfly genus *Papilio*. *Molecular Biology and Evolution* **16(2)**, 286-297.
- Riley ND (1975) *A field guide to the butterflies of the West Indies*. London, Collins.
- Roe AD, Sperling FAH (2007) Patterns of evolution of mitochondrial cytochrome c oxidase I and II DNA and implications for DNA barcoding. *Molecular phylogenetics and evolution* **44(1)**, 325-45.
- Rothschild LW, Jordan HEK (1906) A revision of the American *Papilios*. *Novitates Zoologicae* **13(3)**, 411-752.
- Rozycki R (2004) A “tasso”-like aberration of *Papilio torquatus*. *News of the Lepidopterists' Society* **46(1)**, 5 & 7.
- Rütimeyer KE (1969) A new *Papilio* from Colombia and a new Spingid from New Guinea. *Journal of the Lepidopterists' Society* **23(4)**, 255-257.

- Schaus W (1911) A new *Papilio* from Florida and one from Mexico. *Entomological News* **22(10)**, 438-439.
- Schwartz A (1989) *The butterflies of Hispaniola*. Gainesville, University of Florida Press.
- Scriber JM, Lederhouse RC (1996) Illustrated field notes on *Papilio astyalus pallas* in Costa Rica (Lepidoptera: Papilionidae). *Tropical Lepidoptera* **7(2)**, 119-120.
- Scriber JM, Tsubaki Y, Lederhouse RC (Eds.) (1995) *Swallowtail butterflies: Their ecology and evolutionary biology*. Gainesville, Scientific Publishers.
- Seitz A (1907) *Einleitung. Die Gross-Schmetterlinge des Amerikanischen Faunengebietes*. In: *Die Gross-Schmetterlinge der Erde*. Stuttgart, Alfred Kernen. **5**, 1-8.
- Sharpe EM (1900) On a collection of butterflies from the Bahamas. *Proceedings of the zoological Society of London* **2**, 197-203.
- Simpson GG (1951) The species concept. *Evolution* **5(4)**, 285-298.
- Smith CR, Vane-Wright RI (2008) Classification, nomenclature and identification of lime swallowtail butterflies: a post-cladistic analysis (Lepidoptera: Papilionidae). *Systematics and Biodiversity* **6(2)**, 175-203.
- Smith DS, Miller LD, Miller JY (1994) *The Butterflies of the West Indies and South Florida*. Oxford, Oxford University Press.
- Sourakov (2008) Artificial hybridization and natural speciation in *Cercyonis pegala* (Nymphalidae, Satyrinae). *News of the Lepidopterists' Society* **50(2)**, 49 & 52.
- Staudinger O (1884-88) *I. Theil. Exotische Tagfalter in systematischer Reihenfolge mit Berücksichtigung neuer Arten*. In: Staudinger O, Schatz E (1884-1892) *Exotische Schmetterlinge*. Fürth, G. Löwensohn.
- Staudinger O (1892) Neue Papilio-Formen aus Südamerika. *Deutsche entomologische Zeitschrift "Iris"* **5(2)**, 427-428.
- Sukumaran J, Linkem CW (2009) Choice of Topology Estimators in Bayesian Phylogenetic Analysis. *Molecular Biology and Evolution* **26**, 1-3.
- Swainson W (1829-33) *Zoological illustrations, or original figures and descriptions of new, rare or interesting animals, selected chiefly from the classes of ornithology, entomology, and conchology, and arranged according to their apparent affinities. Second series*. London, Baldwin, Cradock, and Joy & W. Wood.
- Swainson W (1820-23) *Zoological illustrations, or original figures and descriptions of new, rare, or interesting animals, selected chiefly from the classes of ornithology, entomology, and conchology, and arranged on the principles of Cuvier and other modern zoologists*. London, Baldwin, Cradock, J & W Wood.

- Townsend CHT (1893) The larva of *Papilio thersites*, Fab. *Journal of the Institute of Jamaica* **1(8)**, 376-377.
- Tyler HA, Brown KS, Wilson KH (1994) *Swallowtail butterflies of the Americas. A study in biological dynamics, ecological diversity, biosystematics, and conservation*. Gainesville, Scientific Publishers.
- US Fish & Wildlife Service (1999) Multi-species Recovery Plan for South Florida (Revision 5/18/99). Accessed January 1st, 2010 from <http://www.fws.gov/southeast/vbpdfs/species/inverts/ssbu.pdf>
- Van Dinter JBM (1957) *Papilio anchisiades anchisiades* Esper, a Citrus pest of minor importance. *Entomologische Berichten* **17(10)**, 213-216.
- Vázquez L (1947) Papilios nuevos de México. *Anales del Instituto de Biología de México* **18(1)**, 249-256.
- Walker JJ (1882) A life history of *Papilio paeon*, Roger. *Entomologist's monthly Magazine* **19(219)**, 53-55.
- Westwood JO (1847) Description of two new exotic species of the genus *Papilio*. *Transactions of the entomological Society of London* **5(2)**, 36-37.
- Westwood JO (1872) Descriptions of some new Papilionidae. *Transactions of the entomological Society of London* **2**, 85- 110.
- Wheeler WC, Pickett KM (2008) Topology-Bayes versus clade-Bayes in phylogenetic analysis. *Molecular Biology and Evolution* **25**, 447-453
- Wiens JA (1982) Forum: Avian subspecies in the 1980's. *The Auk* **99(3)**, 593-595.
- Young AM, Blum MS, Fales HM, Bian Z (1986) Natural history and ecological chemistry of the Neotropical butterfly *Papilio anchisiades* (Papilionidae). *Journal of the Lepidopterists' Society* **40(1)**, 36-53
- Zakharov^a EV, Caterino MS, Sperling FAH (2004) Molecular phylogeny, historical biogeography, and divergence time estimates for swallowtail butterflies of the genus *Papilio* (Lepidoptera: Papilionidae). *Systematic Biology* **53(2)**, 193-215.
- Zakharov^b EV, Smith CR, Lees DC, Cameron A, Vane-Wright RI, Sperling FAH (2004) Independent gene phylogenies and morphology demonstrate a Malagasy origin for a wide-ranging group of swallowtail butterflies. *Evolution* **58(12)**, 2763-2782.

BIOGRAPHICAL SKETCH

Delano Lewis, the fourth of five children, has been fascinated with insects and the natural world ever since he was a young boy growing up in Manchester, Jamaica. This fascination naturally led him to the field of biology, and he eventually received his Bachelor of Science (B.Sc.) in zoology at Mona, Kingston, Jamaica from the University of the West Indies in 1998. After completing his undergraduate studies, he continued on to graduate school where, after a short stint as a teaching assistant, he secured a graduate assistantship with the Jamaican Iguana Recovery Group doing research on the conservation of the critically endangered Jamaican Iguana, and the impact that an introduced predator, the Indian mongoose, had on the native reptiles of a dry forest ecosystem. His research led to the completion of a Masters of Philosophy (M.Phil.) in zoology in 2002. He started as a part-time instructor at Northern Caribbean University in Jamaica while he was still in graduate school, and accepted a full time faculty position upon his completion. While there, he taught several introductory and advanced biology courses and served as the Coordinator of Laboratories for the Biology Department.

He decided to continue his education and follow his dream of being an insect taxonomist and was accepted at the University of Florida in 2004. He was awarded a Master of Science (M.Sc.) in Entomology from the Department of Entomology and Nematology 2006; his focus was on Lepidoptera taxonomy. The topic of his thesis was “Revision of *Cyllopoda* (Lepidoptera: Geometridae: Sterrhinae: Cyllopodini). He then continued on to the Ph.D. program where his research is on the systematics of a group of Neotropical swallowtail butterflies, the *Heraclides*. Upon completion of his Ph.D. program, Delano hopes to secure a post-doctorate position. He has been married to Dadria Lewis (M.Ed., Ed.S.) for eight years, and they are expecting their first child in July 2010, just shy of their ninth anniversary.