

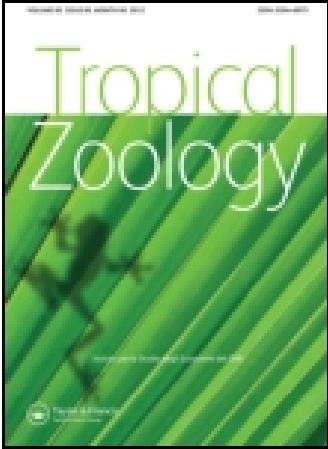
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Biogeographical patterns of the neotropical genus *Battus* Scopoli 1777 (Lepidoptera Papilionidae)

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A phylogenetic approach to the groups of species of the neotropical Troidines currently included in the genus *Battus* Scopoli 1777 has been conducted. In the light of historical and ecological processes of evolution in the neotropical biota, the cladogram of Battiti is discussed. General vicariance patterns, as well as dispersal events which contributed to the present distribution of the taxa, are suggested to have operated at different spatial and temporal points.

KEY WORDS: Insecta, Lepidoptera, *Battus*, taxonomy, cladistics, biogeography, Neotropical region.

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INTRODUCTION

The genus *Battus* Scopoli 1777 is a fairly homogeneous unit. All the species share black wings with green sheens. They have yellow or orange spots on the body, and peculiar fluted androconia on the hindwings. They are endemic to north-central and south America, and all are monophagous on Aristolochiaceae. In the Greater Antilles two species are endemic, while in the Lesser Antilles the genus is represented only by *B. polydamas*.

The genus *Battus* is recognized by MILLER (1987) as a monophyletic taxon within the tribe Troidini on the basis of a series of characters:

1. The upper discocellular vein of the forewing is longer than the medial.
2. The bursa shows a membranous ductus. MILLER (1987), observing this character in the genera *Cressida* Swainson [1832] and *Euryades* C. & R. Felder 1864,

suggests that the plesiomorphic state in the Troidini is a sclerotized ductus, and hence this appears to be an apomorphy in *Battus*.

3. The androconia of the hindwings are fluted. The shape of these scales in *Battus* is different from those of all other Papilionidae. The saccular and channelled shape seems to enhance the surface available for the dispersion of chemical substances.

4. Vein 1A + 2A of the male hindwing is tubular and swollen.

5. The anterior membrane of the ostium exhibits silk protuberances. In some pierid species the females show similar structures, which are unlikely to be homologous. Their function in *Battus* is unknown.

As far as the systematic arrangement of the species is concerned, the old classification of ROTHSCHILD & JORDAN (1906) underwent minor changes by recent authors (FORD 1944, MUNROE 1961, HANCOCK 1983) who recognized two groups of species (the *B. philenor* group and the *B. belus* group) mainly on the simplistic basis of the presence or absence of the series of submarginal spots on the hindwing.

The genus, which involves relatively few species, most of which are endemic, is suitable for phylogenetic and biogeographical studies. Some systematic or nomenclatorial changes from the current species classification have been made (RACHELI & PARISET 1992).

MATERIALS AND METHODS

More than 1700 specimens were examined in Museums or private collections to score external characters. Table 1 shows the species or species complexes, that were employed as OTUs in the phylogenetic analysis.

Character state, according to Table 2 and 3, is based on pattern, male genitalia, and androconial scales. In *Battus* species the peculiar male anal fold of the hindwing has two types of scales (Fig. 1), type I in the anal cell and type II along vein 1A + 2A, that correspond to scales *a* and *b* of BARTH (1950). Preimaginal stages as well as female genitalia were not considered because of lack of material and informations for many species.

Table 1.
List of *Battus* species, and distributions.

<i>B. philenor</i> (Linnaeus 1771) - Southern Canada to Southern Mexico - Polytypic
<i>B. devilliers</i> (Godart [1824]) - Endemic to Cuba - Monotypic
<i>B. zetides</i> (Munroe 1971) - Endemic to Hispaniola - Monotypic
<i>B. polydamas</i> (Linnaeus 1758) - Florida to Northern Argentina - Polytypic
<i>B. streckerianus</i> (Honrath 1884) - Endemic to Peru - Polytypic
<i>B. archidamas</i> (Boisduval 1836) - Pacific coast of Chile - Monotypic
<i>B. madyes</i> (Doubleday 1846) - Ecuador to Argentina - Polytypic
<i>B. eracon</i> (Godman & Salvin 1897) - Pacific coast of Mexico - Monotypic
<i>B. ingenuus</i> (Dyar 1907) - East Mexico to East Ecuador - Monotypic
<i>B. belus</i> (Cramer 1777) - East Colombia, Brazil, Peru, Bolivia - Polytypic
<i>B. laodamas</i> (C. & R. Felder 1859) - Mexico to Central Colombia - Polytypic
<i>B. polystictus</i> (Butler 1874) - SE Brazil to Northern Argentina - Monotypic
<i>B. lycidas</i> (Cramer 1777) - Mexico to Brazil - Monotypic
<i>B. crassus</i> (Cramer 1777) - Costa Rica to Southern Brazil - Polytypic

Table 2.
Characters and character-state data for *Battus* species used in Table 3.

- (1) Sexual dimorphism: 0 = absent, 1 = present
- (2) Tails: 0 = present, 1 = absent
- (3) Male abdomen colour: 0 = dark, 1 = not dark
- (4) Process of harpe perpendicular: 0 = absent, 1 = present
- (5) Scales in S8 UnHWs: 0 = present, 1 = absent
- (6) Ventral abdominal spots: 0 = absent, 1 = present
- (7) Silvery patches UnHWs: 0 = present, 1 = absent
- (8) Abdominal lateral stripe: 0 = present, 1 = absent
- (9) UnHWs submarginal band colour: 0 = red, 1 = yellow
- (10) Androconial scale I: 0 = globe-like, 1 = flat
- (11) Androconial scale II: 0 = not elongated, 1 = elongated
- (12) Blue scales on female abdomen: 0 = absent, 1 = present
- (13) UpHWs costal spot: 0 = absent, 1 = present
- (14) Ridges on pseuduncus: 0 = absent, 1 = present
- (15) Shape of valva: 0 = rounded, 1 = triangular
- (16) Aedeagus: 0 = not bended, 1 = proximally bended, 2 = distally bended
- (17) Aedeagus/valva length: 0 = < 1; 1 = ≥ 1
- (18) Harpa structure: 1 = with central tooth, 2 = without tooth, 3 = with one or two distal teeth, 4 = with three distal teeth

Abbreviations: S = internervular space; UnHWs = underside of the hindwings; UpHWs = upperside of the hindwings.

The 18 characters listed in Table 2 were used for this analysis. They include binary as well as multistate codings (Table 3). The PAUP package (Release 2.4.1, SWOFFORD 1984) was employed. It is based on the «maximum parsimony» principle, often referred to as the «Wagner method» (KLUGE & FARRIS 1969, FARRIS 1970), which searches for the tree(s) of the minimal length in a Manhattan metric.

Table 3.
Matrix of character-states of the OTUs employed in the phylogenetic analysis
(for explanation see Table 2).

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Euryades</i>	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	3
<i>B. philenor</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	3
<i>B. devilliers</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0	3
<i>B. zetides</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	3
<i>B. streckerianus</i>	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	2	1	3
<i>B. polydamas</i>	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	2	0	3
<i>B. madyes</i>	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0	2	1	1
<i>B. polystictus</i>	0	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	0	3
<i>B. eracon</i>	0	1	1	1	1	1	1	0	1	0	1	0	0	1	0	1	0	2
<i>B. archidamas</i>	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	3
<i>B. belus</i>	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	0	2
<i>B. crassus</i>	1	1	1	0	1	1	1	0	1	1	1	0	1	1	0	1	1	2
<i>B. lycidas</i>	0	1	1	1	1	1	1	0	1	0	1	1	0	1	0	1	1	4
<i>B. ingenuus</i>	1	1	1	1	1	1	1	0	1	1	1	0	1	0	0	2	1	2
<i>B. laodamas</i>	0	1	1	1	1	0	1	0	1	1	1	0	1	1	0	1	0	2



Fig. 1. — Androconial scales of the anal area of the hindwings of *Battus ingenuus*: A, type I; B, type II.

The data set (15 taxa, 18 characters) was at the maximum size limit for using an exact algorithm, i.e. one that will find all equally parsimonious trees. We chose the «branch-and-bound method» (HENDY & PENNY 1982) as modified by SWOFFORD in the PAUP package. Multistate characters (chrs 16, 18) were treated as unordered. Tree rooting was obtained by the ROOT = OUTGROUP option, using *Euryades*, a neotropical Troidine genus shown by MILLER (1987) to be a close relative of *Battus*, as the outgroup. The program CONTREE, included in the PAUP package, was employed to produce a strict consensus tree.

RESULTS

Thirty-two equally parsimonious trees (Fig. 2) resulted from this analysis (CI = 0.488). These differ in the minor branches, but the major clades show the same general pattern; this is confirmed by the strict consensus tree (Fig. 3).

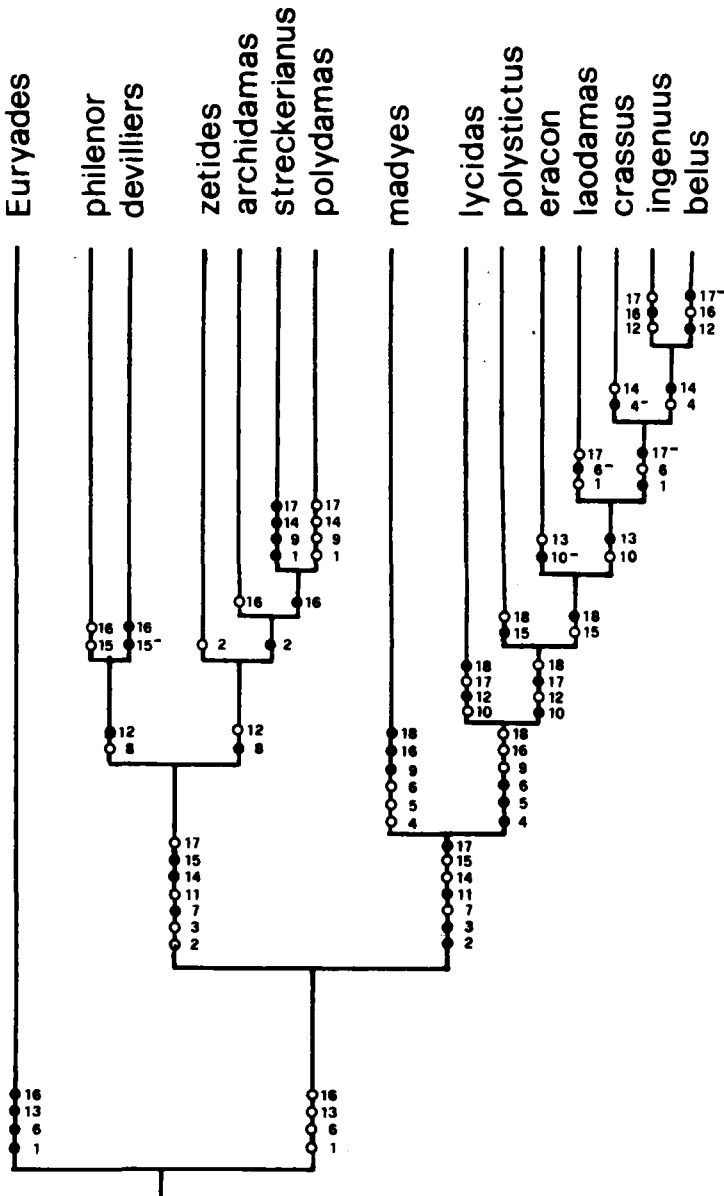


Fig. 2. — Cladistic relationships of the Battiti. One of 32 equally parsimonious trees, showing the distribution of the apomorphies (closed circles) and plesiomorphies (open circles) (a «-» marks reversals).

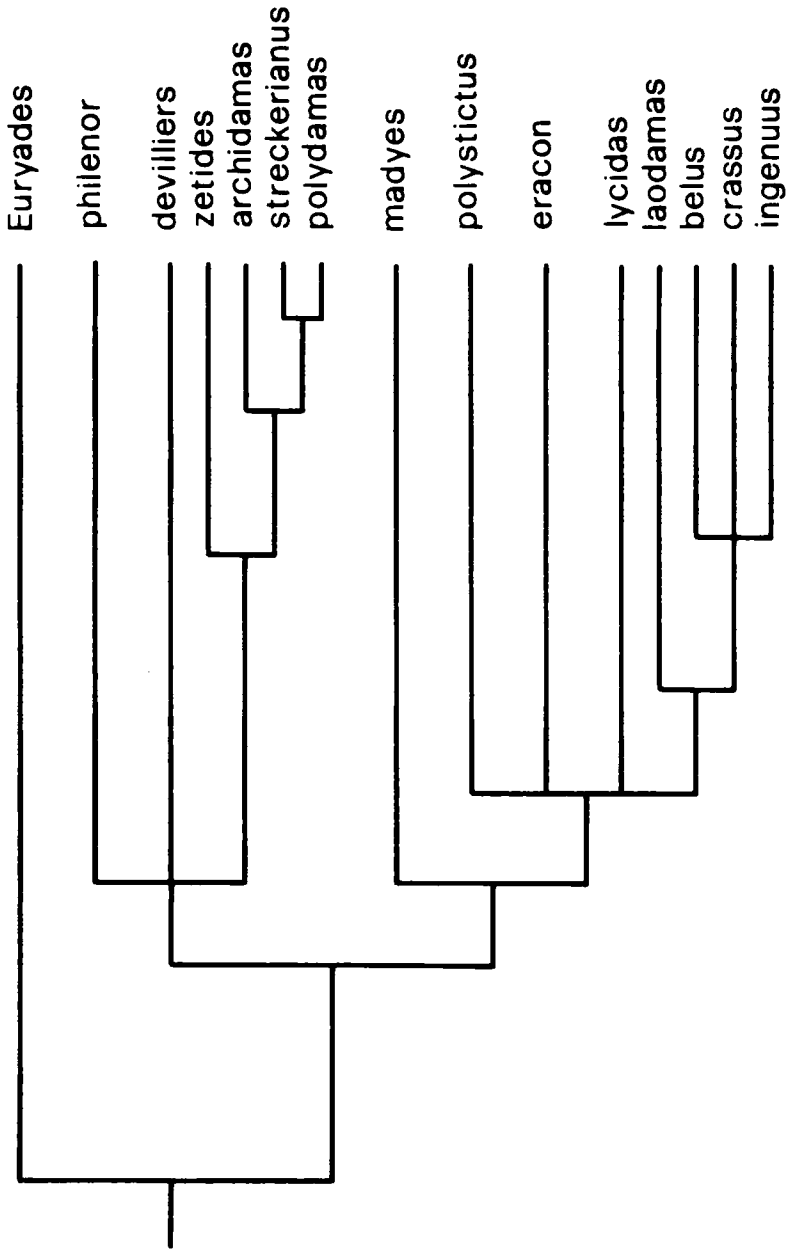


Fig. 3. — Strict Consensus Tree of the 32 most parsimonious trees.

Two major groups emerge from the cladograms: the first fits with a geographical position in the Andean, Transandean and Antillean areas. Three autoapomorphies (chs 7, 14, 15) support this group, which displays relatively few evolutionary novelties. A total of 13 character-state changes are recorded for this clade. The *B.*

archidamas, *B. streckerianus*, *B. polydamas* group, which includes biologically and morphologically separated entities, are terminal taxa in two related clades. A close relationship between *B. philenor* and *B. devilliers* is also suggested by most of the equally parsimonious trees.

The second group comprises taxa whose ranges are mainly Amazonian and Transandean. This clade seems to be less homogeneous and shows a higher trend to diversification. Besides the four autapomorphies (chrs 2, 3, 11, 17) supporting its basal node, 22 other changes are recorded; most of the trees display several reversals in this clade.

The *B. madyes* complex, limited to the Andes, takes a middle position in the cladogram, separated from the other taxa. This complex belongs to the second group in each of the 32 equally parsimonious trees, as shown by four synapomorphies (chrs 2, 3, 11, 17). Nothing is known about the preimaginal stages of these species. It is noteworthy that previous authors (ROTHSCHILD & JORDAN 1906, MUNROE 1961, HANCOCK 1983) placed *B. madyes* with the species of the *polydamas* group based on overall pattern only. In most of the 32 equally parsimonious trees, *B. lycidas* remains partially isolated (i.e. Fig. 1); *B. eracon* and *B. polystictus*, which have widely disjunct ranges, share many character states and occupy a closer position in the trees, though in the Consensus Tree they are all unresolved. *B. laodamas*, *B. crassus*, *B. ingenuus* and *B. belus* appear as the most differentiated species.

DISCUSSION

The main theory of the last 20 years to explain the present-day distribution of animals and plants in the Neotropical Region, is the refugia theory (HAFFER 1967, 1969).

During the Pleistocene, climatic alterations fragmented the Amazonian rain forest into «refugia», or islands of forest where populations were trapped and isolated for a long period of time. This period would have been long enough to lead to speciation before secondary contacts were permitted by climatic conditions.

The refugia theory is attractive because it may provide an explanation for the species richness of the Tropics. Many biologists have used it to justify the distribution and speciation of birds, butterflies, lizards, mammals and plants in America, Africa and Australia (KEAST 1961, 1974; CARCASSON 1963; VUILLEUMIER 1971; MÜLLER 1972; PRANCE 1973, 1978, 1982; VANZOLINI 1973; BROWN et al. 1974; HAFFER 1974, 1977, 1978, 1983, 1985; HAMMEN 1974; BROWN 1975; LIVINGSTONE 1975; HAMILTON 1976; DESCIMON 1977; BROWN & AB' SABER 1979; MAYR & O'HARA 1986; SIMPSON & HAFFER 1978). Alternative hypotheses, mainly ecological, for neotropical species diversity have been suggested by other authors (ENDLER 1977, 1982a, 1982b; COLINVAUX 1979; BEVEN et al. 1984; CONNOR 1986; BUSH 1988; LYNCH 1988).

The wide ranges of many *Battus* species obscure the possible influence of refugia. There are strict Transandean taxa, like *B. laodamas* with clearly outlined subspecies, but also Amazonian/Transandean species, like *B. lycidas* and *B. ingenuus*, with very little variability. *B. crassus*, with two cis- and trans-andean subspecies, could to a certain degree fit HAFFER's model. The range of *B. polystictus*, restricted to Serra do Mar, as well as some populations of *B. belus* in Guyana, Belém and East Peru, may be congruent with Pleistocene refugia.

HAFER's theory, based on rain forest species, is not strictly applicable for the Andean, Transandean or Antillean species, such as *B. streckerianus*, *B. archidamas*, *B. eracon*, *B. philenor*, *B. devilliers* and *B. zetides*. These species, except *B. eracon*, are limited to xeric habitats or habitats characterized by low annual precipitation. *B. madyes* is linked to upper montane rain forests and cloud forests. In the Transandean area, however, the distribution of some species of *Battus* seems to match that of Ithomiinae and Heliconiini (BROWN 1977, 1979, 1982). One can speculate that this type of distribution originated during the late and mid-Tertiary, when the Andes were lower than 2000 m in altitude and «packages» of ancestors were sequestered. The species may have evolved independently, subsequently dividing into north and south vicariants. Today this phenomenon is supported by the pairs of closely related trans- and cisandean species. Among other neotropical Troidini, the transandean *Parides eurimedes* (Cramer 1782) and its cisandean vicariant *P. neophilus* (Geyer 1837), parapatric in Venezuela and Colombia, and the Atlantic *P. zacyntus* (Fabricius 1793) show a vicariant pattern of closely related species. BROWN (1987) explains this phenomenon in terms of Quaternary refugia, but this vicariance seems to be much older than the supposed refugia; it was probably due to paleogeographical or paleoclimatic barriers and it can be geographically substantiated with the interruption of the biota by the Andes. Various Lepidoptera, such as Brassolinae (BLANDIN & DESCIMON 1975, 1977; BLANDIN 1977, 1978) and Riodininae (CALLAGHAN 1986), show a similar trend.

An interpretation of the cladogram of Battiti suggests that long periods of divergence of the taxa occurred at different times. The Battiti might have evolved in isolation in southern America and in the mesoamerican area with subsequent dispersal in both directions following the connection of the isthmus of Darién.

The few Battiti endemics in the Greater Antilles fit a vicariant process with a pattern similar to those of the Danaids *Anetia* Hübner 1823 (ACKERY & VANE-WRIGHT 1984) and of the Ithomids *Greta* Hemming 1934. Pleistocene climatic changes in the Antillean regions were claimed by CLENCH (1963) to have induced the present-day distribution of Lycaenidae. These changes seem not to have influenced *Battus* species except perhaps *B. polydamas*, which in the Lesser Antilles has developed several distinct populations.

From the data obtained on *Battus* it seems unlikely that Pleistocene phenomena have had dramatic effects on its evolutionary history. The picture reflects a multitude of direct or indirect effects. Interestingly, the cladogram separates the species into two groups, r-selected and K-selected. The eggs of the species of the *philenor*-clade are laid in small numbers, while those of the other clade are usually laid in batches of more than 20 eggs. Regrettably, nothing is known about preimaginal stages of *B. madyes*.

HAFER's hypothesis and the «fine-grained» methodological approach (BROWN 1979, 1987; LAMAS 1982) are useful, but they cannot completely explain the high neotropical diversity.

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