A Cladistic Analysis of the genus *Parides* HÜBNER, [1819], based on androconial structures

(Lepidoptera: Papilionidae)

by

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Abstract

The neotropical species of the genus *Parides* have been revised through cladistic numerical technique. The androconial structures of each species were used as the main characters for the analysis. The ingroup *Parides* comprises four main clades, which are discussed in the light of evolutionary and biogeographic evidence.

1. Introduction

The genus *Parides* HÜBNER, [1819], has been studied for a long time, but only recently has it been subjected to cladistic analysis. This showed an unresolved monophylum within the Troidini, encompassing terminal taxa with South American and Oriental distributions. MILLER (1987) hypothesized the monophyly of *Parides* sensu lato by the following apomorphic characters: 1 – Females with a highly sclerotized invagination dorsally to ductus bursae. 2 – A wide ductus bursae. 3 – A large vesica. While the neotropical subgenus *Parides* was characterised by: 1 – Dorso-ventrally oriented signa. 2 – Lower level androconia curled. Several approaches aimed to the recognition of relationships among the species groups resulted in different arrangements (ROTHSCHILD & JORDAN, 1906; MUNROE, 1961; HANCOCK, 1978; MILLER 1987; TYLER et al. 1994; BROWN et al. 1995). All the species considered are endemic to Central and South America, the larvae are monophagous on *Aristolochia* plants (Aristolochiaceae), and the adults are linked to mimicry rings (tab. 1).
The purpose of this study was aimed to determine cladistic relationships in the neotropical *Parides*, using a set of characters from the androconial system, together with features of the male genitalia and exoskeleton. These might suggest new ways of looking at existing relationships between the different taxonomical units belonging to the genus *Parides* sensu stricto.

Tab. 1: Monotypic (M) and polytypic (P) species of *Parides* according to the systematic arrangement of BROWN et al. (1995)

ascanius group

M	*Parides proneus* (HÜBNER, 1825)
P	*Parides bunichus* (HÜBNER, [1821])
M	*Parides ascanius* (CRAMER, 1775)
M	*Parides phalaecus* (HEWITSON, 1869)
M	*Parides agavus* (DRURY, 1782)
M	*Parides gundlachianus* (FELDER & FELDER, 1864)
M	*Parides alopius* (GODMAN & SALVIN, 1890)
M	*Parides photinus* (DOUBLEDAY, 1844)
M	*Parides montezuma* (WESTWOOD, 1842)

aeneas group

P	*Parides chabrias* (HEWITSON, 1852)
M	*Parides hahneli* (STAUDINGER, 1882)
P	*Parides quadratus* (STAUDINGER, 1890)

P Parides *pizarro* (Staudinger, 1884)
M *Parides vercingetorix* (Oberthür, 1888)
M *Parides klagesi* (Ehrmann, 1904)
M *Parides tros* (Fabricius, 1793)
M *Parides orellana* (Hewitson, 1852)
M *Parides burchellanus* (Westwood, 1872)
P *Parides aeneas* (Linnaeus, 1758)
P *Parides panthonus* (Cramer, 1780)
P *Parides echemon* (Hübner, [1813])
P *Parides lysander* (Cramer, 1775)
P *Parides eurimedes* (Stoll, 1782)
P *Parides neophilus* (Geyer, [1837])
P *Parides zacynthus* (Fabricius, 1793)

anchises group
P *Parides childrenae* (Gray, 1832)
P *Parides sesostris* (Cramer, 1780)
P *Parides phosphorus* (Bates, 1861)
M *Parides cutorina* (Staudinger, 1898)
P *Parides panares* (Gray, [1853])
P *Parides vertumnus* (Cramer, 1780)
P *Parides erithalion* (Boisduval, 1836)
P *Parides iphidamas* (Fabricius, 1793)
P *Parides anchises* (Linnaeus, 1758)

2. History of the classification of the genus *Parides*

Linnaeus (1758) included the two species known at that time (*P. anchises* and *P. aeneas*) in his *Papilio Equites Trojani*, and for a long time this was the combination of names followed by subsequent authors. Hübner [1819] introduced the genus *Parides*, but apparently this name was forgotten. The type-species is *Princeps echelus* Hübner, [1815], now considered to be a synonym of *Princeps echemon* Hübner, [1813].

The major early revisionary papers on the Papilionidae by Gray [1853], Bates (1861, 1862), Felder & Felder (1864), and Rothschild & Jordan (1906) shed new light on the systematics of the species of *Parides*, included then in the omni-comprehensive genus *Papilio*. Bates (1861, 1862), who resided in the Amazonia for eleven years laid the basis for a biological vs typological classification of *Parides*. Gosse (1883), who described the male genitalia of 69 Papilionid species, discussed and figured those of *P. vertumnus, P. sesostris, P. childrenae, P.lysander, P. echemon*. Although the genitalia drawings are admirable, the interspecific relationships inferred by this author are inadequate. Rothschild & Jordan (1906), in the subsection A of their *Aristolochia*-swallowtails, outlined the *Ascanius, Aeneas* and *Lysander* groups. Ford (1944a, b) included in the genus *Atrophaneura* all the neotropical and Old World species, recognizing separate the genus *Battus* which comprises the species in the subsection B of Rothschild & Jordan (1906).

Munroe (1961) retained the neotropical species in the subgenus *Parides*. D'Almeida (1966) placed all the neotropical *Aristolochia* feeding species, except those belonging to *Euryades*, in the genus *Battus* with two subgenera *Battus* (s.s.) and *Parides*. It has been shown that *Battus* is distantly related to *Parides* (Munroe, 1961; Miller, 1987), although Parsons (1996a, b) suggests a relationship as sister genera.

Hancock (1978) divided *Parides* into the following groups:
Ascanius group with a) *montezuma* subgroup (4 species); *ascanius* subgroup (7 species);
Aeneas group with a) *coelus* subgroup (7 species); *aeneas* subgroup (18 species);
Lysander group (9 species). Together these total 45 species.

Subsequently, HANCOCK (1983) recognized only the three major groups. The *Ascanius* group assumed to be more primitive than the *Aeneas* and *Lysander* groups because they lack the submarginal series of the red spots on the hindwings.
BROWN (pers. comm., 1980) recognised five natural groups i. e. the *Ascanius, Aeneas, Lysander, Sesostris*, and the *Anchises* groups in a primitive-derived sequence. These hypotheses were condensed in TYLER et al. (1994) and in BROWN et al. (1995) who recognised 34 morpho species especially on the basis of new information of preimaginal stages.
The phylogeny of *Parides* (s. l.) was investigated by MILLER (1987), but his results are tentative. The phylogenetic hypotheses presented by MILLER (1987) left many doubts on the position of *Parides* within Troidini. Alternatively, it is placed in a clade together with *Troides*, or in a separate clade. Moreover, the genus *Parides* is considered a monophyletic unit with three subgenera, i. e. *Parides* (s.s.), comprising all neotropical species as already noted by MUNROE (1961), *Panosmia* and *Atrophaneura,* with an oriental distribution. This latter was ranked as a genus by HANCOCK (1988).
Although *Parides* is the largest subgenus within Troidini, 45 species at that time, MILLER (1987) was unable to detect additional reliable characters. As this author says (MILLER 1987: 428), trying to clarify the phylogenetic relationships within this group: " remains the single largest systematic problem in the Troidini."
PARSONS (1996a, b), in a cladistic analysis aimed to refine the interrelationships of the birdwing *Ornithoptera* using mainly larval character states, showed that *Parides* is the sister group of *Troides* + *Atrophaneura*. *Panosmia* and *Losaria* were considered synonyms of *Atrophaneura*, and *Pachliopta* as a subgenus of *Atrophaneura*. IGARASHI (1984) recognized *Pachliopta* as a genus distinct from *Atrophaneura* but surprisingly he did not make any comment upon the systematic position of *Parides* possibly due to lack of information on preimaginal stages.

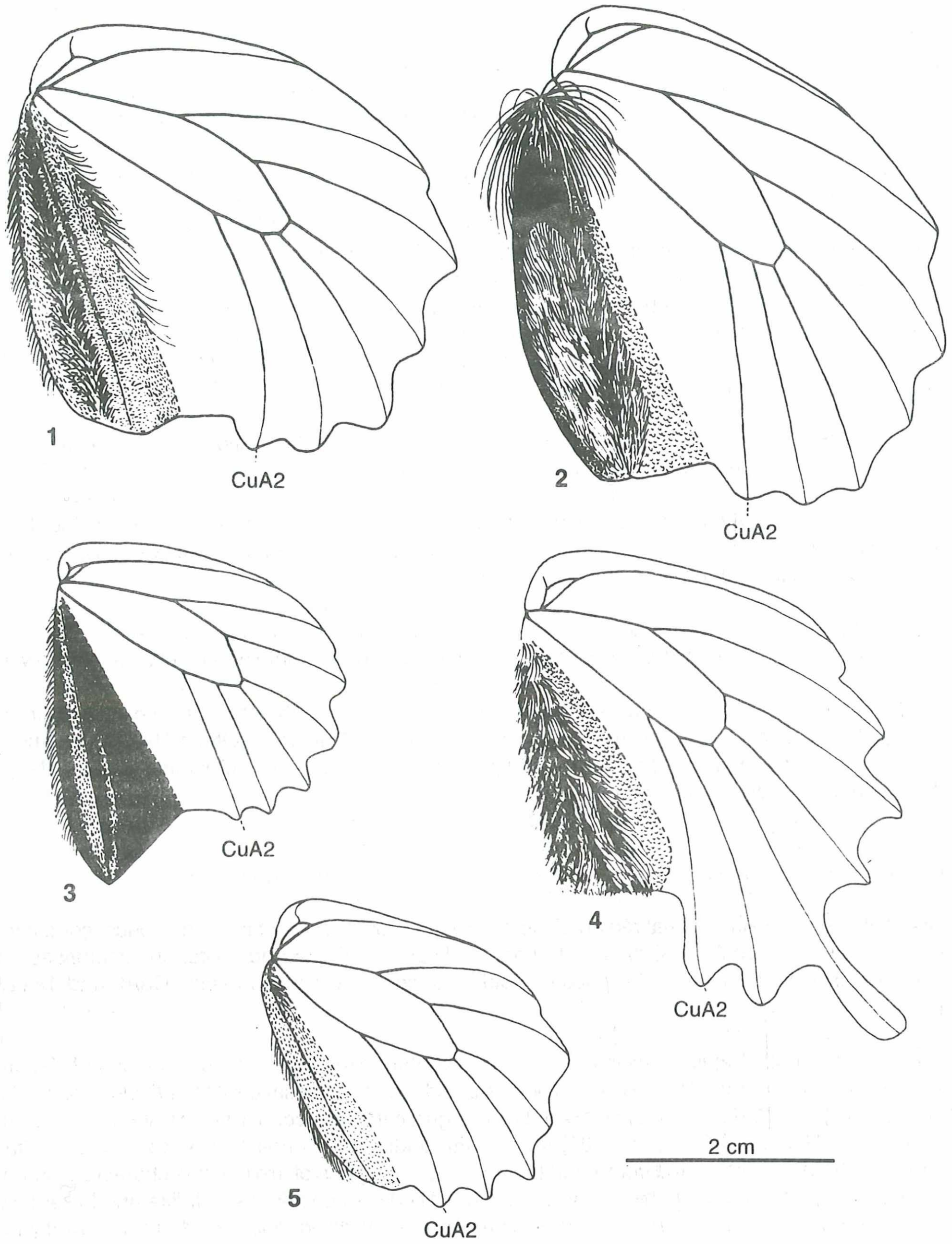
Relationships among the many *Parides* morphospecies have been variously interpreted in the past, especially for the paucity of distributional and biosystematical data. Some groups of species show an extremely complicated net of local populations. The wing patterns make it difficult to distinguish each species. TYLER et al. (1994) recognized five natural groups, although the phylogenetic analysis treating all Papilionidae was limited to only a few species of *Parides*. The data gathered by these authors, although enormously improved compared to 90 years ago, emphasize the still incomplete knowledge of the preimaginal stages and food plants.

3. Material and methods

Males of *Parides* have in the anal region of the hindwings a fold, herafter called the pouch, containing androconial scales (figs 1–5). This is limited anteriorly by vein CuA2 and posteriorly comprises the anal cell. The upper surface of the pouch is folded along a line between veins CuA2 and 1A+2A (fig. 6).

For this character the Papilionidae have had little attention, except for the observations of ZEUNER (1943) for the Troidini, and of BARTH (1950), who studied the androconial organs of *Battus polystictus* (BUTLER, 1874) and *Parides proneus*. MILLER (1987) figured the androconial scales of *P. lysander* and of *P. photinus*. RACHELI & PARISET (1992) studied the androconial organs of all species of *Battus*. PARSONS (1996a) examined and compared the androconial organs of Troidini (his characters 39 and 40), and included the pouch in his analysis. Pouches filled with deciduous hair-like and lower level androconia, occur in *Parides, Troides* and in some species of *Atrophaneura*. All are apparently homologous (MILLER, 1987; PARSONS, 1996a).

A set of 41 characters was used (tab. 2). These characters were analysed using some 2000 specimens, belonging to private or museum collections. Ten males for each nominal taxon, from different localities of their ranges were dissected, except for only one male each of *Parides burchellanus* and *Parides klagesi*.



Figs 1–5: Diagrammatic representation of unrolled pouches in different *Parides* species-groups. Fig. 1 *Parides vertumnus* Fig. 2. *Parides sesostris* Fig. 3. *Parides bunichus* Fig. 4 *Parides chabrias* Fig. 5 *Parides neophilus*.

Tab. 2: Characters and character-state data for *Parides* species.

1. Sexual dimorphism (0 = absent, 1 = present).
2. Males: valvae edged with red scales (0 = present, 1 = absent).
3. Males: red scales on the valva face (0 = present, 1 = absent).
4. Females: ostium edged with red scales (0 = present, 1 = absent).
5. Females: red scales on papillae anales (0 = present, 1 = absent).
6. Females: red scales on the caudal edge of IX sternite (0 = present, 1 = absent).
7. Marginal fringes (0 = white, 1 = red).
8. Number of segments in the female labial palpi (0 = 3, 1 = 2).
9. Harpe expanded but without teeth on the tip (0 = absent, 1 = present).
10. Harpe bent and with teeth (0 = absent, 1 = present).
11. Basal spiny process of the harpe (0 = absent, 1 = present).
12. Fine serration along the distal edge of the harpe (0 = absent, 1 = present).
13. Teeth on the apical fourth of the harpe (0 = absent, 1 = present).
14. Heavy sclerotization along the edge of the harpe (0 = absent, 1 = present).
15. Distal part of the harpe specialized (0 = absent, 1 = present).
16. Teeth between the apex of the harpe and the basal spiny process (0 = absent, 1 = present).
17. Teeth along the whole distal edge of the harpe (0 = absent, 1 = present).
18. Harpe narrow bending apically (0 = absent, 1 = present).
19. Lined teeth on the apex of the harpe (0 = absent, 1 = present).
20. Pseuduncus with lateral processes (0 = absent, 1 = present).
21. Apical process of the harpe slender but blunt (0 = absent, 1 = present).
22. Androconial tuft at the base of the pouch (0 = absent, 1 = present).
23. Strip of androconial hair-like scales edging the anterior margin of the pouch preceeding the coverage of normal scales (0 = absent, 1 = present).
24. Lower level curled androconia (0 = absent, 1 = present).
25. Dark, narrow, oblong scales inside the pouch (0 = present, 1 = absent).
26. Long hair-like androconia (0 = absent, 1 = present).
27. Very short hair-like androconia (0 = absent, 1 = present).
28. Long hair-like androconia yellow (0 = absent, 1 = present).
29. Long and short hair-like androconia white (0 = absent, 1 = present).
30. Dark scales as character 25 filling only the proximal half of the pouch (0 = present, 1 = absent).
31. Long, black hair-like androconia, and character 25 (0 = absent, 1 = present).
32. Androconial tufts as in character 22 white (0 = absent,1 = present).
33. Cushion-like androconia (0 = absent, 1 = present).
34. Pouch bordered by black hair (0 = black hair scarce, 1 = black hair dense).
35. Ventral surface of the pouch covered with black hair (0 = absent, 1 = present).
36. Ventral surface of the pouch with black hair along vein S1b (0 = absent, 1 = present).
37. Androconial structure: character 34 and cushion-like androconia (0 = absent, 1 = present).
38. Androconial structure: tufts (character 22) and long hair-like androconia (0 = absent, 1 = present).
39. Long white hair-like androconia only (0 = absent, 1 = present).
40. Presence of the pouch and its differentiation: (0 = absent, 1 = weakly developed, 2 = multiple structures).
41. Feeding of larvae on only 1–2 species of *Aristolochia*: (0 = present, 1 = absent).

The anal pouch was studied both by SEM (fig. 7) and optical microscope. For SEM preparation a strip of 3x4 mm was cut off at the unrolled anal margin of right HW. It was rinsed in NH_4OH for two minutes, laid on a stub and coated with gold-palladium.

Other structures were directly observed from specimens with optical microscope Wild M5.

A set of characters of the male genitalia was also included in the analysis. Male genitalia preparations, after dissection, were not mounted but preserved in vials with 70% ethanol.

Wing patterns and coloration in *Parides* species are highly variable, both among different species or groups of species, and between individuals of the same species. These characters have been used by various authors to classify *Parides*, but they were excluded from the present study. We regarded them as being subject to too much selective pressure, mainly due to mimicry.

Thirty-three taxonomic units, the same morphospecies recognized by TYLER et al. (1994), became the terminal taxa for the cladistic analysis. The only exception is *Parides vercingetorix* (OBERTHÜR, 1888) which was lumped with *P. quadratus*.
The matrix (tab. 3) was analysed using the Hennig86 program (FARRIS, 1988), which implements the principles of WAGNER parsimony for determining phylogenetic trees. The options for searching minimal length trees (mh*) and extended branch swapping (bb), were used. Polarisation and scoring of characters were determined using as outgroup a hypothetical ancestor to root the cladogram.
We preferred to avoid the use of multistate characters. Character 40 has been scored as a multistate due to the hypothetical absence of any androconial structure in the anal area of a Troidine ancestor. Data was also processed with the successive character weighting procedure (xsteps w; with mh*; bb*; and cc options).

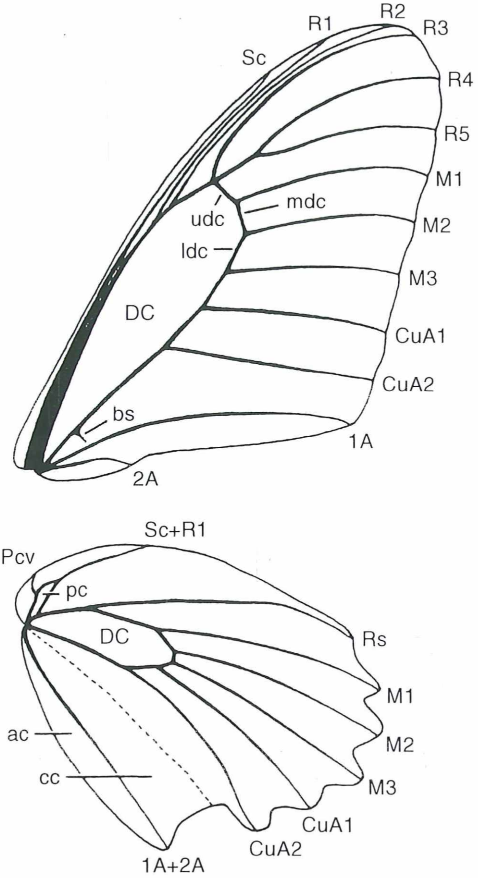


Fig 6. Wing venation of *Parides erithalion* showing unrolled anal area of hindwings.

Tab. 3: Data matrix of character-states of *Parides* for the cladistic analysis

										1										2										3										4	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. anchises	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	1
P. iphidamas	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	1
P. erithalion	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	0
P. phosphorus	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	?
P. cutorina	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	?
P. vertumnus	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	0
P. panares	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	0
P. childrenae	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	2	0

	1 2 3 4
	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1
P. sesostris	1 1 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 1 1 0 0 1 1 0 1 0 0 0 1 0 0 0 2 0
P. alopius	0 1 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 1 2 1
P. photinus	0 1 0 1 0 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 1 2 0
P. gundlachianus	0 0 0 1 0 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 1 2 1
P. bunichus	0 1 0 1 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 1 0 0 0 0 0 1 0 0 0 1 2 1
P. proneus	0 0 1 1 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 1 0 0 0 0 0 1 0 0 0 1 2 0
P. ascanius	0 1 1 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 1 0 0 0 0 0 1 0 0 0 1 2 0
P. montezuma	0 1 0 1 1 0 0 1 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1 1 0 0 1 0 0 0 0 0 0 0 0 0 1 2 1
P. agavus	0 1 1 1 1 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 1 0 0 0 0 0 1 0 0 0 1 2 1
P. phalaecus	0 1 1 1 1 0 0 1 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1 1 0 0 1 0 0 0 0 0 1 0 0 0 1 2 0
P. klagesi	0 1 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 1 0 0 0 0 0 0 0 0 0 1 2 ?
P. chabrias	0 1 0 1 0 0 0 1 1 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 1 0 0 0 1 0
P. hahneli	0 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 1 0 0 0 1 0
P. pizarro	0 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 1 0 1 0 1 0 0 0 0 0 0 1 0 0 0 1 0
P. quadratus	0 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 1 1 0 1 0 1 0 1 1 0 0 0 1 0 0 0 1 0 0 1 0 0 0 2 0
P. aeneas	1 1 1 1 0 1 0 1 0 1 0 0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 1 0 0 1 0 0 2 1
P. tros	1 1 1 1 0 1 0 1 0 1 0 0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 0 0 1 0 0 0 1 1 0 0 1 0 0 2 0
P. orellana	0 1 1 1 0 0 0 1 0 1 0 0 1 0 0 0 0 1 0 0 0 0 0 1 1 0 0 0 1 0 0 0 1 1 0 0 1 0 0 2 ?
P. burchellanus	0 1 0 1 1 0 0 1 0 1 0 0 1 0 0 0 0 1 0 ? 0 0 0 1 0 1 0 0 1 0 0 0 1 1 0 0 1 0 0 2 ?
P. panthonus	1 1 0 0 0 0 0 1 0 1 0 0 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 1 0 0 0 1 1 0 0 1 0 0 2 1
P. lysander	1 1 0 0 0 0 1 1 0 1 0 0 1 0 0 0 0 1 1 0 1 0 0 1 1 0 0 0 1 0 0 0 1 1 0 0 0 0 0 2 0
P. echemon	1 1 0 0 0 0 1 1 0 1 0 0 1 0 0 0 0 1 1 0 1 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 1 1
P. eurimedes	1 1 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 1 1
P. neophilus	1 1 0 1 0 1 1 1 0 1 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 1 1
P. zacynthus	1 1 0 1 0 0 1 1 0 1 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 1 1

4. Results

The study of scale structures led to the identification of different morphological structures in and outside the anal pouch of *Parides* species. The morphology of the unrolled pouch for each species of *Parides* is given in tab. 4.

Tab. 4: Morphology of the unrolled pouch in each species of *Parides*.

P. proneus — Pouch filled with dense, white, hair-like scales [ch. 26]. Wide, short, apically bent scales are present basally (lower-level androconia of Miller, 1987) [ch. 24]. Underside of pouch with long and black hair-like scales [ch. 35]. *P. bunichus, P. ascanius, P. phalaecus, P. agavus* show the same scale types.

P. gundlachianus — Similar to *P. proneus* but hair-like androconia inside the pouch yellow [ch. 28]. *P. photinus* is similar to *P. gundlachianus*.

P. alopius — Pouch filled with long, yellow hair-like scales [ch. 28]. Lower-level androconia present [ch. 24]. Pouch edged by evident black hair [ch. 34]. Black hair absent on underside of pouch.

P. montezuma — Pouch filled with long, white hair-like scales [ch. 28]. Lower-level androconia present [ch. 24]. Black hair absent on the underside of the pouch.

P. hahneli — Pouch covered by very minute, yellow, hair-like scales [ch. 27]. Lower-level androconia absent [ch. 24]. Underside of the pouch showing black hair along S1b [ch. 36]. *P. chabrias* and *P. pizarro* are similar to *P. hahneli.*

P. quadratus — Pouch filled with short, white, hair-like scales, "cushion-like" [ch. 33]. Lower-level androconia present [ch. 24]. Long, white, hair-like scales forming a distinct tuft at the base of the pouch [ch. 22]. Underside with black hair along S1b [ch. 36]. *P. vercingetorix* has the same character states.

P. klagesi — Pouch filled with long, white, hair-like scales [ch. 39]. Lower-level androconia present [ch. 24]. Black hairs absent on the underside.

P. tros — Pouch filled with dark, narrow, oblong scales [ch. 25]. Lower level androconia present [ch. 24]. Pouch bordered by dense black hairs [ch. 34]. Black hair absent on the underside. On the outer margin of the pouch a narrow strip of white, hair-like scales.

P. orellana — Pouch filled with "cushion-like" scales [ch. 33]. Pouch bordered by dense black hairs [ch. 34]. Black hair absent on the underside. *P. burchellanus, P. aeneas, P. panthonus* are similar to *P. orellana.*

P. echemon — Pouch filled with dark, narrow, oblong scales [ch. 25]. Pouch bordered by dense black hairs [ch. 34]. Black hairs absent on the underside. *P. eurimedes, P. neophilus*, and *P. zacynthus* show the same character states as *P. echemon.*

P. lysander — Pouch filled with white, hair-like scales [ch. 39]. Lower-level androconia present [ch. 24]. Black hair absent on the underside.

P. childrenae — Outer half of the pouch covered with long, white, hair-like scales [ch. 26]. Lower-level androconia present [ch. 24]. A tuft of long, black, hair-like scales is present at the base of the pouch [ch. 22]. Inner half of the pouch covered with dark, narrow, oblong scales [ch. 30]. Underside of the pouch showing black hair along S1b [ch. 36]. *P. sesostris* shows the same characters.

P. phosphorus — Pouch filled with long, white, hair like scales [ch. 26]. A strip of androconial hair-like scales edges the anterior margin of the pouch [ch. 23]. Lower-level androconia present [ch. 24]. Black hairs absent on the underside. *P. cutorina, P. panares, P. vertumnus, P. erithalion, P. iphidamas*, and *P. anchises* have the same character states.

Cladistic analysis of the matrix produced eight equally parsimonious trees using the (bb*;) (mh*;) options. The general topology is retained in the consensus tree (nelsen; option), which confirms the recognition of two major clades in the genus *Parides* (Fig. 8). Using the options (xsteps w; m*;) resulted a tree of length 301, ci 77, ri 94 (Fig. 9) Monophyly of *Parides* is supported by characters 2, 29, 40.

One of the two synapomorphies supporting the monophyly of *Parides*, i. e. lower-level curled androconia, (Miller, 1987), appears not to be universally distributed in the genus *Parides*, being absent in the *chabrias* and *neophilus* groups.

A new feature of the evolutionary lineages of *Parides* lies in the position of the *anchises* group which becomes the plesiomorphic part of the taxon for this set of characters. There is not yet a good resolution inside this group, the terminal taxa belonging to the *anchises-iphidamas-erithalion* species complex are poorly resolved. The androconial structures, the wing pattern, and male genitalia of this complex are very similar.

The *ascanius* group becomes its sister-taxon. Contrary to current classifications, *Parides klagesi* is a primitive exponent of this group, although the resolution of this clade is somewhat variable. Brown (pers. comm.) has noticed that both sexes of this species show a quadrate whitish spot in space 2 of the forewings. This character is quite peculiar of the *ascanius* group.

The second clade, comprising the *chabrias* and the *aeneas* groups, becomes the more apomorphic and its resolution is extremely stable.

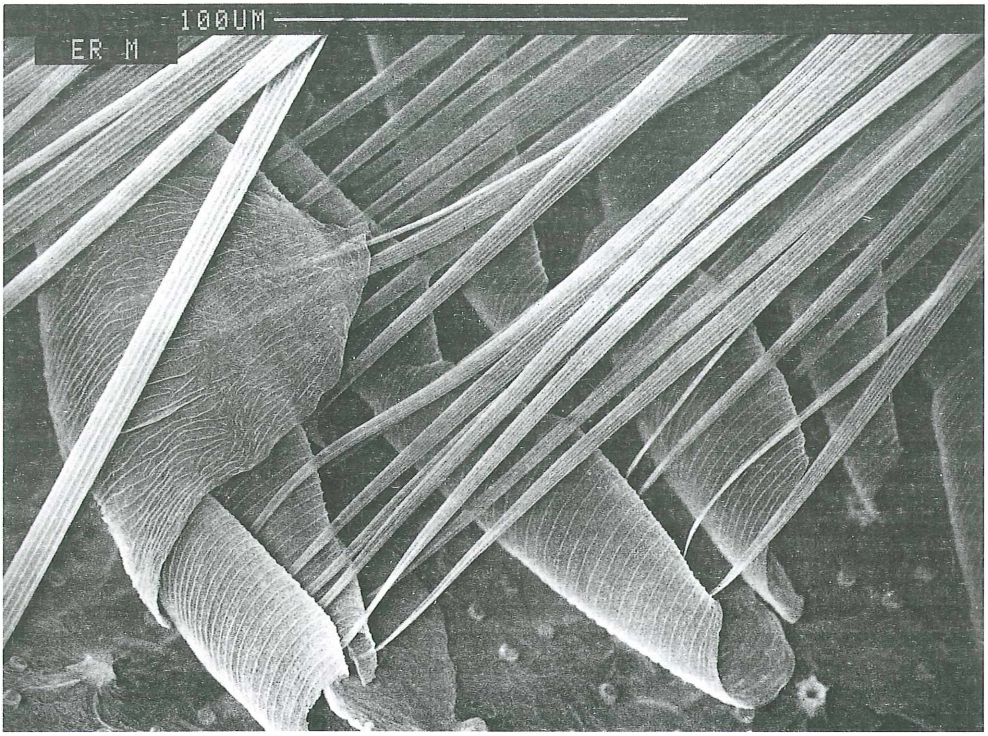


Fig. 7. Hair-like white androconia and lower-level curled androconia of *Parides erithalion*.

5. Discussion

The evolutionary and distributional patterns of *Parides* obtained from this study can be summarized as follows from the evidence of the more stable clades. Based on the analysis of characters mainly of androconial structures and male genitalia, the topology of the various lineages of *Parides* differs from the classification of Tyler al. (1994), although the sets of characters were different and only a few species were assayed by these authors. The main difference is that our results give an inversion in the trend of primitive-derived groups. The phylogenetic classifications of Hancock (1978, 1983) differ considerably in the species groups arrangement. The species groups of *Parides*, defined mainly on colour patterns by various authors, seem to be due largely to convergence, being placed in two distantly related lineages in the tree. Brown et al. (1995: 433) proposed the *ascanius, aeneas* and *anchises*-groups. The present analysis suggests a plesiomorphic-apomorphic trend of the four main lineages *anchises, ascanius, chabrias* and *aeneas*.

Parides terminal taxa which are taxonomically treated as polytypic species and are more linked to mimicry rings, are the more advanced in the trees. Most of the recognized monotypic species which are mainly confined to the Andes, the mesoamerican area, and to SE Brazil, tend to remain at the base of the cladogram.

Hammond (1991) has discussed the patterns of geographical variation and of evolution of the Nearctic Nymphalid *Speyeria* butterflies. The models for mono- and polytypic species are different. Monotypic species show a cohesive gene pool, are vagile and migrants. Polytypic species lack this cohesion, comprise multiple, fragmented populations which have the possibility to become independent

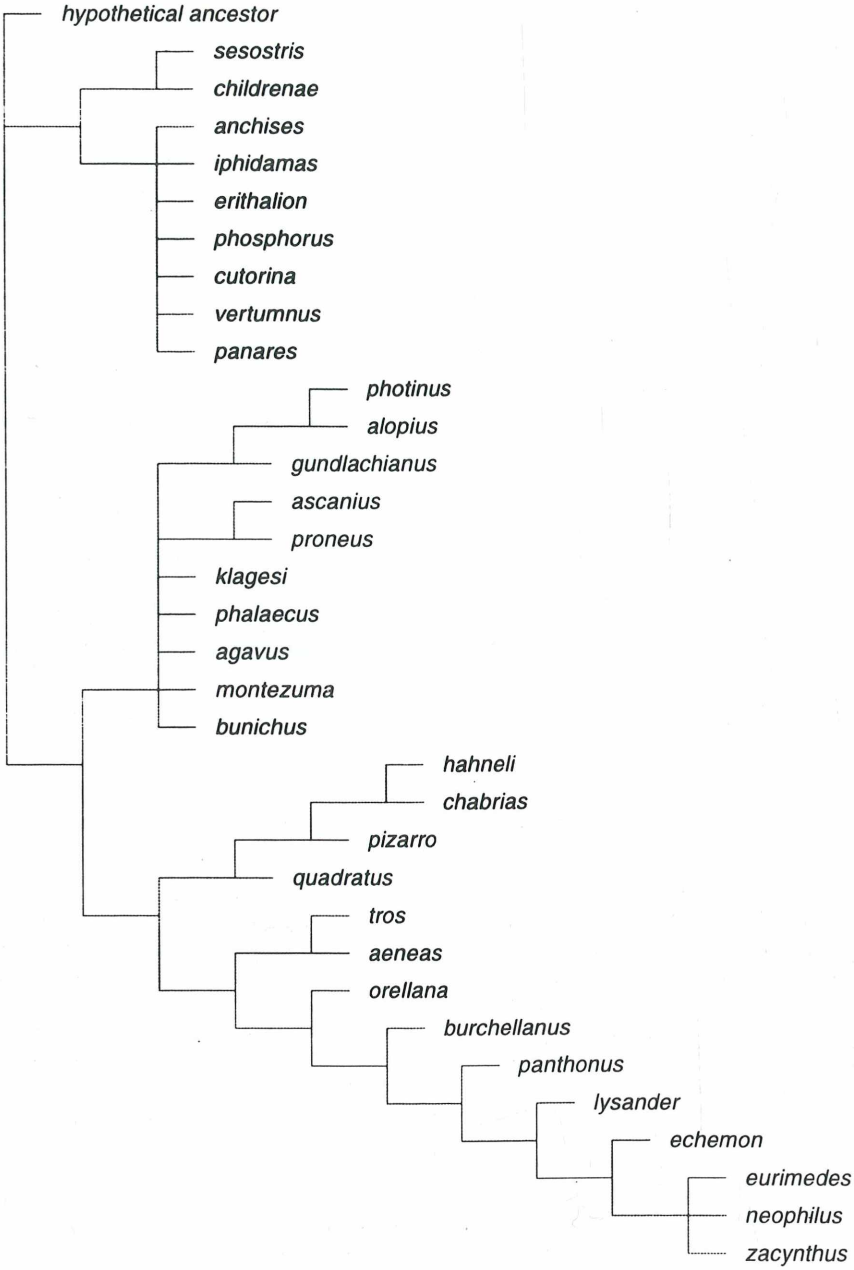


Fig. 8. Consensus tree obtained with (nelsen) option. Tree length 92, ci 45, ri 80.

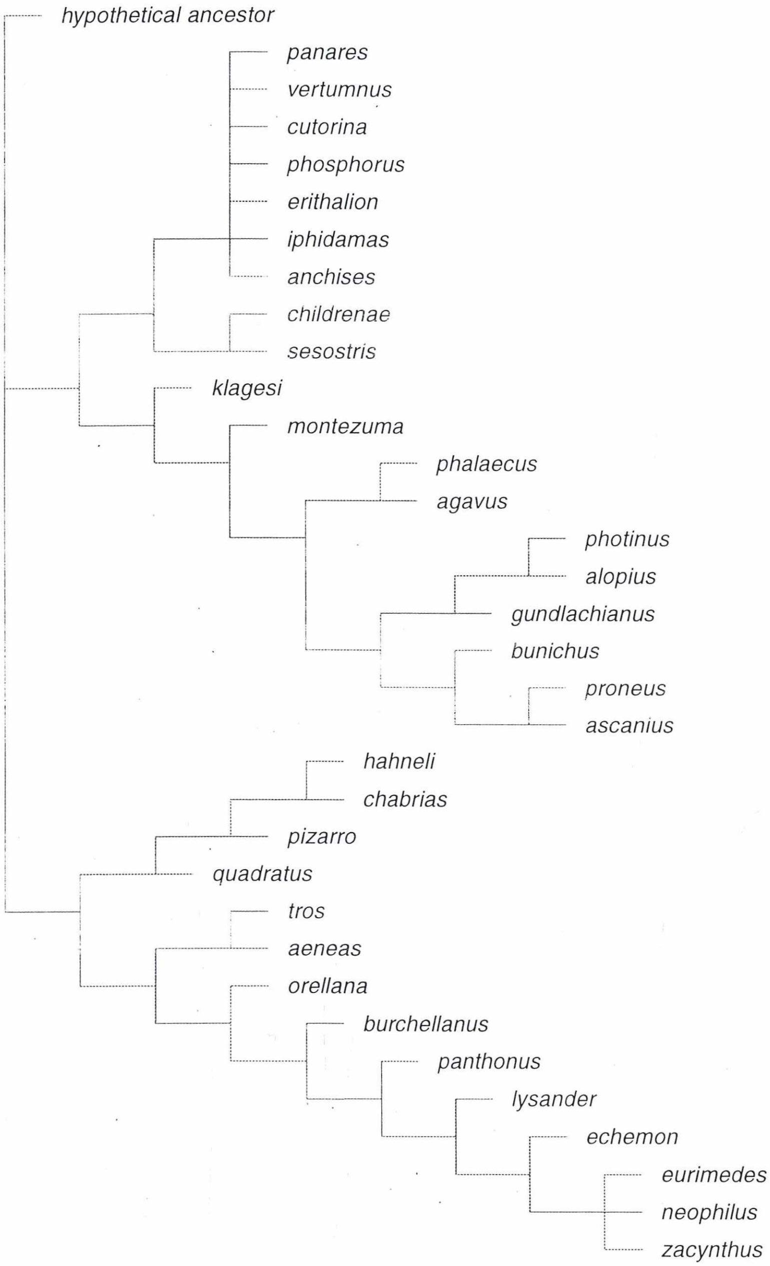


Fig. 9. One of the eight most parsimonious trees obtained using (mh*;) (bb*;) (x steps w; m*;) options. Tree length = 301; ci= .77; ri = .94.

evolutionary units. Applying this model to *Parides* species, monotypic species such as *P. klagesi, P. montezuma, P. tros, P. orellana*, although apparently neither migrants nor vagile, remain as the more primitive species in different lineages. Some of the polytypic species, in the trees the more advanced, show a tendency to have unresolved clades (*P. anchises, P. iphidamas, P. erithalion, P. eurimedes, P. neophilus, P. zacynthus*). This phenomenon can be speculatively related to isolation mechanisms (refugia?) which led to speciation only recently. Male genitalia, androconial structures, and to some extent colour designs of wings in these species are not so well differentiated as to distinguish them. The refugial hypothesis might be substantiated then for the more advanced taxa. The allopatric distribution of *P. eurimedes, P. zacynthus* and *P. neophilus* seems to corroborate this hypothesis (see BROWN, 1987). For the stem taxa, vicariant processes (Andean orogenesis) and bridge effects (Isthmian connection) might be hypothesised. These phenomena may have been further causal (or casual) factors for the differentiation and evolution of the genus. Perhaps the subdivision in four main lineages one of which includes all the monotypic species, is not due to chance alone.

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