

SYSTEMATICS OF VAGRANTINI BUTTERFLIES (LEPIDOPTERA: NYMPHALIDAE). PART 2. DISCUSSION ON CLADES AND CHARACTER DISTRIBUTIONS

Djunijanti Peggie

Division of Zoology, Research Center for Biology, Indonesian Institute of Sciences
Jl. Raya Jakarta Bogor Jakarta Km. 46, Cibinong 16911, Indonesia

Abstract

Cladistic analysis of the Indo-Australian heliconiine butterflies showed that they belong to the Heliconiinae. The name Vagrantini was suggested by Penz and Peggie (2003) to include Vindula, Smerina, Vagrans, Phalanta, Cupha, Terinos, Lachnoptera, Algia, Algiachroa, and Cirrochroa. Vindula is shown as sister group to the rest of the genera, and Terinos forms a sister-group relationship with Lachnoptera and the Cirrochroa group-of-genera. The monophyly of the Cupha group-of-genera and the Cirrochroa group-of-genera are supported.

Introduction

Taxonomical studies on the Indo-Australian heliconiine genera were conducted by Parsons (1989, 1999). Though limited, review on *Terinos* was provided by Brooks (1930), on *Phalanta* by Fox (1964), and on *Vindula* by Nieuwenhuis (1962). It is generally agreed that these genera, *Acraea*, *Heliconius*, *Cethosia* and *Argyreus* are closely related. Corbet & Pendlebury (1978, 1992) noted that the Indo-Australian genera form a taxonomic continuum that is not readily separable. Corbet & Pendlebury (1978, 1992) and Ackery (1988) indicated that the genera belong to argynnines, but the presence of stink clubs in *Cirrochroa* through *Smerina* may suggest that these genera are more closely related to the Neotropical heliconiines. *Cethosia* and *Vindula* were suggested to belong to the Neotropical Heliconiines (Barrett & Burns, 1951; Corbet & Pendlebury, 1956, 1978, 1992; Brown, 1981; Haribal, 1992; Parsons, 1989, 1999) based on larval morphology and food plants. However, Harvey (in Nijhout, 1991) included *Cethosia* in the Acraeinae. Baltazar (1991) included *Vindula* together with *Argyreus*, *Cirrochroa*, *Cupha*, *Algia*, *Phalanta*, *Terinos*, and *Vagrans* in the subfamily Argynninae, whereas *Cethosia* was included in the subfamily Heliconiinae. Penz & Peggie (2003) showed that within Heliconiinae there are four main groups: Acraeini, Heliconiini, Vagrantini and Argynnini. Peggie (2003), however, showed that these Indo-Australian genera are inclusive within Argynnini. These relationships will be better understood with further studies on the true argynnines (T. Simonsen, in prep.).

Materials and Methods

Taxa were selected to include most species of the ingroups and some closely related outgroups (see Peggie, 2003). The body and wings were examined for potential

characters. The primary sources for character definitions include Penz (1999), Penz & Peggie (2003), which were based on prior studies by Michener (1942), Emsley (1963), and Brown (1981). Other characters used by Corbet and Pendlebury (1992), and Parsons (1989, 1999) were also evaluated and included.

The list of characters can be seen in previous publication (see Appendix 1 - Peggie, 2003). Observations on the characters across the taxa were recorded as a matrix of taxa and characters (see Appendix 2 - Peggie, 2003). Cladistic programs Winclada and NONA (Nixon, 1999, 2000; Goloboff, 1996) were used to analyze the data matrix. One of the most parsimonious trees was selected to map characters. This preferred tree (Fig. 1) forms the basis for subsequent discussion on character distributions.

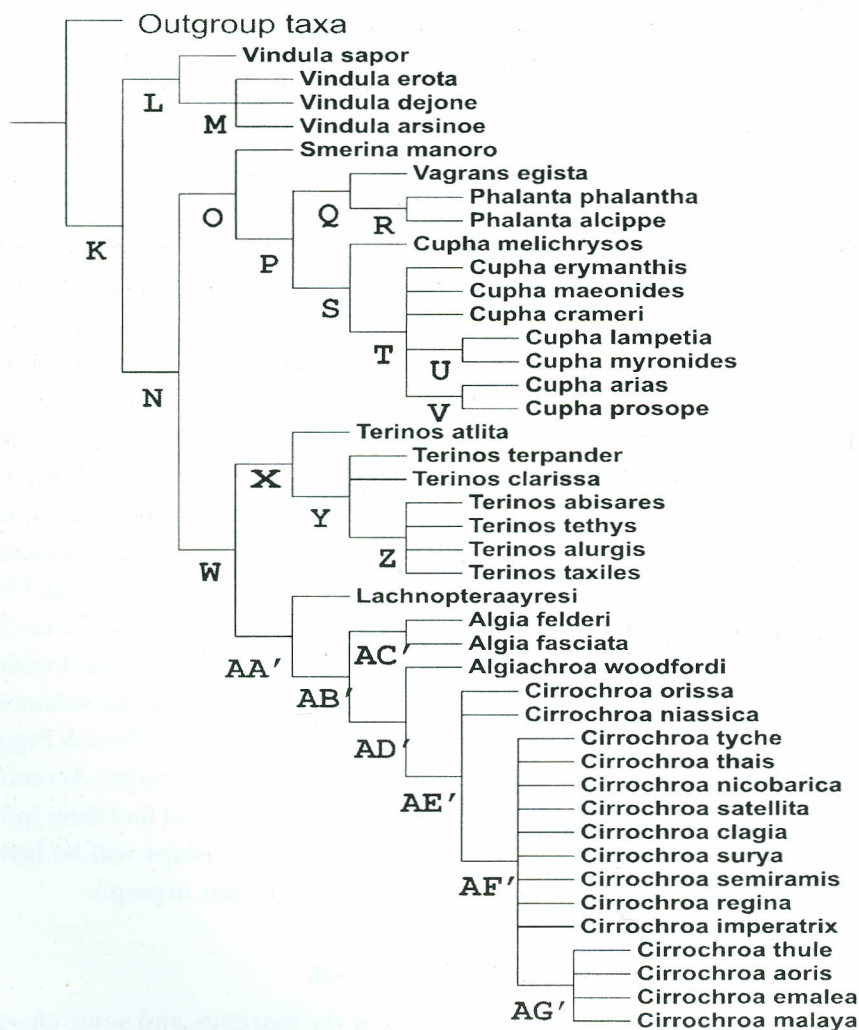


Figure 1. Ingroup taxa of the preferred tree with clades indicated.

Results and Discussion

The arrangement of the outgroup taxa is in concordance with previously suggested classification. The monophyly of *Acraea* clade is supported as indicated previously by Eltringham (1912), Van Son (1963), and Pierre (1987). The monophyly of *Philaethria* and *Heliconius* clade is supported as in the work of Michener (1942), Emsley (1963), Penz (1999), Penz & Peggie (2003). The sister-group relationship between *Heliconiina* and *Cethosia* is indicated in this analysis, as suggested by Brown (1981), Penz (1999) and Penz & Peggie (2003). This view is not in line with Harvey's (in Nijhout, 1991) indication of *Cethosia* - *Acraea* sister-group relationship and Brower's (2000) hypothesis of *Heliconiina* - *Acraeini* sister-group relationship.

The relationships of the ingroup taxa are discussed below:

Clade K includes all genera regarded as *Vagrantini* by Penz & Peggie (2003). Clade K is supported by homoplasious characters 20 (antennae gradually clubbed) with the exception of *Smerina* in which it is abruptly clubbed, and *Cupha* and clade AB' (*Algia*, *Algiachroa* and *Cirrochroa*) in which it is almost not clubbed; 37 (anterior margin of the abdominal T8 conspicuously narrower than the posterior margin of the T7), also in *Pardopsis* and *Philaethria*, though the anterior width of T8 is similar to the posterior margin of T7 in *Algia* and *Algiachroa*; 38 (presence of apophysis of abdominal T8) with reversal or absence in *Terinos* and most *Cupha* (although present in *C. erymanthis*); 43 (presence of gnathos), also in *Philaethria* and *Heliconius*, and absent in *Smerina*, *Terinos atlita*, and clade AB' (*Algia*, *Algiachroa* and *Cirrochroa*) with the exception of *Cirrochroa satellita* in which the gnathos is present; and 76 (numerous sensilla in female foreleg tarsus), also seen in *Pardopsis*, *Philaethria* and *Heliconius* but reversed at clade Q (*Vagrans* and *Phalanta*), in which the sensilla are few.

Clade L. Monophyly of *Vindula* is supported by synapomorphic characters 13 (hw humeral vein forked) as observed by Penz (1999); 58 (juxta bulbous with distal edges strongly dentate); 67 (expansion of vesica as a pair of heavily sclerotized and modified sclerites); 75 (first tarsomere of female foreleg conspicuously narrower than those distal to it); 93 (presence of appendix bursa); plus some homoplasious characters 14 (presence of hw M3 tail), also in *Vagrans*; 16 (hindwing cell open), also in *Philaethria*, *Cupha* and clade AA' (*Lachnoptera*, *Algia*, *Algiachroa* and *Cirrochroa*); 28 (presence of a single pair of pulvillar processes), also in *Euptoieta*; 31 (male pre-tarsal claws straight at the middle), also in *Acraea*, *Cethosia*, and *Euptoieta*; 40 (contour of posterior edge of T8 incurved, i.e. concave), as in *Philaethria* and *Terinos*; 42 (absence of fenestrula or dorsal window of uncus), also in *Acraea*, *Philaethria*, *Heliconius*, and *Cethosia*. Warren (1944) indicated that the presence of the fenestrula or dorsal window of the uncus is a uniting feature for *Argynnini*. Other homoplasious characters include: 49 (saccus elongate proximally), also in the basal clades: *Pardopsis*, *Acraea*, *Philaethria*, *Heliconius*, *Cethosia*, and also

clade AB' (*Algia*, *Algiachroa* and *Cirrochroa*); 94 (presence of signum), also present in *Philaethria* and *Cethosia*; 99 (base of apophyses posteriores uniformly well sclerotized from ventral to dorsal edge), as in clade Q (*Vagrans* and *Phalanta*); and 100 (sub-papillary glands well sclerotized), as in *Pardopsis*, *Acraea*, and *Cethosia*.

Parsons (1999) suggested a close relationship between *Vindula* and *Cethosia* based on larval features and their passifloraceous foodplants. Corbet & Pendlebury (1992) indicated that *Vindula* together with *Terinos* are connectant genera between Heliconiina and Argynnina. Their early stages and foodplants fit best into Heliconiina whereas some male genitalic characters are shared with Argynnina. The placement of *Vindula* (and *Terinos*) has puzzled Eliot (pers. comm., 2000) as to whether *Vindula* should be placed near *Cethosia* or with the rest of Harvey's subtribe uncertain. This analysis shows that *Vindula* is sister to the rest of subtribe uncertain except for *Euptoieta*.

Clade M. *Vindula* part - are supported by homoplasious character 60 (presence of setae on transtilla), also in *Cupha*, *Lachnoptera*, and clade AD' (*Algiachroa* and *Cirrochroa*). This is a weak character as the absence of setae on *V. sapor* may due to a problem in cleaning the specimens.

Clade N is supported by synapomorphic character 44 (gnathos not fused ventrally) though the gnathos is absent in *Smerina*, *Terinos atlita*, and most clade AB' (*Algia*, *Algiachroa* and *Cirrochroa*) except *Cirrochroa satellita*; and homoplasious characters 57 (shape of juxta flat, thin and lamellate), with exception of *Vagrans* and clade AB' (*Algia*, *Algiachroa* and *Cirrochroa*) in which the juxta is bulbous; and 82 (female wide membranous pouch between abdominal T7 and T8 lightly textured) as in *Cethosia*; but *Lachnoptera ayresi* has very well developed paired abdominal glands.

Clade O monophyly is supported by homoplasious characters 2 (fw R1 arises from the cell apex or very close to apex), as in *Cethosia* and *Lachnoptera*; 22 (labial palpal second segment inflated and third segment very small), as in *Euptoieta*, *Childrena childreni*, *Argyreus hyperbius*, and *Lachnoptera*; and 87 (presence of thick setae on S7), which also occurs in *Lachnoptera*. In this clade, the African genus *Smerina* is shown to be sister to the *Vagrans* + *Phalanta* + *Cupha* group-of-genera. Corbet (1948) suggested that *Smerina* most closely resembles *Cirrochroa* in general appearance.

Clade P (*Vagrans* + *Phalanta* + *Cupha*) is supported by synapomorphic characters 5 (fw R4 ends on costal margin); 6 (fw discocellular M2-M3 connected with cubitus at the base of Cu1a); 72 (presence of stylus of valva), as indicated by Roepke (1938), Fox (1964), and Parsons (1999); 83 (clavatium very reduced); and 92 (bursa almost as long or longer than the abdomen) as recognized by Corbet & Pendlebury (1992), Parsons (1999); and homoplasious characters 3 (forewing vein R2 arising from vein R5), as in the basal clades up to *Clossiana* and also in *Lachnoptera*; 4 (fw vein R4 arising distad or at about the same position as end of R2), as in *Cethosia*, *Euptoieta*, *Lachnoptera*, *Algia* and

parts of *Cirrochroa* clade AG' (*C. thule*, *C. aoris*, *C. emalea*, and *C. malaya*); 46 (presence of small plate as extension of appendix angularis), as in *Algia*.

Clade Q. *Vagrans* + *Phalanta* monophyly is supported by homoplasious characters 40 (contour of posterior edge of T8 outcurved or convex), as in *Heliconius*, *Euptoieta*, *Algia felderi* and clade AE' (*Cirrochroa*); 76 (few sensilla in female foreleg tarsus), as in *Acraea*, *Cethosia*, *Euptoieta*, *Clossiana*, *Childrena childreni* and *Argyreus hyperbius*. This sensilla character is qualitatively related to sensillar abundance, as Penz (1999) noticed that the sensilla are much more numerous in the Heliconiina. Some other characters supporting the clade are: 78 (apical tarsomere of female foreleg shorter than penultimate), as in *Pardopsis*, *Acraea*, *Cethosia*, *Euptoieta*, and parts of *Cupha* clade V (*C. arias* and *C. prosope*); 98 (apophyses posteriores longer than or equal to the height of papilla anales), as in *Acraea meyeri*, *Heliconius erato*, *Euptoieta*, *Childrena childreni* and *Argyreus hyperbius*; and 99 (base of apophyses posteriores uniformly well sclerotized from ventral to dorsal edge), as in *Vindula*.

Clade R. Monophyly of *Phalanta* species is supported by homoplasious character 79 (notched condition of last tarsomere of female foreleg), present also in *Euptoieta*.

Clade S. *Cupha* monophyly is supported by homoplasious characters 1 (fw Sc extended less than 1/2 length of costal margin), also in *Terinos* and clade AB' (*Algia*, *Algiachroa* and *Cirrochroa*); 8 (fw cell about 1/3 fw length), also in *Terinos* and clade AB' (*Algia*, *Algiachroa* and *Cirrochroa*); 16 (hindwing cell open), as in *Philaethria*, *Vindula* and clade AA' (*Lachnoptera*, *Algia*, *Algiachroa* and *Cirrochroa*); 20 (antennae thread-like with almost no club), as in clade AB' (*Algia*, *Algiachroa* and *Cirrochroa*); 38 (absence of apophyses of T8), as in the basal clades up to *Childrena childreni* and *Argyreus hyperbius*, and in *Terinos*, although the apophyses are present in *Cupha erymanthis*; and 60 (presence of setae on transtilla), also seen in most of *Vindula* clade M (*V. erota*, *V. dejone*, *V. arsinoe*), *Lachnoptera*, and clade AD' (*Algiachroa* and *Cirrochroa*).

Clade T is supported by homoplasious character 51 (arch formed by tegumen + pedunculum smaller than the arch formed by vinculum + saccus), also in *Philaethria*, *Clossiana*, *Childrena childreni*, *Argyreus hyperbius* and *Phalanta phalantha*. This is an extremely variable character.

Clade U. The clade *Cupha lampetia* + *Cupha myronides* is supported by homoplasious character 36 (length of S7 2/3 or more length of S6), also in *Pardopsis*, *Acraea*, *Heliconius erato*, *Cethosia*, *Euptoieta*, *Clossiana*, *Childrena childreni*, and many of *Cirrochroa* clade AF' (*C. tyche*, *C. thais*, *C. nicobarica*, *C. satellita*, *C. clagia*, *C. surya*, *C. semiramis*, *C. regina*, *C. imperatrix*, *C. thule*, *C. aoris*, *C. emalea*, and *C. malaya*).

Clade V. The clade *Cupha arias* + *Cupha prosope* is supported by homoplasious character 78 (apical tarsomere of female foreleg shorter than penultimate), as in *Pardopsis*, *Acraea*, *Cethosia*, *Euptoieta*, and clade Q (*Vagrans* and *Phalanta*).

Clade W shows that *Terinos* is sister to the African genus *Lachnoptera* and the *Algia* + *Algiachroa* + *Cirrochroa* group-of-genera. The clade is supported by synapomorphic character 6 (fw discocellular M2-M3 connected with cubitus proximal to or basad the base of CuA1); and homoplasious characters 10 (absence of basal spur), as in *Pardopsis*, *Acraea*, *Euptoieta*, and *Clossiana*; 77 (presence of pretarsal pad of female foreleg), also in *Philaethria*, *Heliconius erato*, and *Vindula sapor*; 78 (apical tarsomere of female foreleg longer than penultimate), also in *Philaethria* and *Heliconius erato*; and 83 (presence of well-developed stink-club), as in *Philaethria* and *Heliconius erato*.

Clade X. *Terinos* monophyly is supported by synapomorphic character 19 (presence of androconial patch on upperside hindwings). *Lachnoptera* (see clade AA') also has the androconial patches on both forewings and hindwings. Other character support for clade X includes 71 (presence of spiny projection at the center of valva); and homoplasious characters 38 (absence of the apophyses of abdominal T8), also in the basal clades up to *Childrena childreni* and *Argyreus hyperbius*, and also in most *Cupha* except *C. erymanthis*; and 40 (contour of posterior edge T8 incurved, i.e. concave) as in *Philaethria* and *Vindula*. This cladistic analysis shows that *Terinos* is sister to *Lachnoptera*, *Algia*, *Algiachroa*, and *Cirrochroa*, although Parsons (1999) suggested that *Terinos* is closely related to *Cupha*, *Phalanta*, and *Vagrans*, based on larval and pupal morphology, and foodplant association.

Clade Y. Monophyly of most species of *Terinos* is defined by homoplasious character 21 (hairy eyes), as in *Smerina*.

Clade Z. Monophyly of parts of *Terinos* is supported by the homoplasious character 11 (forewing termen about the same length as dorsum), as in *Cethosia*, *Vagrans*, *Lachnoptera*, and *Algia*.

Clade AA'. Monophyly of *Lachnoptera*, *Algia*, *Algiachroa* and *Cirrochroa* is supported by synapomorphic character 70 (crista present); and homoplasious characters 16 (hw cell open), as in *Philaethria*, *Vindula*, and *Cupha*; 23 (tegula about $\frac{1}{2}$ or longer than $\frac{1}{2}$ the length of mesoscutum), as in *Euptoieta*, *Childrena childreni*, *Argyreus hyperbius*, and *Smerina*; 46 (presence of large plate as extension of appendix angularis), as in *Cethosia*, *Euptoieta*, *Childrena childreni* and *Argyreus hyperbius*, although the plate in *Algia* is small; 60 (presence of setae on transtilla), as in most *Vindula* clade M (*V. erota*, *V. dejone*, *V. arsinoe*) and *Cupha*, with reversal at *Algia*; 65 (presence of coecum penis), as in *Pardopsis*, *Acraea pharsalus*, *Heliconius erato*, and *Clossiana*, with reversal in *Algiachroa* and *Cirrochroa satellita*.

Clade AB' indicates that the *Algia*, *Algiachroa* and the *Cirrochroa* group-of-genera is supported by homoplasious characters 20 (antennae thread-like with almost no club), as in *Cupha*; 34 (apodeme at the anterior edge of second abdominal segment small), as in *Pardopsis* and *Acraea*; 49 (saccus elongate proximally), as in *Pardopsis*, *Acraea*, *Philaethria*,

Heliconius erato, *Cethosia*, and *Vindula*; 57 (juxta bulbous and elongated), as in *Euptoieta*, *Clossiana*, *Childrena childreni*, *Argyreus hyperbius*, *Vindula*, and *Vagrans*; 66 (absence of expansion of vesica at aedeagus opening), as in the basal clades up to *Euptoieta*, and *Vagrans*; and 89 (ductus seminalis attachment at some distance distal to antrum), as in *Pardopsis* and *Acraea*. This group-of-genera was recognized by Parsons (1989, 1999). Parsons (1989) removed *Cupha woodfordi* from *Cupha* and introduced the generic name *Algiachroa* for the species. Corbet & Pendlebury (1992) indicated the close relationship of *Algia* to *Cirrochroa*, without mention of *Algiachroa woodfordi*.

Clade AC'. *Algia* monophyly is supported by synapomorphic character 15 (presence of yellowish cream submedian band on upperside of hindwing); and homoplasious character 46 (small plates as extension of appendix angularis), as in clade P (*Vagrans*, *Phalanta* and *Cupha*).

Clade AD'. Monophyly of *Algiachroa* and *Cirrochroa* is defined by synapomorphic character 64 (presence of spines on external wall of aedeagus). This is the first mention of this feature for the heliconiine group. I am unaware of any mention of it in any heliconiine publication. Miller (1987) used the term *cornuti* also for the spines on external wall of aedeagus (c.f. *cornuti* on vesica membrane) although acknowledged that the *cornuti* on the aedeagus of different papilionid genera are not homologous.

Clade AE'. *Cirrochroa* monophyly is supported by homoplasious character 40 (contour of posterior edge of T8 outcurved, i.e. convex), as in *Heliconius erato*, *Euptoieta*, clade Q (*Vagrans* and *Phalanta*), and *Algia felderi*. The resolution within the genus *Cirrochroa* may change with future study on the species level involving all species and more applicable characters.

Clade AF'. Part of *Cirrochroa* is supported by homoplasious character 36 (length of S7 2/3 or more the length of S6), as in *Pardopsis*, *Acraea*, *Heliconius erato*, *Cethosia*, *Euptoieta*, *Clossiana*, *Childrena childreni*, and clade U (*Cupha lampetia* and *Cupha myronides*).

Clade AG'. Monophyly of part of *Cirrochroa* (*C. thule*, *C. aoris*, *C. emalea*, and *C. malaya*) is supported by homoplasious character 4 (forewing vein R4 arises distad or at about the same position as end of R2), also in *Cethosia*, *Euptoieta*, clade P (*Vagrans*, *Phalanta* and *Cupha*), *Lachnoptera*, and *Algia*.

Conclusion

This analysis using adult morphological characters demonstrated that the ingroup taxa belong to the argynnines, and there is resolution among the genera of the subtribe uncertain. The name **Vagrantini** was suggested by Penz and Pegg (2003) to include *Vindula*, *Smerina*, *Vagrans*, *Phalanta*, *Cupha*, *Terinos*, *Lachnoptera*, *Algia*, *Algiachroa*, and *Cirrochroa*. Previously *Vindula* and *Terinos* were regarded intermediate between Heliconiina and the argynnines. This study indicated that *Vindula* is sister to the rest

of the Indo-Australian and the two Afrotropical genera, although the monophyly is supported only by homoplasious characters. *Terinos* forms a sister group relationship with *Lachnoptera* and the *Cirrochroa* group-of-genera.

The Afrotropical genus, *Smerina*, is shown to be sister to *Vagrans-Phalanta-Cupha* with homoplasious characters supporting the relationship. Interestingly, the homoplasious characters are also found in *Lachnoptera*, the other Afrotropical genus. In this study, *Lachnoptera* is shown as sister to *Cirrochroa* group, with the support of a synapomorphic character, the presence of crista, and some homoplasious characters which are not necessarily shared with *Smerina*.

This analysis also showed the support for the monophyly of the *Cupha* group-of-genera and the *Cirrochroa* group-of-genera, which have long been suggested (Fruhstorfer, 1912; Corbet & Pendlebury, 1978, 1992; Parsons, 1989, 1999). The *Cupha* group-of-genera consists of *Cupha*, *Phalanta*, and *Vagrans*. The *Cirrochroa* group-of-genera consists of *Cirrochroa*, *Algia*, and *Algiachroa*.

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