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Adult Morphology and the Higher Classification of *Bia* Hübner (Lepidoptera: Nymphalidae) [1]

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Abstract. The South American nymphalid *Bia* Hübner, 1819, treated for over 150 years by most lepidopterists as a member of the Satyrinae, has been shown by recent work on early stages and DNA to share characters with the Morphinae: Brassolini. Examination of the wing patterns and androconial organs of *Bia*, described in detail for the first time, reveals unusual features otherwise only known from brassolines. In particular, the tufted posterior androconial organ of the hindwing forming palisades is a synapomorphy for *Bia* and several genera of Brassolini, including *Caligo*. The genus *Bia* is formally transferred from the Satyrinae to the Morphinae: Brassolini as the sole member of the subtribe Biina Herrich-Schäffer, 1864, **stat. nov.,** co-ordinate with Brassolina Boisduval, 1836, and Naropina Stichel, 1925.

Key words. Systematics, Satyrinae, Morphinae, Brassolini, *Caligo*, androconia, Neotropics, butterflies

The brothers Kratos and Zelos, and their sisters Nike and Bia, were the personifications of strength, rivalry, victory and force. These four winged gods stood beside the throne of Zeus.
http://www.theoi.com/Ouranos/Kratos.html

1. INTRODUCTION

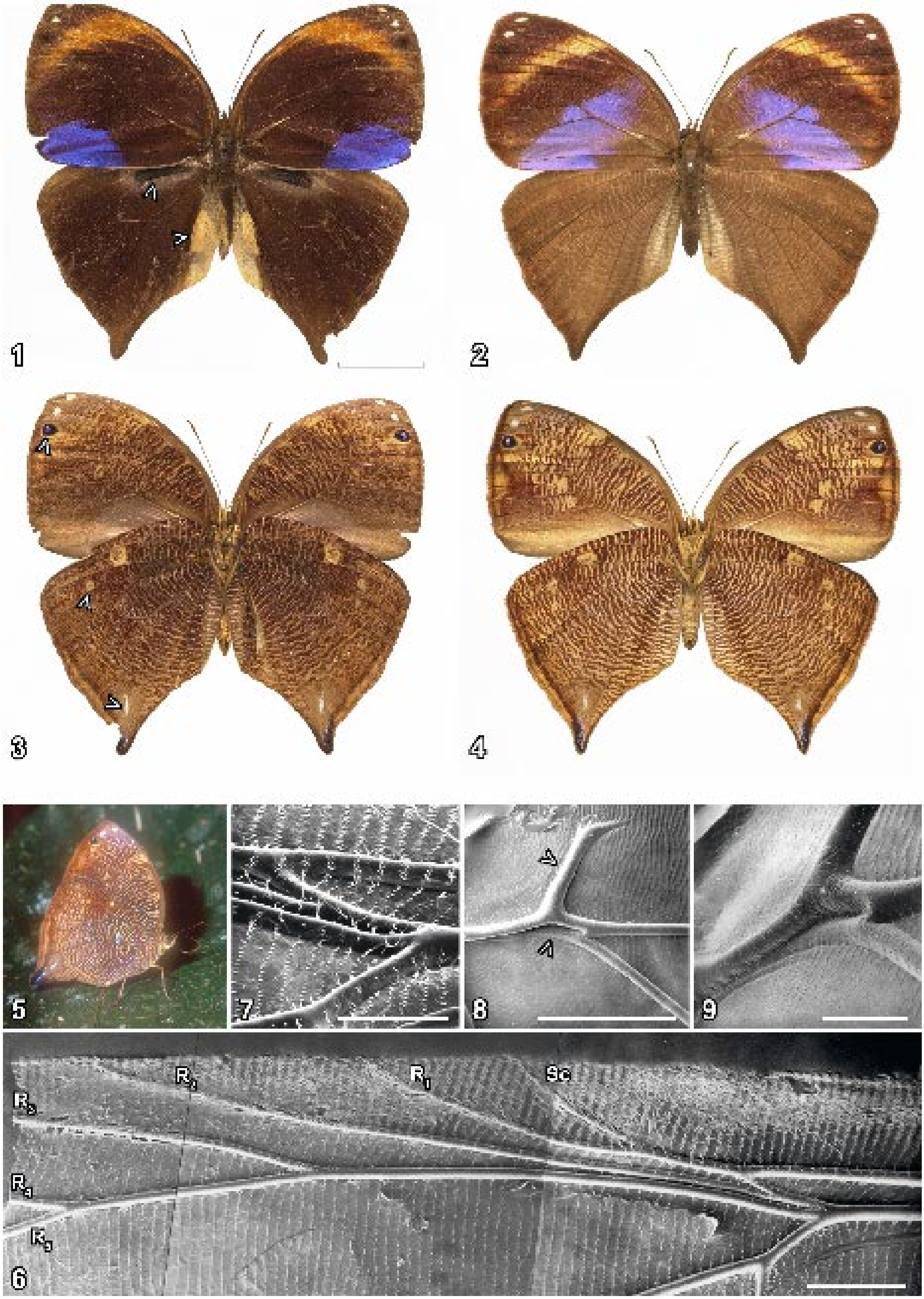
The genus *Bia* Hübner, 1819, has long been a puzzle to systematists. At present only one species is recognised, *Bia actorion* (Linnaeus, 1763). However, our investigations and those of Gerardo LAMAS (pers. comm., Lima 2004) indicate that there may be two or more sibling species, and this will be addressed in a future paper (LAMAS, BOPPRÉ, HOARE & VANE-WRIGHT in prep.).

In general facies *Bia* is markedly divergent from other butterflies, and both sexes are instantly recognisable as members of the genus (Figs 1–4). The butterflies are restricted to lowland and lower-montane forests of South America, occurring in dense undergrowth where the canopy is not fully closed. Individuals fly along trails and in clearings in damp, marshy areas, and are active from dawn to dusk. They often settle on rotting fruits, on which they feed, or on vegetation about a metre above the ground, when they may reveal their yellowish and blue upper side pattern. Mark and recapture studies indicate that males can live for at least 20 days, and are generally loyal to a particular patch of forest. In flight, the iridescent blue patches sported by most individuals flash conspicuously. If threatened, the butterflies dash into the base of a bush, where they are very difficult to reach. As they settle after an escape flight, the wings are closed to reveal only the cryptic, ripple-pattern underside (Fig. 5). This, together with the sudden disappearance of the distinctive blue colour, makes them difficult to locate. Interactions between males are frequent, and courtship is lengthy and complex, including tandem flight patterns, contact during flight, and male flight over perched females that apparently may respond by flashing their wings. Until very recently their early stages and host plants were unknown (BARTLETT 1876; HALL 1939; MASTERS 1970; FREITAS et al. 2002; Keith WILLMOTT, pers. comm., London 2004).

Bia adults have tri-carinate antennae and small forelegs in both sexes, and the genus undoubtedly belongs to the Nymphalidae *sensu* ACKERY et al. (1999). Its systematic position within the family has, however, been very uncertain. With no convincing evidence to support MILLER's (1968) suggestion of a relationship to the melanitine Satyrinae, D'ABRERA (1988: 846; 2001: 340), for example, has continued to locate *Bia* amongst the Pronophilina, the dominant group of typical Satyrinae found in mountainous regions of South America. This reflects a convention first adopted by KIRBY (1871) in his 'Catalogue', and subsequently followed by WEYMER (1911: 276) in 'Seitz', and by GAEDE (1931: 524) in 'Lep. Cat.'. MIELKE & CASAGRANDE (1998) list the Biini immediately after the Pronophilini.

FREITAS & BROWN (2004), in contrast, conclude that *Bia* should be placed as a monobasic subfamily (Biinae) within their "satyroid clade", reflecting a view going back to HERRICH-SCHÄFFER (1864) that gives *Bia* very high taxonomic rank. In most of their analyses, *Bia* appeared in various relationships with the Satyrinae, Mor-

1 In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)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phini, Brassolini and Calinaginae, although in a successive weightings analysis it appeared as the stem group of the Brassolini (FREITAS & BROWN 2004: fig. 2). Recent publications by BROWER (2000) and FREITAS et al. (2002) have provided, respectively, valuable new data on the molecular systematics and early stages that are consistent with the idea that *Bia* is a member of the Brassolini, one of the two South American tribes that belong to the Morphinae. This view, that *Bia* is a brassoline, was first put forward by CLARK (1947), tentatively supported by DEVRIES et al. (1985), and recently accepted by YOSHIMOTO (2003).

Here we re-investigate the adult morphology of *Bia* and question why its membership of the Brassolini was not recognised previously. CLARK (1947, 1948) failed to provide any evidence, and inaccurate or incomplete subsequent work has obscured its natural relationships. The peculiarities of the androconial systems reported here demonstrate that, even without the evidence now available from knowledge of DNA sequences and early stage morphology, the clear relationship of *Bia* to the owl butterflies (*Caligo* Hübner, 1819) and other Brassolini has literally been "staring us in the face" for over 200 years.

2. SYSTEMATIC HISTORY

LINNAEUS (1763a,b) described *Papilio actorion* from "Indiis", for which HÜBNER (1819: 51) introduced the genus *Bia*, with *Papilio actoriaena* Hübner, 1819 (an objective synonym of *Papilio actorion*: HEMMING 1964), as the only included species. GODART (1824: 446), however, consigned *P. actorion* to *Morpho* Fabricius, 1807, in which he also included many species now placed in the Amathusiini and Brassolini.

In his outstanding contribution to *The Genera of Diurnal Lepidoptera*, WESTWOOD (1850: 321) accepted Hübner's genus for *actorion*, noting *Bia* as a "very interesting … butterfly" belonging to the "Nymphalidae". It must be appreciated, however, that Westwood's classification of the Nymphalidae differed significantly from current practice. He likened *Bia* not only to various butterflies in the "Satyridae", but in particular among his "Nymphalidae" to such genera as *Siderone* Hübner, 1823 (now in Charaxinae), *Heteropsis* Westwood, 1850 (now Satyrinae), *Kallima* Doubleday, 1849 (Nymphalinae) and *Amathusia* Fabricius, 1807, *Zeuxidia* Hübner, 1826, and *Discophora* Boisduval, 1836 (Morphinae: Amathusiini).

In contrast, HERRICH-SCHÄFFER (1864) suggested that *Bia* should have very high taxonomic rank, placing it as the sole member of a new family, the Biidae [as "Bina"], one of just 16 family groups into which he divided the entire Rhopalocera. In so doing, he compared *Bia* with butterflies now placed in the Brassolini and Danaini, but not the Satyrinae.

As noted by WESTWOOD (1850), *Bia* has the bases of forewing veins Sc, Cu and 2A conspicuously inflated. This apparently persuaded WALLACE (1854) to place *Bia* in the Satyridae: "the beautiful *Bia Actorion,* which, though classified with the Nymphalidae, exactly agrees with this family [Satyridae] in its haunts and mode of flight … [and] in many structural points." Wallace concluded that it formed "a very satisfactory link connecting the two families." In assigning *Bia* to the satyrines, he has been followed by a majority of lepidopterists ever since – e.g. FELDER (1861), DIETRICH (1862), KIRBY (1871), DRUCE (1876), MÜLLER (1877), STAUDINGER (1888), SCHATZ & RÖBER (1889), WEYMER & MAASSEN (1890), WEYMER (1911), GAEDE (1931), HALL (1939), EHRLICH (1958), HAYWARD (1958, 1964), FORSTER (1964), MILLER (1968), D'ABRERA (1988, 2001), HARVEY (1991), MIELKE & CASAGRANDE (1998), RACHELI & RACHELI (2001). However, at least two authors before the recent period linked this curious little butterfly firmly with the Morphinae – but in different ways.

REUTER (1896), in his remarkable but often neglected thesis, placed *Bia* in the Morphinae, as one of three tribes: Morphini, Amathusiini and Biini (GODART 1824, by including *actorion* as a discrete subgroup "IIA" within *Morpho*, set a precedent for this). REUTER separated the Morphinae from the Brassolini, including the latter within the much larger Satyrinae. On the other hand, and possibly taking a lead from HERRICH-SCHÄFFER, CLARK (1947, 1948) unhesitatingly placed *Bia* as a brassolid, but without giving any reason. Frustratingly, in the first of these two papers, CLARK stated confidently but without explanation, "Brassolidae [are] easily recognisable by adult characters"; no justification at all was given in his second paper. For various reasons, both REUTER (1896, 1898) and CLARK (1947, 1948) have largely been ignored.

Figs 1–9: *Bia actorion* (L.) *sensu lato*. Adult butterflies and wing venation (both specimens from Suapure, Venezuela). **1** male upperside (upper arrow: anterior alar organ; lower arrow: posterior alar organ; BMNH(E) #693091); **2** female upperside (BMNH(E) #693105); **3** underside of 1 (upper arrow: border ocellus in forewing cell M_1; mid arrow: border ocellus in hindwing cell R_5; lower arrow: border ocellus/diagonal white stripe in hindwing cell Cu_{1a}); **4** underside of **2**; **5** live individual at rest (Venezuela, Bolivar State, Jasper Falls 27.x.2000); **6** forewing radial venation from anterior apex of discal cell to separation of R_4 and R_5 (subcostal and radial veins labelled; BMNH electron micrographs #E3/273–5, composite SEM); **7** detail of 6 to show origin of radial veins from discal cell; **8** hindwing precostal area (upper arrow: precostal vein; lower arrow: precostal cell; BMNH electron micrograph #E3/270, SEM); **9** detail of 8 (BMNH electron micrograph #E3/271). Scale bars: 1–4: 10 mm; 6: 1 mm; 7: 0.5 mm; 8–9: 1 mm.

MILLER (1968) followed conventional wisdom in accepting *Bia* as a member of the Satyridae (he regarded them as a family) in which, like Reuter, he also included the Brassolini but not Morphini or Amathusiini. MILLER used the name Biinae to designate one of seven subfamily divisions for the group, and further subdivided the Biinae into three named tribes: the Melanitini, Antirrheini, and the monobasic Biini, commenting that "*Bia* is far too aberrant to be referred to either of the other two biine tribes." He also suggested that "within the Satyridae the brassolines are allied to the New World Biinae, particularly through such genera as *Narope* [Brassolini]" (MILLER 1968: 23).

Miller thus united *Bia* with the new world Antirrheini (*Antirrhea* Hübner, 1822, and *Caerois* Hübner, 1819), and the old-world Melanitini: *Melanitis* Fabricius, 1807, *Cyllogenes* Butler, 1868, *Gnophodes* Westwood, 1851, *Parantirrhoea* Wood-Mason, 1880, and *Bletogona* C. & R. Felder, 1867 (for placement of this last genus, see UÉMURA 1987). In addition, but in a very ambiguous manner, Miller also listed *Manataria* Kirby, 1908, at the end of his account of the Biinae. This peculiar genus represents a small group of South American brown butterflies of very uncertain affinity that he likened to the old world Elymniini: Lethina, as well as some members of his Biinae. In contrast, FORSTER (1964; see also RACHELI & RACHELI 2001) had earlier placed *Manataria* within the Satyrini: Euptychiina, the dominant group of lowland Satyrinae found in Latin America. MIELKE & CASAGRANDE (1998) understandably listed *Manataria* at the end of the Satyrinae as "tribe uncertain".

VANE-WRIGHT (1972a) recognised that the three higher taxa linked within the Biinae by MILLER (1968) represent an unnatural assemblage. Based on evidence from eggs, larvae and adults, DEVRIES et al. (1985) formally transferred the Antirrheini to the Morphini, as a subtribe. They also suggested that *Bia*, mainly on the evidence of its external abdominal androconia similar to those found in *Caligo* and related genera, might belong to the Brassolini, and these views were echoed by ACKERY (1984: 16, 1988: 104). In BROWER's (2000) molecular investigation, *Bia* grouped with *Caligo*, and these two genera then grouped with *Opsiphanes* Doubleday, 1849, a result consistent with CLARK's assertion and the suggestion of DEVRIES et al. This contention is further supported by the work of FREITAS et al. (2002) on the early stages.

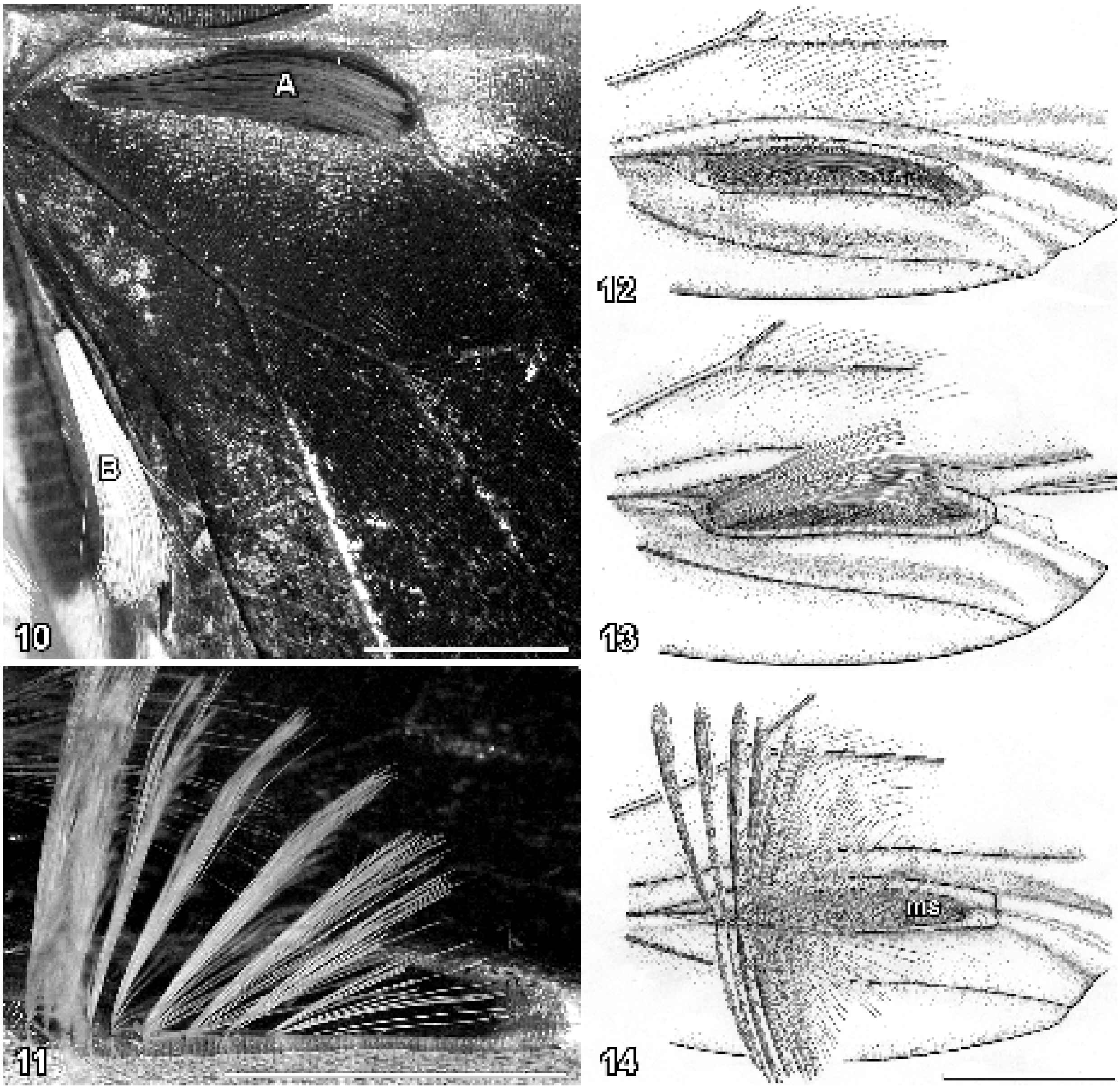
Currently, of the subgroups included by MILLER in the Biinae, only the evening browns and their relatives of the Old World tropics (Melanitini), together with the peculiar New World *Manataria*, appear to belong securely to the Satyrinae as currently conceived (ACKERY 1988; BROWER 2000; WAHLBERG et al. 2003). YOSHIMOTO (2003) has formally raised the Melanitini (to include *Manataria*) to tribal rank within the Satyrinae. Following DEVRIES et al. (1985), the Antirrheina are now widely accepted to as a subtribe of the Morphini (ACKERY 1988; HARVEY 1991; BROWER 2000). But what conclusions should be drawn with respect to *Bia*?

Appreciating the peculiarity of *Bia* is confounded by MILLER's description of the adult insect, which is inaccurate with respect to the labial palpi and forewing radial venation (the latter error has recently been repeated by YOSHIMOTO 2003), and incomplete most notably with respect to the androconial organs. In the following sections we first correct MILLER's (1968) account of the palpi and forewing venation. This is followed by observations on its wing patterns and an extensive account of the androconial organs. We then review recently published work on the early stages, hostplant relationships and molecular systematics, before offering a general discussion. Finally, we summarise a revised provisional classification for Satyrinae and Morphinae (Appendix I).

3. THE LABIAL PALP AND FOREWING RADIAL VENATION

Labial palp. MILLER's (1968: 33) account of the adult morphology of *Bia* is fundamentally incorrect on two points. First, regarding the labial palp, he states that "the third segment … is very long, over half the length of the second segment". Such an arrangement would be highly autapomorphic, but is simply not the case. As first shown by SCHATZ & RÖBER (1889: pl. 39), the third segment is much shorter, about one quarter the length of the second, as found in very many Nymphalidae.

Forewing radial venation. In contrast, as MILLER correctly appreciated, the forewing radial venation of *Bia* is highly autapomorphic, but his description ("forewing radial veins arise from a single branch") and illustration (MILLER 1968: 33, fig. 29) are inaccurate. The forewing radial system comprises two main branches, R_{1+2} and R_{3+4+5}, which arise in very close proximity at the anterior apex of the discal cell (Figs. 6, 7). After about 0.5 mm, R_{1+2} divides. R_1 then fuses with the subcostal vein for about 1 mm before separating again and finally running free to the costa (such an anastomosis occurs in many butterflies). R_2 runs free to the costa, but for the first 2 mm or so of its length it remains extremely close to R_{3+4+5}. After this parallel section, R_{3+4+5} gently diverges before separating, at about 5 mm from the apex of the discal cell, into R_3 and R_{4+5}; about 2 mm or so further on the latter separates into R_4 and R_5, with all the separate branches of R eventually running free to the costa. The real peculiarity of this system is the 'joint' origin (Fig. 7) of two branches of the radius as R_{1+2} and R_{3+4+5}, and their extremely close, parallel course that continues as R_2 and R_{3+4+5} (Fig. 6).

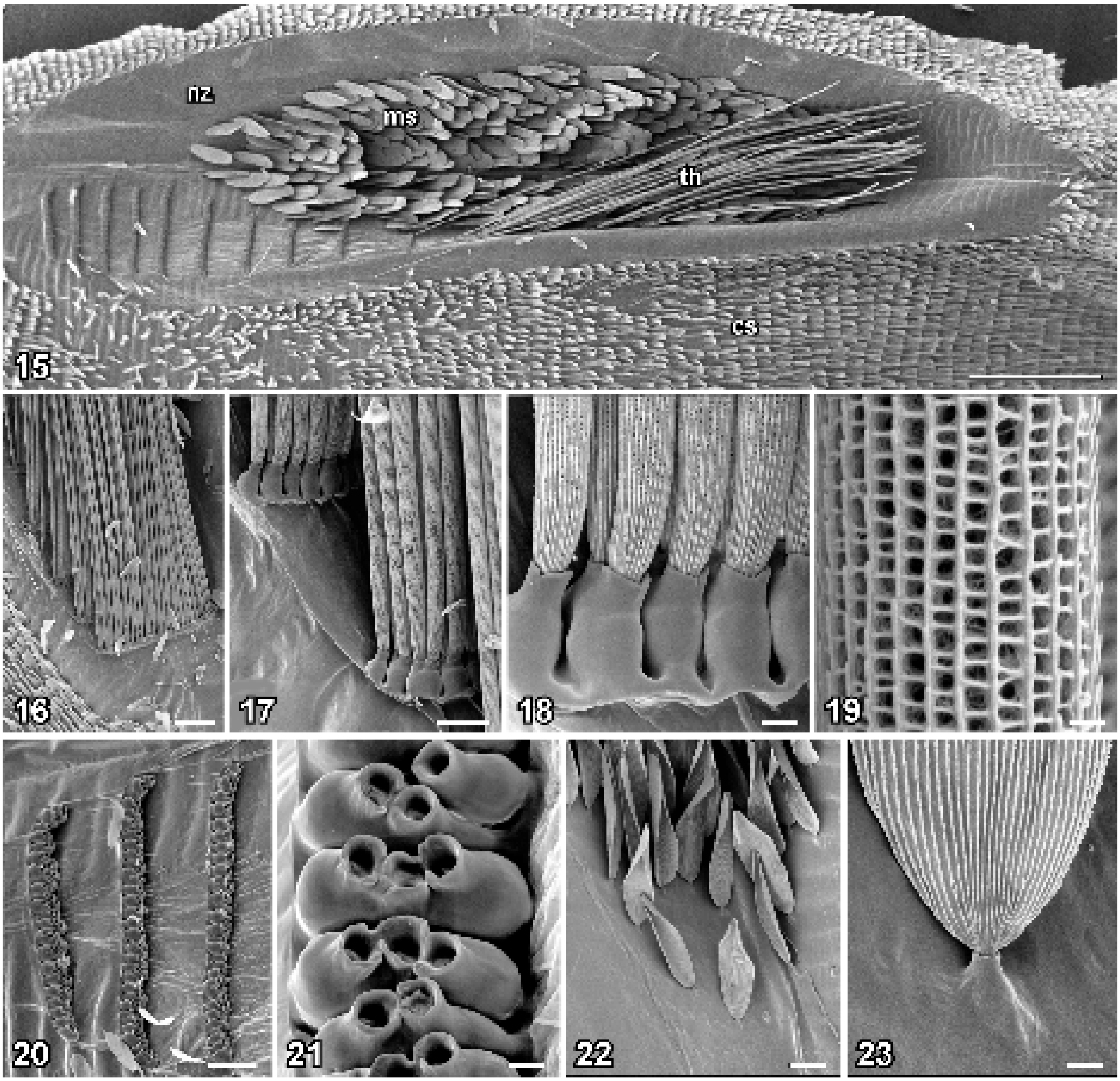


Figs 10–14: *Bia actorion* (L.) *sensu lato*. Hindwing androconial organs. **10** anterior (A) and posterior (B) alar organ; **11** posterior hair tuft fully erect; **12** pocket between 2A and 3A exposed with tuft closed (BMNH(E) #693030); **13** tuft partly erect revealing part of scale patch (BMNH(E) #693232); **14** tuft fully erect, patch of modified scales (ms) visible (BMNH(E) 693196). Scale bars: 10–14: 5 mm.

4. WING PATTERN

The underside pattern of *Bia* is very reduced compared with the nymphalid groundplan (NIJHOUT 1991: 24). Almost the entire area of both wings is covered by a ripple pattern (Figs. 3–5) (NIJHOUT 1991: 37), relieved only by marginal and submarginal bands on both wings, three or four specialised border ocelli and the parafocal elements on the forewings, and some very reduced ocelli and a few other markings on the hindwings, including the small but characteristic diagonal white stripe in cell Cu_{1a} (Figs. 3–5).

The forewing border ocelli, although small, are distinctive, occurring very close to the wing margin, with the two or three anterior ocelli (R_4 and R_5, and in some individuals, R_3) being reduced to white 'pupils' only (Figs. 3, 4). The posterior ocellus (in cell M_1), although better developed, is somewhat oblate, with the proximal side a little drawn out to form a blunt point. The parafocal elements of the forewing are not overwhelmed by the ripple pattern (cf. NIJHOUT 1991: 37), but form a distinctive line that deviates more or less markedly at the intervenous stripe in cell M_3. On the hindwing the border ocelli are reduced to vague spots, present only in

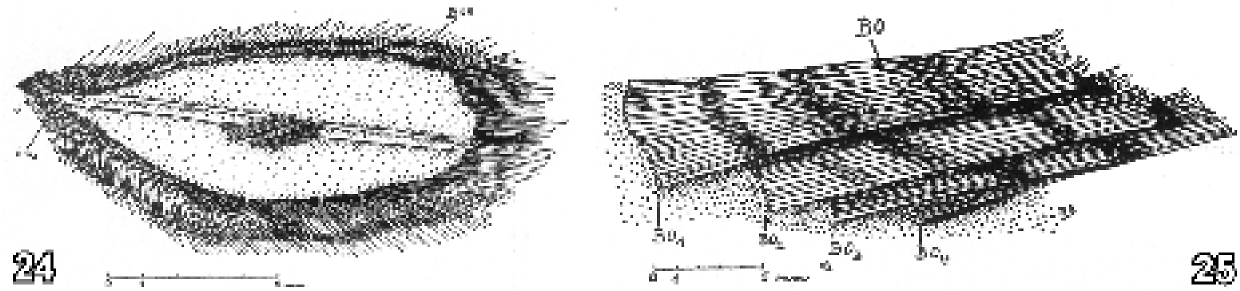


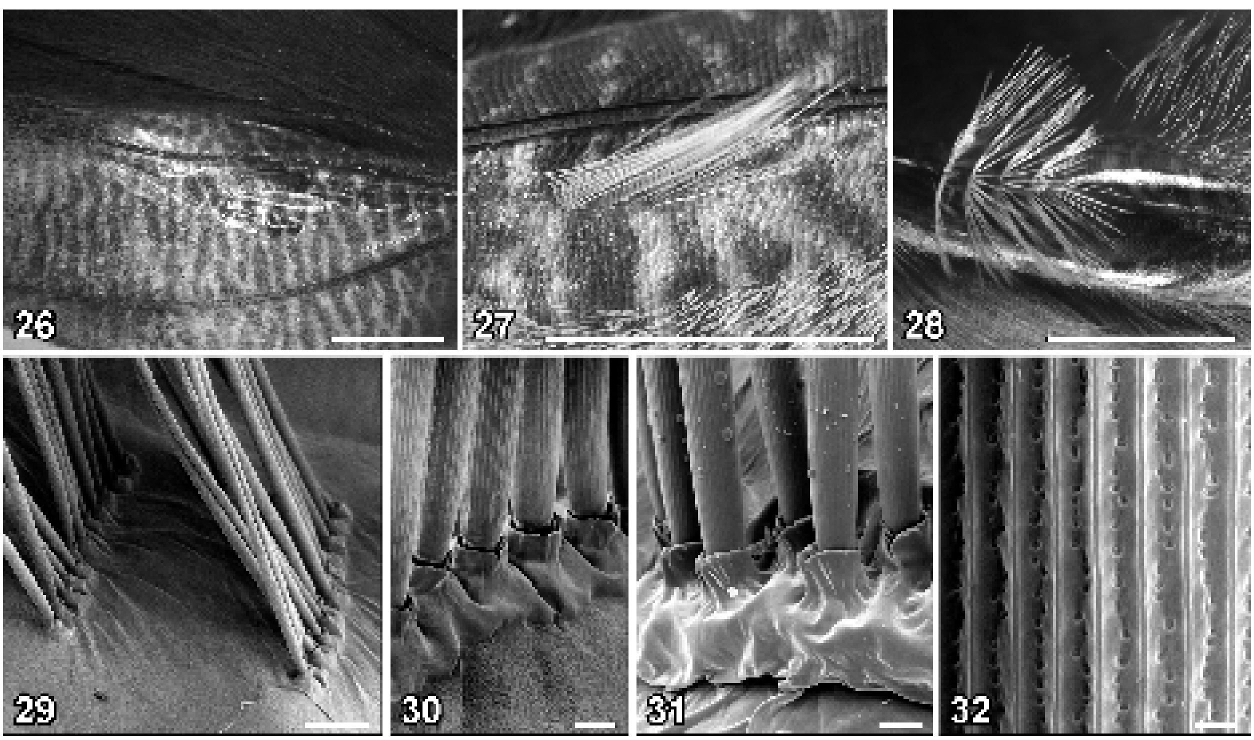
Figs 15–23: *Bia actorion* (L.) *sensu lato*. Scanning electron micrographs of hindwing posterior androconial organs. **15** entire organ with hairs from ten anterior tuft rows broken off to reveal a patch made of modified scales (ms) (22, 23), surrounding naked zone (nz), tuft hairs (th), and covering scales (cs) of wing area adjacent to vein 3A; **16** bases of a five rows of palisade-forming tuft hairs; **17**, **18** bases of a row showing conjoined sockets; **19** fine structure of hair; **20** part of patch with hairs lifted off to reveal sockets; **21** detail from sockets with hairs removed; **22**, **23** details of scales and sockets comprising patch (ms in 15). Scale bars: 15: 1 mm; 16: 200 µm; 17: 50 µm; 18: 10 µm; 19: 2 µm; 20: 100 µm; 21: 10 µm; 22: 100 µm; 23: 10 µm.

three adjacent anterior cells, R_1, R_5 and M_1, plus a diagonal whitish stripe in Cu_{1a} (which is also a specialised border ocellus – see Discussion). Although the three anterior hindwing ocelli occur in cells that, in terms of serial homology, correspond to the forewing cells that always have border ocelli, unlike the forewing, on the hindwing the ocelli are located far from the margin (Figs. 3, 4).

5. ANDROCONIAL SYSTEM

Alar androconial organs. According to MILLER (1968: 34), "there is a patch of mealy scales on the upper end of the cell along crossvein rs-m1, and a long hair tuft lies along 2A." As long ago and more accurately pointed out by MÜLLER (1877), the males of *Bia* possess a "tuft of long pale leather-brown hairs near the inner margin of the hind-wings, which can be erected or depressed at will, and when at rest, are enclosed in a long pocket, and also by a patch with long black silky hair





Figs 24, 25: *Caligo arisbe* Hübner, 1822. Hindwing posterior androconial organs (from BARTH 1953: figs 6, 7). Barth has called the structure 'apparatus assisting evaporation of the secretion'. An_1: analis of hindwing; dotted: naked area; BOR: ring of bristles; BO: bristles. [Note: obviously, the scale bar in 25 is incorrect.]

Figs 26–32: *Caligo eurilochus* (Cramer). Macrophotographs (26–28) and scanning electron micrographs (29–32) of hindwing posterior androconial organs. **26** hair tuft surrounded by a large shiny zone; **27**, **28** partly (27) and fully (28) erected hair tuft; **29–31** tuft rows showing conjoined sockets of palisade-forming tuft hairs; scanning electron micrographs: **32** fine structure of hair. Scale bars: 26–28: 5 mm; 29: 100 µm; 30, 31: 20 µm; 32: 2 µm.

near the anterior margin of the hind-wings. This latter patch is covered by a bare spot on the under side of the fore-wings, close to the inner margin." (cf. Figs. 1, 10).

Close examination of the hair tuft of the posterior alar organ (Figs. 11–21) reveals a peculiar arrangement of the hairs from which it is formed. The tuft comprises several rows of transversely inserted hairs, the length of the hairs, the distance between the rows, and the number per row all diminishing posteriorly (Figs. 11, 15; th), so that the entire tuft fits into a pocket formed between veins 2A and 3A. The whole organ, in its retracted state, is about 6–7 mm in length. When the hairs are erect, single lines become apparent, forming palisades (Figs. 11, 12, 14). The fine structure of these hairs (Fig. 19) is typical for many Lepidoptera androconia but their bases are peculiar in being conjoined (Figs. 18, 21). Underneath the hair tuft there is a large patch of modified scales (Figs. 14, 15; ms) that was overlooked by MÜLLER (1877). The scales are densely packed and partly upstanding, but do not show any peculiar features under SEM (Figs. 22, 23) or have sockets (Fig. 23) suggestive of glandular nature. Under a strong electron beam, these scales twist, something that happens to some scales but is relatively unusual. Adjacent to the posterior organ on the side abutting vein 3A is an extensive area of the wing with covering scales that are less dense and with scattered hairs (Fig. 15; cs), unlike the main areas of the wing.

In several specimens, the upperside forewing cell Cu_{1b} has a mane composed of hairs that are significantly longer and more densely packed than those found on the rest of the wing. This may represent another androconial organ, perhaps characteristic of one or more of the sibling species of which *Bia* may be composed, and is subject to further study.

MÜLLER (1877) found all kinds of "hair-tufts and felted patches" on the wings of male butterflies, including various Satyrinae and Morphinae. For *Caligo* he noted "Hind-wing of the male with a small tuft of hair near the inner margin, opposite to the middle of the abdomen." However, he apparently did not realize that the arrangement of the posterior hair tuft in *Bia* shares some peculiar features with *Caligo* (BARTH 1953; cf. figs. 24, 25), *Penetes* Doubleday, 1849, *Catoblepia* Stichel, 1902, *Opsiphanes* (ELTRINGHAM 1926; BARTH 1952), *Blepolenis* Röber, 1906, and *Caligopsis* Seydel, 1924, and some other brassolines. The most striking similarity is that the rows of tuft hairs arise from conjoined sockets (Figs. 24, 25, 27–32), a configuration currently unknown elsewhere in the butterflies. However, each row in these other genera comprises only a single line of scales (Fig. 29), not a double or triple line as in *Bia* (Figs. 17, 20, 21). Also, the number of rows of hairs (Figs. 27, 28) forming the posterior alar organ is always less, sometimes as few as 3 rather than 11–15 found in *Bia*. The major difference is the lack of a scale patch, but the surrounding zone (Figs. 24, 26) is comparable, normally much larger and conspicuous as a shiny, nacreous area (= "Reibefläche" of STICHEL 1909).

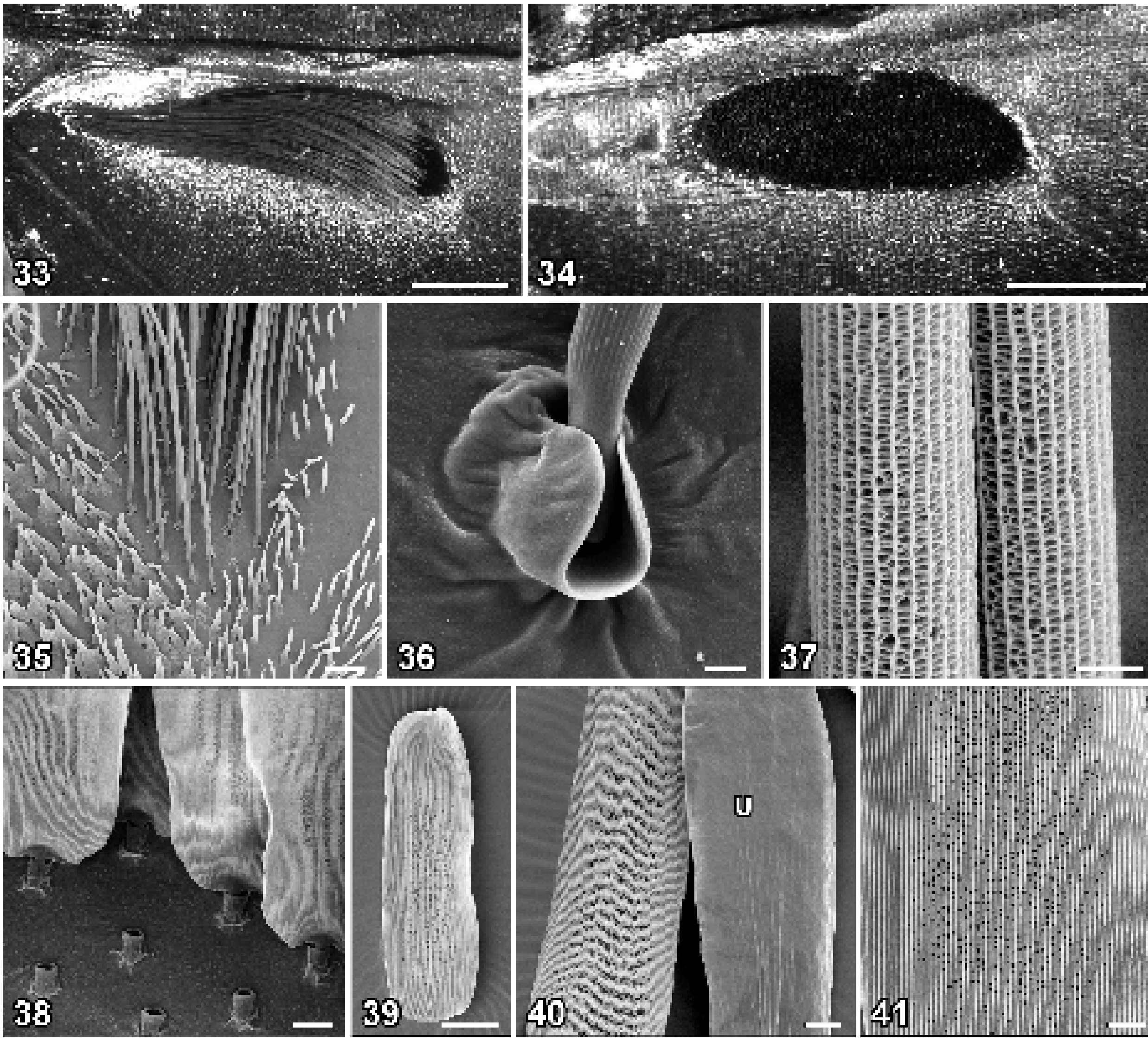
The anterior alar androconial organ of *Bia* consists in part of a pencil of hairs about 6–7 mm long (Fig. 33) inserted on the upperside close to the base of the hindwing discal cell (Fig. 10), and aligned approximately with the radial sector. It is evident that this pencil can be erected, as the hair sockets are modified to form an obvious 'click' mechanism (Fig. 36) comparable to that observed in the forewing alar organ of the morphine *Antirrhea* (Vane-Wright 1972b). These hairs do not otherwise exhibit special morphological peculiarities (Fig. 37), but when decumbent (Fig. 33) they virtually cover an extensive patch of modified scales (Fig. 34). This scale patch was not mentioned by MÜLLER (1877), but MILLER (1968: 34, fig. 29) referred to it (or the organ as a whole) as "a patch of mealy scales on the upper end of the cell." Probably a dual organ in the terminology of BOPPRÉ & VANE-WRIGHT (1989: 123), the hairpencil and its patch lie directly opposite a completely naked area on the underside of the forewing (MÜLLER 1877). A dual anterior alar organ of this type located in the hindwing discal cell is not typical for the Brassolini, but many members of the tribe have androconial organs of various sorts, including hairpencils located at various positions on the wings (cf. STICHEL 1909). *Caligo*, for example, has a conspicuous area of scales on the upper surface of the hindwing discal cell (Figs. 70–74) but, unlike *Bia*, this patch in *Caligo* is not associated with a hairpencil. *Eryphanis* Boisduval, 1870, has a patch and a hairpencil (ELTRINGHAM 1926), but the latter does not rest on the former.

Abdominal androconial organs. STICHEL (1909) mentions for many brassolines, including *Caligo, Penetes, Opsiphanes, Catoblepia,* and *Eryphanis*, "Reibewülste" or "drüsenartige Wülste" (rubbing or glandular bulges) that occur laterally on the male abdomina; no further characterisation is given. *Brassolis* Fabricius, 1807, *Dynastor* Doubleday, 1849, *Dasyophthalma* Westwood, 1851, *Narope* Doubleday, 1849, *Opoptera* Aurivillus, 1882, and *Selenophanes* Staudinger, 1887, lack them. These structures were not mentioned by MÜLLER (1877), but they have been described in considerable detail by BARTH (1952, 1953), and also by WASSERTHAL & WASSERTHAL (1977; as "scent pads"). Some of these structures are figured here for *Caligo eurilochus* (Cramer, 1775) (Figs. 63–69).

For the first time we describe lateral abdominal pads in *Bia* (Figs. 42, 44–46). Unfortunately, the condition of the specimens available to us is not suited for detailed study. However, in contrast to *Caligo*, the pads of *Bia* are located on the tergites (Figs. 42–46), not within the pleurae (Fig. 63). Moreover, in *Bia* the pads are comprised of three relatively simple scale types (Figs. 47–60), none of which matches the single highly specialised type (Figs. 64–69) of *Caligo*. The abdominal pads of *Caligo* can be protruded (WASSERTHAL & WASSERTHAL 1977). One set specimen of *Bia* in the collection of the BMNH shows the pads protruded, appearing as warty, shiny structures (Figs. 61–62). Another difference between *Caligo* and *Bia* concerns the resting position: in *Caligo*, when the butterfly is at rest, the pads are enclosed by the anal area of the hindwings, and thus must come automatically in contact with the posterior alar organs. In *Bia*, however, the posterior alar organ at rest is enfolded, and contact with abdominal pads would require a special behaviour. While *Caligo* exhibits dual androconial organs, those of *Bia* appear to be binate (BOPPRÉ & VANE-WRIGHT 1989). Although there are many differences in detail, the abdominal pads of *Bia* are grossly similar those found in Brassolini, and androconial organs of this general type are unknown from other taxa.

6. EARLY STAGES AND HOSTPLANT RELATIONSHIPS

Until the publication by FREITAS et al. (2002), the life cycle of *Bia* was undescribed. Here we summarise their results with reference to features of the early stages considered likely to be of significance for higher classification.

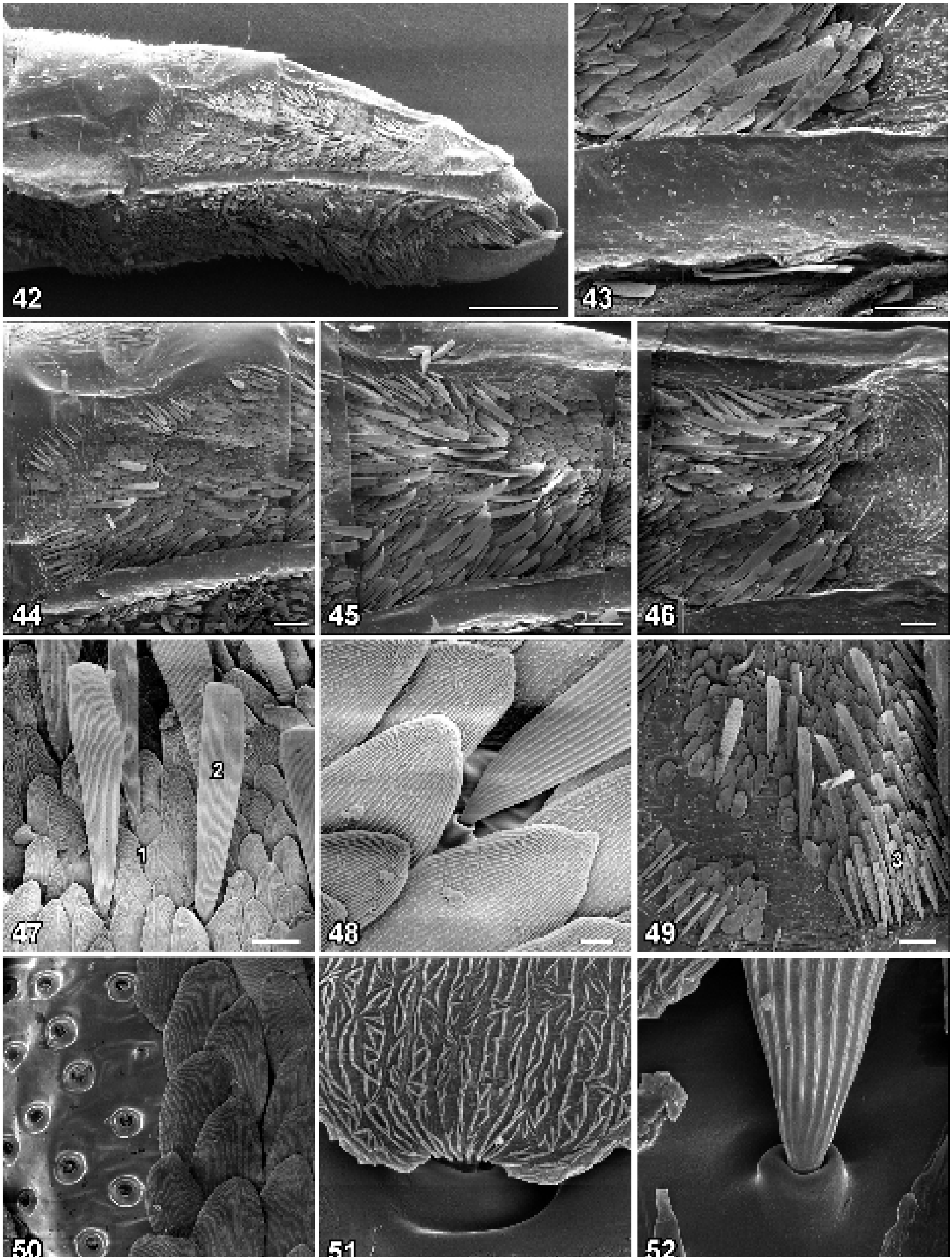


Figs 33–41: *Bia actorion* (L.) *sensu lato*. Macrophotographs (33, 34) and scanning electron micrographs (35–41) of hindwing anterior androconial organs. **33** hair tuft in resting position, obscuring **34** patch with modified scales; scanning electron micrographs: **35**, **36** hair bases exhibiting 'click' mechanism; **37** fine structure of hair; **38–41** patch scale bases and scale fine structure are unexceptional but the scale undersides are not perforated (40, U). Scale bars: 33, 34: 2 mm; 35: 100 µm; 36, 37: 5 µm; 38: 20 µm; 39: 50 µm; 40: 20 µm; 41: 10 µm.

Egg. Spherical, with 25–30 longitudinal ribs and as many as 50 transverse ridges (FREITAS et al. 2002: 120, fig. 1a). The eggs are thus comparable to those of Brassolini, which have 30–60 transverse ridges (e.g. *Narope*: CASAGRANDE 2002: figs. 1,2), and are unlike those of Satyrinae, which never have as many (FREITAS 1999).

First instar larva. The head capsule lacks scoli but has numerous long, branched or plumose setae (FREITAS et al. 2002: figs. 1b,c). A very similar condition can be seen in some Brassolini (e.g. *Narope*: CASAGRANDE 2002: fig. 4). FREITAS et al. (2002: 119) note that the newly hatched larvae are active, moving around the hostplant unlike "the sluggish behaviour of typical satyrines".

Later instar larvae. Later instars have three pairs of scoli on the head capsule (FREITAS *et al.* 2002: 121, figs 1i,j,k), typical of most Brassolini other than *Brassolis* (cf. DEVRIES 1987: fig. 32 E, 1–8; CASAGRANDE 2002: fig. 3e). According to FREITAS et al. (2002: 121), Satyrinae only have one pair of such scoli; however, while this is generally the case, arguably *Elymnias* Hübner, 1818, also has three pairs (IGARASHI & FUKUDA 1997: 85–89). The form of the head scoli in *Bia* is, however, highly autapomorphic, especially the dorsal pair (FREITAS et al. 2002: fig. 1k). The bifid caudal projec-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tions (FREITAS et al. 2002: figs. 1b,f,g,h,i) are like those seen in many Brassolini (e.g. *Caligo*: CASAGRANDE 1979), and are thus grossly similar to all members of the Satyrine clade as conceived by FREITAS & BROWN (2004), including Amathusiini, Calinaginae and Apaturinae. The numerous secondary body setae give a "hairy" appearance, as in many Brassolini (e.g. *Caligo*: CASAGRANDE & MIELKE 2000a: fig. 3) and Amathusiini (IGARASHI & FUKUDA 1997).

Pupa. Squat and sculptured (FREITAS et al. 2002: fig. 1 l,m), and thus quite similar to e.g. *Opsiphanes* (DEVRIES 1987: fig. 32B) and *Dasyopthalma* (CASAGRANDE & MIELKE 2000b: figs 6–8; 2003: figs. 4–6).

Hostplants. *Astrocaryum* G.Mey, 1818, and *Geonoma* Willd., 1805 (Arecaceae) (FREITAS et al. 2002). Arecaceae are recorded as foodplants of species of the brassoline genera *Brassolis, Opsiphanes, Catoblepia* and *Dasyophthalma*, and are also utilised by some species of Morphini, Amathusiini and Satyrinae (ACKERY 1988). Among the Brassolini, *Geonoma* is recorded as the host of *Dasyophthalma* species (CASSANGRANDE & MIELKE 2000b, 2003), both *Geonoma* and *Astrocaryum* are recorded as hosts for *Opsiphanes* (PENZ et al. 2000), and *Astrocaryum* as a host for *Brassolis* (ACKERY 1988).

7. MOLECULAR EVIDENCE

BROWER (2000) carried out a cladistic analysis of 103 species of Nymphalidae based on sequence data obtained from a 378 base-pair region of the *wingless* gene. In addition to *Bia*, his sample included species representing 6 genera conventionally included in the Morphinae *sensu lato* (*Morpho, Caerois, Antirrhea*, *Amathusia, Caligo* and *Opsiphanes*), and 13 genera included in the Satyrinae (*Haetera* Fabricius, 1807*, Melanitis, Lethe* Hübner, 1819*, Mycalesis* Hübner*,* 1818, *Tisiphone* Hübner*,* 1819, *Megisto* Hübner*,* 1819, *Oressinoma* Westwood, 1852*, Taygetis* Hübner*,* 1819, *Cercyonis* Scudder, 1875 , *Corades* Doubleday, 1848*, Lymanopoda* Westwood, 1851*, Pedaliodes* Butler, 1867, and *Steroma* Westwood, 1851). In his preferred solution (a most parsimonious cladogram produced using the successive approximations weighting option in PAUP 3.1: SWOFFORD 1991), all 20 of these genera, including *Bia*, formed a monophyletic group. This was divided into two subclades, one including the 13 genera conventionally included in the Satyrinae plus *Amathusia*. The remaining five conventional morphines, plus *Bia*, formed the other group. Within this latter clade, *Bia* grouped as sister to *Caligo*, with *Opsiphanes* as sister to these two, with these three forming the sister group to (*Morpho* (*Antirrhea* + *Caerois*)).

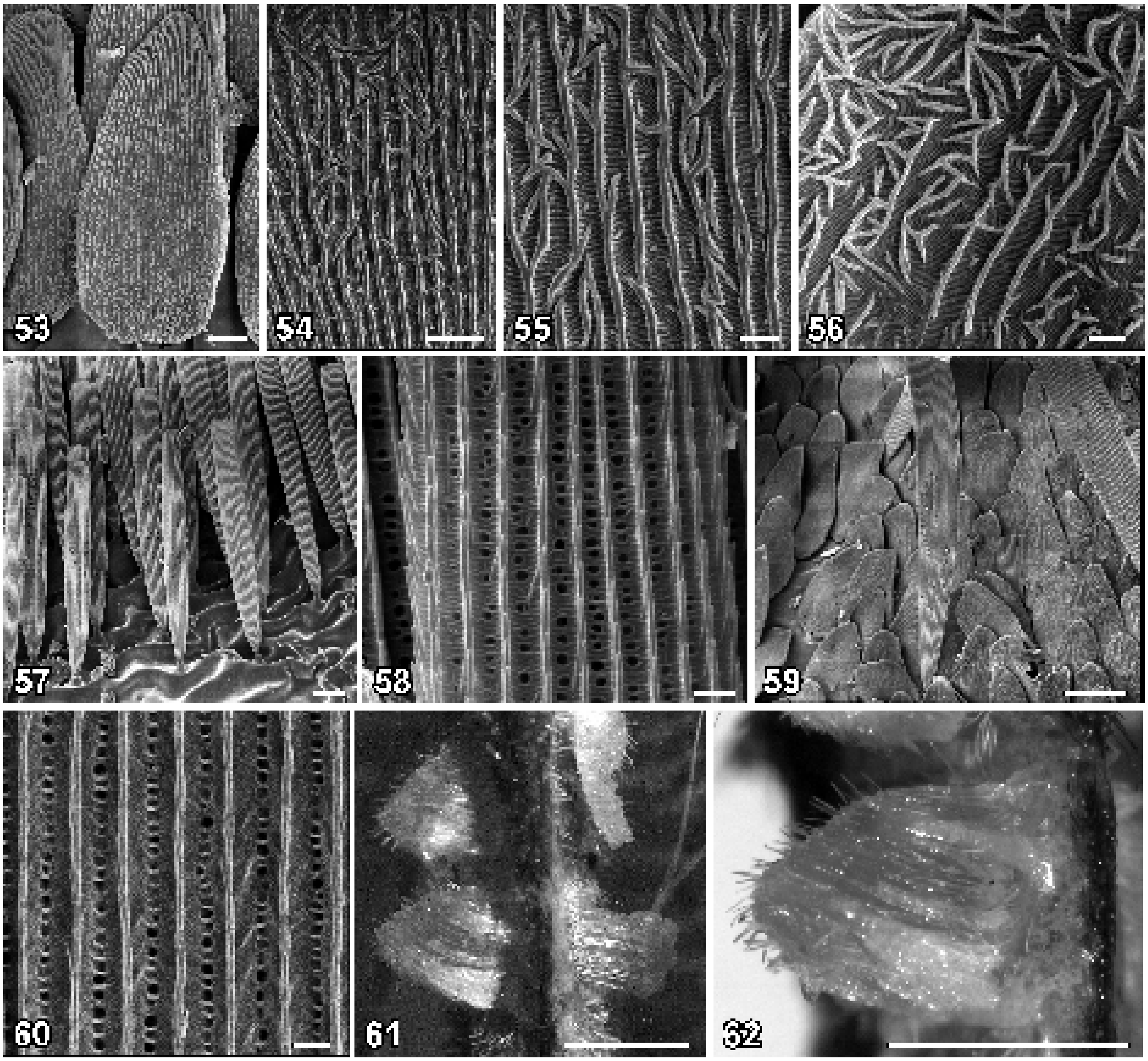
WAHLBERG et al. (2003) presented results from a cladistic analysis of 54 Nymphalidae, based on sequence data for one mitochondrial gene (COI, 1450 bp) and two nuclear gene sequences (EF-1α, 1064 bp; and *wingless*, 412–415 bp). His species sample represented three conventional morphine and nine conventional satyrine genera, including *Manataria* but not *Bia*. Although all of these genera grouped within a single major subclade, this grouping also encompassed both of their exemplar Charaxinae, and the enigmatic *Calinaga* Moore, 1857 (Calinaginae). This last genus (not available to Brower) grouped as sister to the two Charaxinae, and in some analyses these three together appeared as the sister group to (*Caligo* + *Morpho*). The remainder of the clade formed a paraphyletic assemblage of the nine conventional Satyrinae including *Melanitis* and *Manataria*, together with *Stichophthalma* C. & R. Felder, 1862 (Amathusiini). *Manataria* appeared as sister to *Melanitis*, and did not group with any of the Satyrini or Elymniini included in the analysis. This offers support for the inclusion of *Manataria* within the Melanitini as dealt with by YOSHIMOTO (2003), and not in the lethines (Elymniini) as vaguely speculated by MILLER (1968), or in the Euptychiina (Satyrini) as suggested by FORSTER (1964).

8. DISCUSSION

MILLER (1968: 33) made two errors in his account of *Bia*. First, he stated that the third segment of the labial palpus was abnormally long, exceeding half the length of the second. As revealed even by his own diagram (MILLER 1968: fig. 30), this is simply inaccurate. The gross morphology of the *Bia* palp is commonplace and unremarkable, being directly comparable to brassolines such as *Aponarope* Casagrande, 1982 (CASAGRANDE 2002: fig. 103), and many other nymphalids.

MILLER's description of the forewing venation was also wrong: two branches of the radius (R_{1+2} and R_{3+4+5}) arise from the cell, not one. MILLER (1968: fig. 29) was misled because the anterior of the two branches arising from the cell, R_{1+2} and its continuation as the basal part of free R_2, lies parallel to R_{3+4+5}, the two sections initially running very close together (Fig. 7). He was nonetheless correct to regard the venation as very peculiar.

Figs 42–52: *Bia actorion* (L.) *sensu lato*. Scanning electron micrographs of abdominal androconial organs. **42** lateral view of abdomen from segment 3 to apex, showing position of lateral pads on tergites of segments; **43** channel-like strukture formed by pleurae; **44–46** pads on segment 4–6; **47** short (type 1) and long (type 2) androconial scales clothe all three pads; **48** detail of 47; **49** small marginal scales (type 3); **50**, **51** scale bases of type 1; **52** scale base of type 2. Scale bars: 42: 1 mm; 43: 100 µm; 44, 45: 200 µm; 46: 100 µm; 47: 50 µm; 48: 10 µm; 49: 100 µm; 50: 20 µm; 51, 52: 5 µm.



Figs 53–62: *Bia actorion* (L.) *sensu lato*. Scanning electron micrographs of abdominal androconial organs. **53–56** details of scale type 1; **57**, **58** details of scale type 3; **59**, **60** details of scale type 2; macrophotographs: **61**, **62** dorsal views of abdomen of unique museum specimen in which the pads are exerted. Scale bars: 53: 10 µm; 54: 5 µm; 55, 56: 2 µm; 57: 20 µm; 58: 2 µm; 59: 50 µm; 60: 2 µm; 61–62: 1 mm.

Although the forewing radial vein configuration of *Bia* is unique among the butterflies, it can be compared in some ways with the Brassolini: Naropina (genera *Narope* and *Aponarope*), in which three branches of the radius arise in close proximity from the discal cell, with either a single anastomosis of Sc+R_1 (CASAGRANDE 1989: fig. 5), or a double anastomosis giving a short section Sc+R_{1+2}, with Sc+R_1 and R_2 eventually running separately to the costa (STICHEL 1904: pl. 1, fig. 5; CASAGRANDE 1989; 1996: fig. 29). The venation of *Bia* is also comparable to that of certain amathusiines, such as *Discophora*, in which the forewing radial system similarly arises from the discal cell as two branches that run closely parallel. However, the two branches in *Discophora* are R_1 and Rs (not R_{1+2} and R_{3+4+5}). In this genus R_1 forms a long anastomosis with Sc before separating, then forms an anastomosis with R_2 before they separate and run free to the costa (BASCOMBE et al. 1999: fig. 9.38).

But even if MILLER had been right regarding the palp, two such autapomorphies would have told us little about relationships. The odd venation even when correctly described, simply underscores the generic distinctness of this peculiar nymphalid. This would also be true with respect to the absence of tibial spurs, another unusual feature of *Bia* observed by MILLER (1968: 33, fig. 31). In this context it may be significant that *Narope* also lacks tibial spurs, whereas its close relative *Aponarope* does not (CASAGRANDE 2002: figs. 30a,b, 103a,b). However, before drawing any detailed conclusions about the relationships of *Bia*, we first discuss a series of wider questions regarding its higher classification.

Does *Bia* belong to the satyrine clade? In nymphalid butterflies other than *Bia*, ripple patterns (NIJHOUT 1991) are found in the Nymphalina (e.g. *Nymphalis* Kluk, 1802*, Aglais* Dalman, 1816*, Polygonia* Hübner, 1819), Satyrinae (many species, including *Melanitis, Elymnias* and *Ypthima* Hübner, 1818), Morphinae (all Brassolini; Morphini: Antirrheina; and a few Amathusiini, including *Thauria* Moore, 1894, and *Discophora*), and certain Charaxinae (including *Palla* Hübner, 1819, and *Anaea* Hübner, 1819). Thus the capacity to produce underside ripple patterning appears to be a characteristic (with the exception of the Nymphalina) of the satyrine clade *sensu* WAHLBERG et al. (2003) as based on molecular evidence, or the satyroid clade *sensu* FREITAS (1999) other than the supposedly basal Apaturinae (FREITAS & BROWN 2004) as based on early stage characters. Other than in the Nymphalina, ripple patterns are unknown elsewhere in the Nymphalidae, including the very small subfamily Calinaginae (considered internal to the satyrine clade by BROWER 2000, WAHLBERG et al. 2003, and FREITAS & BROWN 2004), and the Apaturinae (not included in the satyrine clade by BROWER 2000 or WAHLBERG et al. 2003). Based on many characters including features of the thorax, EHRLICH (1958) placed *Bia* in the Nymphalidae: Satyrinae. With the recent addition of molecular and early stage data, there is now little doubt that *Bia* belongs to the satyrine clade *sensu* WAHLBERG et al. (2003), and its ripple pattern (Figs. 3–5) is further evidence from adult morphology consistent with this conclusion.

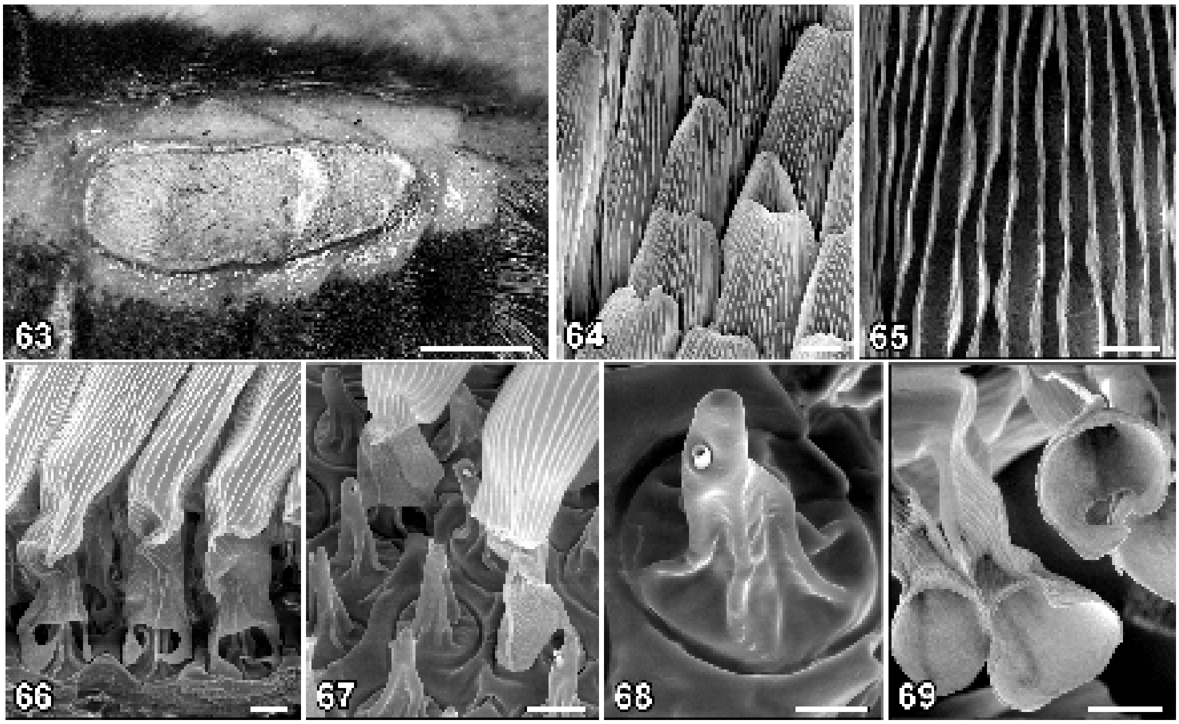
Why isn't *Bia* a satyrine? As reviewed above, most authors have included *Bia* within the Satyrinae, including EHRLICH (1958), MILLER (1968), and HARVEY (1991). The emergent view, however, is that *Bia* belongs to the Morphinae: Brassolini (CLARK 1947, 1948; DEVRIES et al. 1985; BROWER 2000; FREITAS et al. 2002; VANE-WRIGHT 2003; YOSHIMOTO 2003). The question then naturally arises, what are the distinguishing features of the Satyrinae, and does *Bia* exhibit them or not?

Unfortunately, from a morphological perspective, no uniquely diagnostic features for the Satyrinae have been recognised (DEVRIES et al. 1985; HARVEY 1991; ACKERY et al. 1999). Traditional but non-unique characters include the closed hindwing discal cell, feeding on monocots, and the fleshy, bifid larval tail (MILLER 1968; ACKERY et al. 1999). Although *Bia* has all of these features, none is diagnostic for Satyrinae with respect to Morphinae. EHRLICH (1958) listed a number of characters for all subfamilies of the Nymphalidae that he recognised. For the Morphinae and Satyrinae the only clear separation he gave was another traditional character, the inflated forewing veins Sc, Cu and 2A—never clearly seen in the Morphinae, but present in many Satyrinae. In this respect *Bia* is a typical satyrine and unlike the morphines. However, the expression of this character varies widely. For example, it is virtually unexpressed in Satyrinae: Melanitini, while only vein Sc is inflated in Satyrinae: Ragadiini. Moreover, inflated forewing veins occur elsewhere in the Nymphalidae, well outside the satyrine clade (EHRLICH 1958; ACKERY et al. 1999).

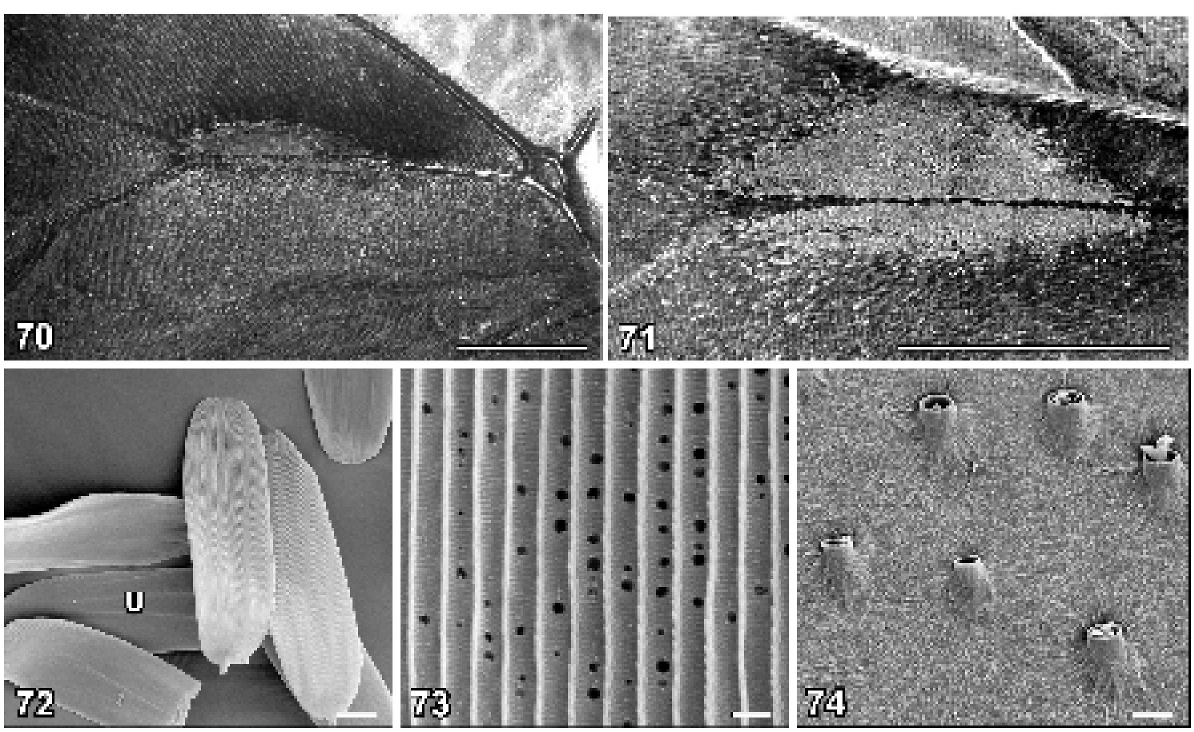
Why don't the Brassolini belong to the Satyrinae? Even if *Bia* were most closely related to the Brassolini, we must also consider the possibility that the Brassolini are simply nested, to the exclusion of the Morphini and Amathusiini, within the Satyrinae, as proposed by MILLER (1968). DEVRIES et al. (1985) re-affirmed EHRLICH'S (1958) position by including the Brassolini and Amathusiini within the Morphinae, doing so primarily on the basis of three putative larval characters. However, DeVries later retained the Morphinae and Brassolinae as separate subfamilies, and commented that the latter were "closely related to the Satyrinae" (DEVRIES 1987: 245). HARVEY (1991), partly due to an error in interpreting ACKERY (1988) (see ACKERY et al. 1999), also kept the Brassolinae as a separate subfamily. Given all this uncertainty, and the fact that the larval characters introduced by DEVRIES et al. (1985) remain unverified for many relevant taxa, we must question whether or not it is correct to link the brassolines with the morphines, and whether or not they can legitimately be excluded from membership of the Satyrinae, either alone, or together with the Morphini.

Do the Brassolini belong to the Morphinae? In the molecular investigations of both BROWER (2000) and WAHLBERG et al. (2003), their exemplar Brassolini grouped exclusively with their exemplar Morphini, while the two Amathusiini (*Amathusia* in BROWER, *Stichophthalma* in WAHLBERG et al.) appeared elsewhere, either within a monophyletic Satyrinae (BROWER 2000: fig. 4), or as part of a paraphyletic assemblage made up of Satyrinae, Morphinae, Charaxinae and Calinaginae (WAHLBERG et al. 2003: fig. 4). This is consistent with the conclusion of EHRLICH (1958) that the Satyrinae and Morphinae *sensu lato* are closely related, as also suggested by KUZNETZOV & STEKOLNIKOV (2001), who linked the Morphinae *sensu* EHRLICH (1958) with the Satyrinae as a monophyletic family. The conclusions of FREITAS & BROWN (2004: fig. 5) also suggest that the Brassolini are more closely related to the Morphini (and the Amathusiini) than they are to the Satyrinae.

SCOTT (1985) considered that the larval "fuzzy head" characterised the Morphinae *sensu* EHRLICH (1958) as a



Figs 63–69: *Caligo eurilochus* (Cramer). Macrophotograph (63) and scanning electron micrographs (64–69) of abdominal androconial organs. **63** lateral view of abdominal segments 4-6 showing pad, located in the pleural area between the tergites and sternites; scanning electron micrographs: **64–69** scales making up pad; they exhibit unusual scale structure (65), and, in particular, highly specialised sockets (66–68); note tube leading from interior and funnel-like base that fits over the specialised sockets (69). Scale bars: 63: 2 mm; 64: 20 µm; 65: 5 µm; 66, 67: 20 µm; 68: 10 µm; 69: 20 µm.



Figs 70–74: *Caligo eurilochus brasiliensis* (Cramer). Macrophotographs (70, 71) and scanning electron micrographs (72–74) of hindwing anterior androconial organs. **70** patch immediately anterior to vein Rs (note also very small precostal cell); **71** detail of patch; scanning electron micrographs: **72** scales comprising patch (U: underside); **73** detail of scale surface; **74** scale sockets. Scale bars: 70–71: 5 mm; 72: 50 µm; 73: 2 µm; 74: 20 µm.

monophyletic group. If so, this raises doubts about inclusion of the Amathusiini within the Satyrinae. Certainly the larvae of various Amathusiini do have "fuzzy" heads (e.g. IGARASHI & FUKUDA 1997: pls. 126–133), comparable to Brassolini and Morphini. However, it is evident that the head capsule of *Melanitis*, for example, is also quite "fuzzy", and more work is needed on this character. Another character linking the Amathusiini to the Brassolini is the presumed repugnatorial neck gland of the larvae (ELIOT, *in* CORBET & PENDLEBURY 1992: 137). Our conclusion is that, despite the weakness of the present evidence, we should maintain the Morphinae *sensu* EHRLICH (1958), to include Morphini, Amathusiini and Brassolini.

Is *Bia* a brassoline?

In BROWER's (2000) analysis, and in some of the analyses of FREITAS & BROWN (2004), *Bia* groups with the Brassolini to form a monophyletic group, either with just the Morphini (BROWER 2000; FREITAS & BROWN 2004: fig.1) or with the Morphini + Amathusiinae in addition (FREITAS & BROWN 2004: fig. 3). So the Brassolini do not appear to belong to the Satyrinae *sensu stricto*. Given the evidence from early stages reported by FREITAS et al. (2002) that seem so suggestive that *Bia* is a brassoline (summarised in section 7 above), it is perhaps surprising that FREITAS & BROWN (2004: fig. 5) placed *Bia* as a monobasic subfamily separate from both Morphinae and Brassolinae. Apparently they did so because *Bia* behaved ambiguously in their analyses: "it appeared in three different positions in the trees" (FREITAS & BROWN 2004: 372). Can any strong support or challenge to the hypothesis that *Bia* is a brassoline be drawn from our re-examination of adult morphology?

ACKERY et al. (1999) stated that the "Brassolini … currently lack convincing autapomorphies". Although MILLER's (1968) arguments for including the Brassolini within the Satyrinae were unconvincing, he did identify one relatively distinctive character for the group apparently overlooked by ACKERY et al. – the basal separation of the hindwing veins Sc and R_1 to produce a distinct precostal cell (STICHEL 1909). MILLER correctly pointed out that this feature recurs in a few groups included in the Satyrinae (e.g. *Elymnias*: SCHATZ & RÖBER 1889: pl. 39), and essentially the same character is found in some other butterflies, including many Papilionidae (SMITH & VANE-WRIGHT 2001), various Charaxinae (SCHATZ & RÖBER 1888: pls. 28, 29), *Parthenos* Hübner, 1819 (Limenitidinae: SCHATZ & RÖBER 1887: pl. 25), various Danaini (ACKERY & VANE-WRIGHT 1984), and even *Morpho* itself (SCHATZ & RÖBER 1885: pl. 1, fig. 1). Thus, although characteristic of all Brassolini, the precostal cell is not uniquely diagnostic for the group.

Within the Brassolini, as demonstrated by STICHEL (1904, 1909), the precostal cell varies significantly in size and form. In some genera (e.g. *Opoptera*) it is very large (STICHEL 1904: pl. 2, fig. 1), and most brassolines approach this condition. In *Eryphanis, Caligopsis* and *Caligo*, however, the precostal cell is much smaller, with a narrow, ovoid 'lumen' (STICHEL 1904: pl. 2, figs. 4, 5), unlike the widely open 'parallelogram' seen in other genera. *Bia* has a slight basal separation of these veins, as correctly observed over 150 years ago by WESTWOOD (1850), but this can only be appreciated readily by examination of a cleared wing preparation or use of SEM. The form this takes in *Bia* (Figs. 8, 9) is like a miniaturised *Eryphanis* or *Caligo* (Fig. 70). However, given the homoplasious distribution of this character as noted above, to include *Bia* within the Brassolini on this basis would be unconvincing.

The configuration of the forewing ocelli of *Bia* closely approximates that seen in several brassoline genera, notably *Opoptera*, *Catoblepia*, and many species of *Opsiphanes*. This is also true for the curvilinear path of the parafocal elements that occurs in some of the species belonging to these genera, including the deviation in cell M_3. Overall, this gives a reminiscent 'Gestalt' to both the upperside and underside pattern of the forewing apex of *Bia* and these three genera. On the hindwing underside the position of the ocellar marking in cell R_1 also corresponds closely to that occupied by the large and fully-developed border ocellus in underside cell R_1 of the same genera. The suggestion of a border ocellus in hindwing cell R_5 is unusual in most brassolines, while an ocellus in M_1 is only seen in a few genera, notably *Brassolis* and *Dasyophthalma*. However, in many species of *Narope* small border ocelli similar to those of *Bia* occur in all hindwing underside cells R_1–Cu_{1b} (e.g. CASAGRANDE 2002: figs. 29, 95). Most Brassolini have an extremely well developed border ocellus in hindwing underside cell Cu_{1a}, reaching its maximum development both in size and basal displacement to give the huge eyespot characteristic of the owl butterflies (*Caligo*). Of this there is no obvious trace in *Bia*, unless we interpret the curious diagonal white stripe that occurs in cell Cu_{1a} adjacent to the tail-like extension formed around Cu_{1b} (also unique to this genus: the tail of *Opoptera* is formed around M_3) as a modified remnant of the ocellar pupil. This appears to be confirmed by the very similar underside white stripe that occurs in cell Cu_{1a} of some species of *Narope*, such as *N. cyllastros* Doubleday, 1849, and *N. cyllene* Felder, 1859 (CASAGRANDE 2002: figs. 28, 29, 34, 35; cf. fig. 50).

Male genitalia are widely used in insect systematics, but these highly plastic structures are often difficult to interpret for higher taxonomy (SMITH & VANE-WRIGHT 2001). Most members of the satyrine clade have relatively simple male genitalia, and this is true for *Bia*

(HAYWARD 1958, 1964). Indeed, the genitalia of *Bia* are quite similar to *Narope*, except that the ganthos is directed ventrally (as in Brassolina), unlike the upswept structure found in Naropina (CASAGRANDE 1996: figs. 10–12, 31, 32).

As with the precostal cell, the wing patterns of *Bia* and perhaps even the male genitalia are suggestive of a relationship with the Brassolini, but are not wholly convincing. In contrast, several features of the androconial organs provide what we consider to be strong evidence for such a relationship. Notably, hair-tufts arranged in palisades with conjoined sockets and abdominal pads occur in many Brassolini, and in *Bia*, but not in the Satyrinae.

9. CONCLUSIONS

Evidence from all life stages, including several adult characters described here, and DNA sequence data, supports the view that *Bia* is a member of the morphine tribe Brassolini. Even though *Bia* is very small for a brassoline (forewing length 25–32 mm) and highly autapomorphic, it may ultimately prove to be internal to the tribe as a whole, and not sister to the rest of the group as suggested by one of the analyses made by FREITAS & BROWN (2004: fig. 2).

Until recently there has been no accepted subtribal classification for the Brassolini. However, CASAGRANDE (1996, 2002) has separated the Naropina Stichel (to include only *Narope* and *Aponarope*) from all of the remaining genera, which she included in the Brassolina. In addition to its marked autapomorphic features (e.g. forewing radial venation, inflated forewing veins, minute hindwing precostal cell, basally fused dorsal horns of larval head), *Bia* shares putative synapomorphies with both the Naropina (e.g. loss of tibial spurs; unique form of hindwing underside border ocellus in cell Cu_{1a}; possibly the plumose hairs on larval head) and the Brassolina (e.g. tufted alar organs composed of palisade rows and abdominal pads, as found in *Caligo* and several other genera). In the circumstances, we propose, pending more extensive analysis, to place *Bia* in the Biina Herrich-Schäffer, 1864, as a third subtribe of the Brassolini Boisduval, 1836 (see Appendix I). However, it seems quite possible that the Biina will ultimately be subsumed within the Brassolina, or subsume the Naropina.

BOPPRÉ (1984) commented that “androconial organs are … analogous structures, convergently evolved many times … [and] of limited taxonomic value, although they certainly provide good characters in some groups”. Despite this rather cautious view, our experience over the intervening 20 years suggests that detailed investigations of androconial organ morphology (e.g. BOPPRÉ & VANE-WRIGHT 1989), even though loss and independent gain of these organs are indeed frequent evolutionary phenomena, can provide extremely valuable insights into systematic relationships (e.g. VANE-WRIGHT et al. 2002; cf. HALL & HARVEY 2002). This can also be true of androconial chemistry, as in the Danaini (VANE-WRIGHT & BOPPRÉ 1993; SCHULZ et al. 1993), although SCHULZ et al. (2004) found relatively little evidence for phylogenetic relationships from their analyses of Ithomiini pheromones. In the case of the two Neotropical tribes of Morphinae, abdominal coremata are diagnostic for the Morphini, while palisade alar organs and abdominal pads appear to be autapomorphic for Brassolini (including *Bia*), even though they are not expressed by all members of the group.

We conclude that a combined morphological and chemical investigation into the scent organs of *Bia* and other Brassolini would be a most interesting and potentially instructive challenge. Such a study would be in the best tradition of Clas NAUMANN, our dear departed friend, inspiration and mentor, to whose memory this paper is most respectfully dedicated. To him, gaining knowledge and understanding was always more important than merely accumulating information.

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Zusammenfassung. Die südamerikanische Nymphaliden-Gattung *Bia* Hübner, 1919, wurde für mehr als 150 Jahre von den meisten Lepidopterologen als Mitglied der Satyrinae betrachtet. Neuere Berichte zu Präimaginalstadien sowie DNA-Analysen haben jedoch gemeinsame Merkmale mit den Morphinae: Brassolini aufgedeckt. Untersuchungen der Flügelmuster und der androconialen Organe von *Bia*, hier erstmals im Detail vorgestellt, zeigen ungewöhnliche Merkmale, die sonst nur von Brassolinen bekannt sind. Insbesondere das büschelförmige posteriore androconiale Organ der Hinterflügel, das Palisaden bildet, stellt eine Synapomorphie für *Bia* und verschiedene andere Gattungen der Brassolini, inclusive *Caligo*, dar. Die Gattung *Bia* wird daher formal von den Satyrinae zu den Morphinae: Brassolini übertragen, als einzigem Taxon des Subtribus Biina Herrich-Schäffer, 1864, **stat. nov.**, zusammen mit Brassolina Boisduval, 1836, und Naropina Stichel, 1925.

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APPENDIX I

Classification the satyrine clade *sensu* EHRLICH (1958) and KUZNETZOV & STEKOLNIKOV (2001), within the Nymphalidae Rafinesque, 1815, following break-up of the Biinae *sensu* MILLER (1968). Despite various changes, the current system still owes much to Miller (see HARVEY 1991). However, Miller overlooked some potentially important genera that clearly belong here, such as *Penthema* Doubleday, 1848, and *Xanthotaenia* Westwood, 1858, and these need to be located (KIRCHBERG, 1942, firmly included *Xanthotaenia* in the Amathusiini). The Melanitini currently include *Melanitis*, *Cyllogenes*, *Gnophodes*, *Parantirrhoea*, *Bletogona* and *Manataria* (UÉMURA 1987; WAHLBERG et al. 2003; YOSHIMOTO 2003). In future it seems possible that the Amathusiini could be relocated within the Satyrinae, while the grouping as a whole will probably be expanded to subsume the Charaxinae Guenée, 1865, and the Calinaginae Moore, 1895 (WAHLBERG et al. 2003). The suggestion of FREITAS & BROWN (2004) that the Apaturinae Boisduval, 1840, also belong here is contradicted by current molecular evidence (BROWER 2000; WAHLBERG et al. 2003).

Type genera are given in square brackets (for further details regarding these generic names see http://www.nhm.ac.uk/entomology/butmoth/index.html). The family group names, authorities, dates and type genera are in accordance with the as yet unpublished 'GloBIS' system for the nomenclature and classification of the butterflies (LAMAS et al. 2000, in prep.). Note that there is currently no widely accepted sub-tribal system for the Amathusiini. The work of KIRCHBERG (1942) will be invaluable in trying to formulate any effective subdivision. PARSONS (1998) has suggested that *Morphopsis* Oberthür, 1880, *Taenaris* Hübner, 1819 (including *Morphotenaris* Fruhstorfer, 1893), *Hyantis* Hewitson, 1862, and *Faunis* Hübner, 1819, may form a subgroup (for which the oldest available family-group name would be Hyantina Röber, 1905 [*Hyantis* Hewitson, 1862]). The Discophorina Stichel, 1902, are recognised by BASCOMBE et al. (1999).

Note that YOSHIMOTO (2003), following MILLER (1968), incorrectly attributed the following family-group names to Miller: Melanitini, Mycalesina, Ypthimina and Coenonymphina. By following Miller, Yoshimoto also misattributed Lethina to Clark, 1948; Melanargiina to Verity, 1920; gave the original date for Satyrinae Boisduval incorrectly as 1836; and misspelled Antirrheini as "Antirrhini". (Antirrhini Miller, 1968, is an objective synonym and homonym of Antirrhaeidi Reuter, 1896, the latter based on Westwood's invalid emendation "*Antirrhaea*"—see COWAN 1970—and which is properly corrected to Antirrheini Reuter, 1896, or Antirrheina Reuter, 1896, depending on adopted rank.)

MORPHINAE Newman, 1834 [*Morpho* Fabricius, 1807]
- MORPHINI Newman, 1834 [*Morpho* Fabricius, 1807]
  - ANTIRRHEINA Reuter, 1896 [*Antirrhea* Hübner, 1822]
  - MORPHINA Newman, 1834 [*Morpho* Fabricius, 1807]
- BRASSOLINI Boisduval, 1836 [*Brassolis* Fabricius, 1807]
  - BIINA Herrich-Schäffer, 1864 [*Bia* Hübner, 1819] **stat. nov.**
  - NAROPINA Stichel, 1925 [*Narope* Doubleday, 1849]
  - BRASSOLINA Boisduval, 1836 [*Brassolis* Fabricius, 1807]
- AMATHUSIINI Moore, 1894 [*Amathusia* Fabricius, 1807]

SATYRINAE Boisduval, 1833 [*Satyrus* Latreille, 1810]
- HAETERINI Herrich-Schäffer, 1864 [*Haetera* Fabricius, 1807]
- MELANITINI Reuter, 1896 [*Melanitis* Fabricius, 1807]
- ELYMNIINI Herrich-Schäffer, 1864 [*Elymnias* Hübner, 1818]
  - LETHINA Reuter, 1896 [*Lethe* Hübner, 1819]
  - ZETHERINA Reuter, 1896 [*Zethera* C. Felder, 1861]
  - ELYMNIINA Herrich-Schäffer, 1864 [*Elymnias* Hübner, 1818]
  - MYCALESINA Reuter, 1896 [*Mycalesis* Hübner, 1818]
- ERITINI Miller, 1968 [*Erites* Westwood, 1851]
- RAGADIINI Herrich-Schäffer, 1864 [*Ragadia* Westwood, 1851]
- SATYRINI Boisduval, 1833 [*Satyrus* Latreille, 1810]
  - HYPOCYSTINA Miller, 1968 [*Hypocysta* Westwood, 1851]
  - YPTHIMINA Reuter, 1896 [*Ypthima* Hübner, 1818]
  - EUPTYCHIINA Reuter, 1896 [*Euptychia* Hübner, 1818]
  - COENONYMPHINA Tutt, 1896 [*Coenonympha* Hübner, 1819]
  - MANIOLINA Grote, 1897 [*Maniola* Schrank, 1801]
  - EREBIINA Tutt, 1896 [*Erebia* Dalman, 1816]
  - DIRINA Verity, 1953 [*Dira* Hübner, 1819]
  - PRONOPHILINA Reuter, 1896 [*Pronophila* Doubleday, 1849]
  - SATYRINA Boisduval, 1833 [*Satyrus* Latreille, 1810]
  - MELANARGIINA Wheeler, 1903 [*Melanargia* Meigen, 1828]