

A survey of androconial organs in the Riodinidae (Lepidoptera)

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A comprehensive survey of the occurrence and morphology of alar, abdominal and appendage androconial organs in the Riodinidae is presented based on light microscopy and scanning electron microscopy. Although historically poorly studied, the group actually possesses among the greatest diversity of androconial organs in the butterflies, including coremata, reported here for the first time outside the Lycaenidae and Nymphalidae, and hindleg hair-pencils, reported here for the first time in the true butterflies. Twenty-five percent of riodinid species are reported to have androconial organs. The mode of function of these organs and their role in courtship is discussed where known, based on field observations. A number of taxonomic changes are made at the tribal, generic and species level, predominantly in the Symmachiini, based on the occurrence and structure of androconia. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, 136, 171–197.

ADDITIONAL KEYWORDS: – abdominal androconia – alar androconia – coremata – courtship – leg androconia – morphology – perching – pheromones – scale structure.

INTRODUCTION

The existence of specialized scales in adult male Lepidoptera has long been recognized, and they were first named androconia by Scudder (1877). Müller (1877a) believed that such structures had evolved as a result of sexual selection and that they were involved in the dissemination of scents or pheromones to influence female behaviour, a theory that has now been proven by experiments on the courtship of nymphalid and pierid butterflies (Tinbergen, 1941; Magnus, 1958; Brower *et al.*, 1965; Pliske & Eisner, 1969; Rutowski, 1977). While such ethological and chemical studies remain scarce, more accounts exist of the gross occurrence and structure of butterfly androconial organs, but these typically address only one or two species. Broader studies, including general overviews (Müller, 1877a; Barth, 1960; Vane-Wright, 1972a; Boppré, 1984), and surveys of higher groupings, such as the Papilionidae (Miller, 1987), Pieridae (Dixey, 1913, 1932), Nymphalidae (Danainae: Müller, 1877b; Boppré & Fecher, 1977; Ackery & Vane-Wright, 1984; Boppré & Vane-Wright, 1989) and Lycaenidae (Eliot, 1973) are rarer. No such broad studies exist for the family Riodinidae.

This paper presents an overview of the occurrence and ultrastructure of androconial organs in the Riodinidae, with discussions on their function, where

known, and systematic significance. Modified scales found in both sexes, such as the abdominal setal tufts in *Stalachtis* Hübner, 1818 (Harvey, 1987), are assumed to be used for defensive purposes (Müller, 1877a), and are not considered here. The Riodinidae contains approximately 1300 species, the large majority of which are confined to the Neotropics (all subfamilies except the Nemeobiinae), where the family constitutes 15–20% of the total butterfly fauna (Heppner, 1991; Robbins *et al.*, 1996). Although the group is conspicuous for its external and internal morphological and ecological diversity, its systematics and biology are perhaps the most poorly known of any butterfly group.

What little is known of mate location and courtship behaviour in riodinid butterflies, and the fact that many genera exhibit seemingly tight niche packing (Hall 1999a), suggests that androconia should be widespread and varied in the family. The males of many species consistently perch in the same small well-defined areas, typically along streams, at forest edges and on hilltops and ridgetops, in much the same manner that birds and other vertebrates and insects have been described to lek (Höglund & Alatalo, 1995) (Fig. 1). Such prominent topographical features are believed to act as rendezvous sites for the sexes that enhance mating success in rare species (Scott, 1968, 1975; Shields, 1968; 1983). It is well established that

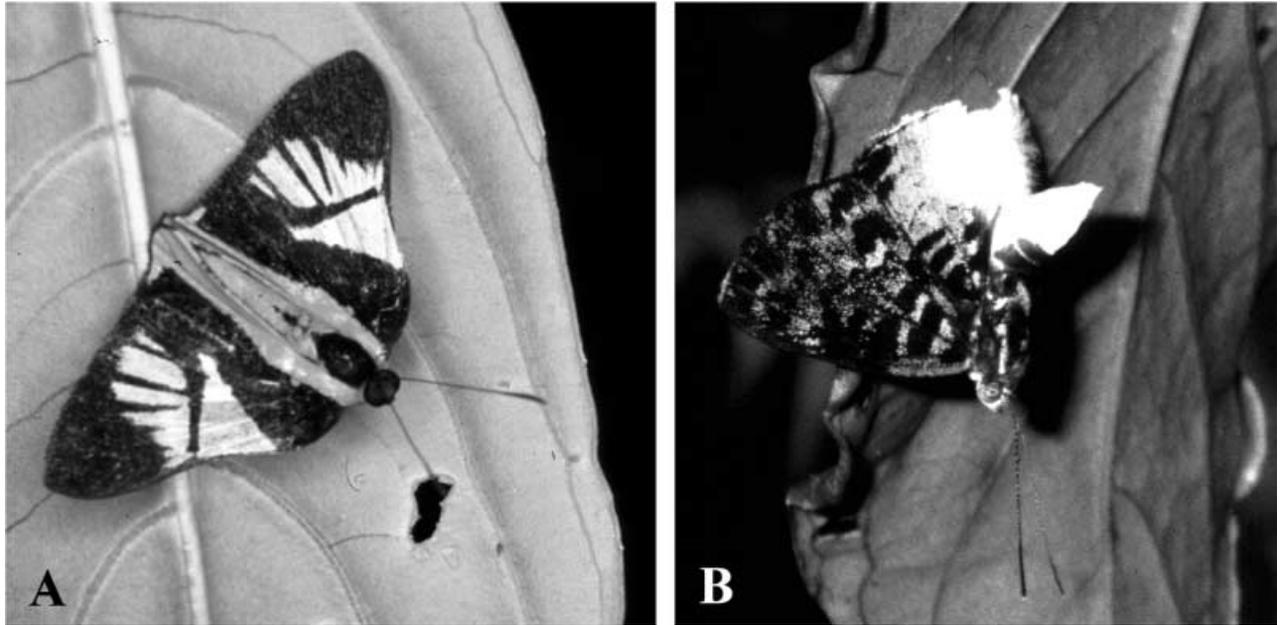


Figure 1. Perching males. A, *Symmachia jugurtha* Staudinger, El Durango, Esmeraldas, Ecuador. B, *Menander hebrus* Cramer, Pimpilala, Napo, Ecuador; curled abdomen is telescoped outwards and presumed to be disseminating pheromones from concealed androconial scales along anterior margins of distal tergites (note left-hand wings are bent downwards out of sight).

most such riordinid groups exhibit interspecific differences in male perching behaviours in terms of perching time, height and microhabitat type (Callaghan, 1983; Brévignon & Gallard, 1995; Hall, 1999a), and these have been explained in terms of premating isolating mechanisms (Callaghan, 1983). However, there are numerous examples where closely related groups of species perch on the same patch of vegetation during the same time period (Callaghan, 1983; Hall, 1998, 1999a; unpubl. data), suggesting that different courtship behaviour and sex pheromonal chemistry must also play an important role in premating isolation (Hall, 1999a).

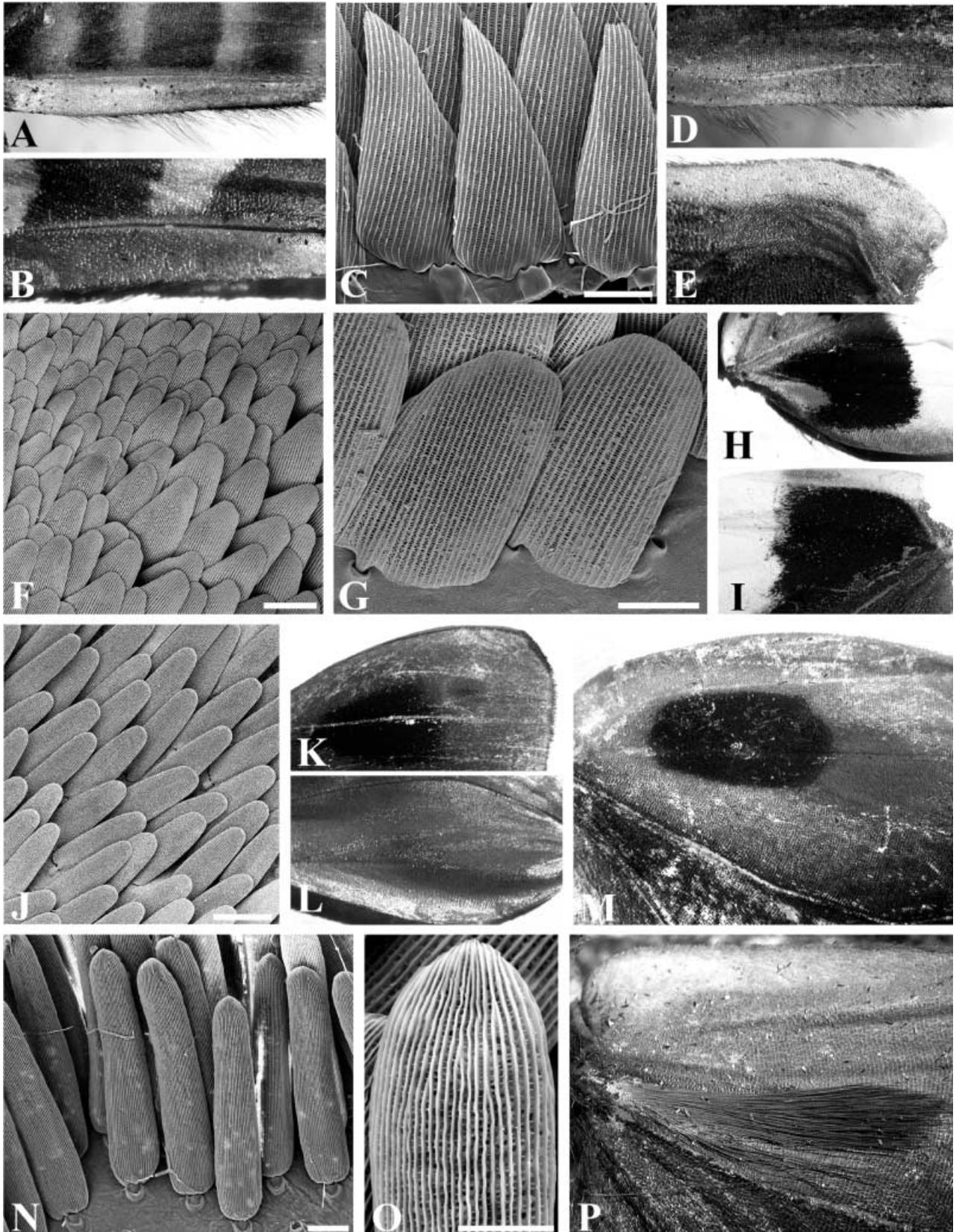
METHODS

It has not been practical to examine critically every riordinid species for potential male androconial organs, but during the course of our systematic research

over many years we have examined the external morphology of virtually all species and the internal abdominal morphology of approximately two-thirds of the species, including representatives from all genera and the majority of species groups. We therefore believe this review to be reasonably complete. The ultrastructure of androconial organs was primarily examined using specimens from the AME: Allyn Museum of Entomology, Sarasota, FL, USA; BMNH: The Natural History Museum, London, UK; JHKW: Collection of Jason P. W. Hall & K. R. Willmott, Washington, DC, USA; and USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. Descriptions of riordinid perching and courtship behaviour are based on observations by JPWH in Ecuador.

Androconial scales were studied using light microscopy and scanning electron microscopy (SEM). Abdomens and legs were usually first placed in hot

Figure 2. Alar androconia: Nemeobiinae. A, *Zemerus emesoides* C. & R. Felder, androconial scales along vein 2A at anal margin of VFW; B, C, *Dodona durga* (Kollar), androconial scales along vein 2A at anal margin of VFW (B) and androconial scales magnified (C); D–G, *Saribia tepahi* (Boisduval), androconial scales along vein 2A at anal margin of VFW (D), androconial scales around base of cell R1 on DHW (E), transitional area of scales magnified [androconial scales at top left] (F) and two androconial scales magnified (G); H–J, *Abisara gerontes* (Fabricius), androconial patches at base of VFW (H) and DHW (I) and androconial scales magnified (J); K–O, *Abisara rutherfordii* Hewitson, androconial patches in apex of DFW (K), at anal margin of VFW (L) and costa of DHW (M), and androconial scales of DHW magnified (N,O); P, *Abisara tantalus* Hewitson, setal tuft in discal cell of DHW. Scale bars: C, G, 20 µm; F, J, N, 50 µm; M, 10 µm.



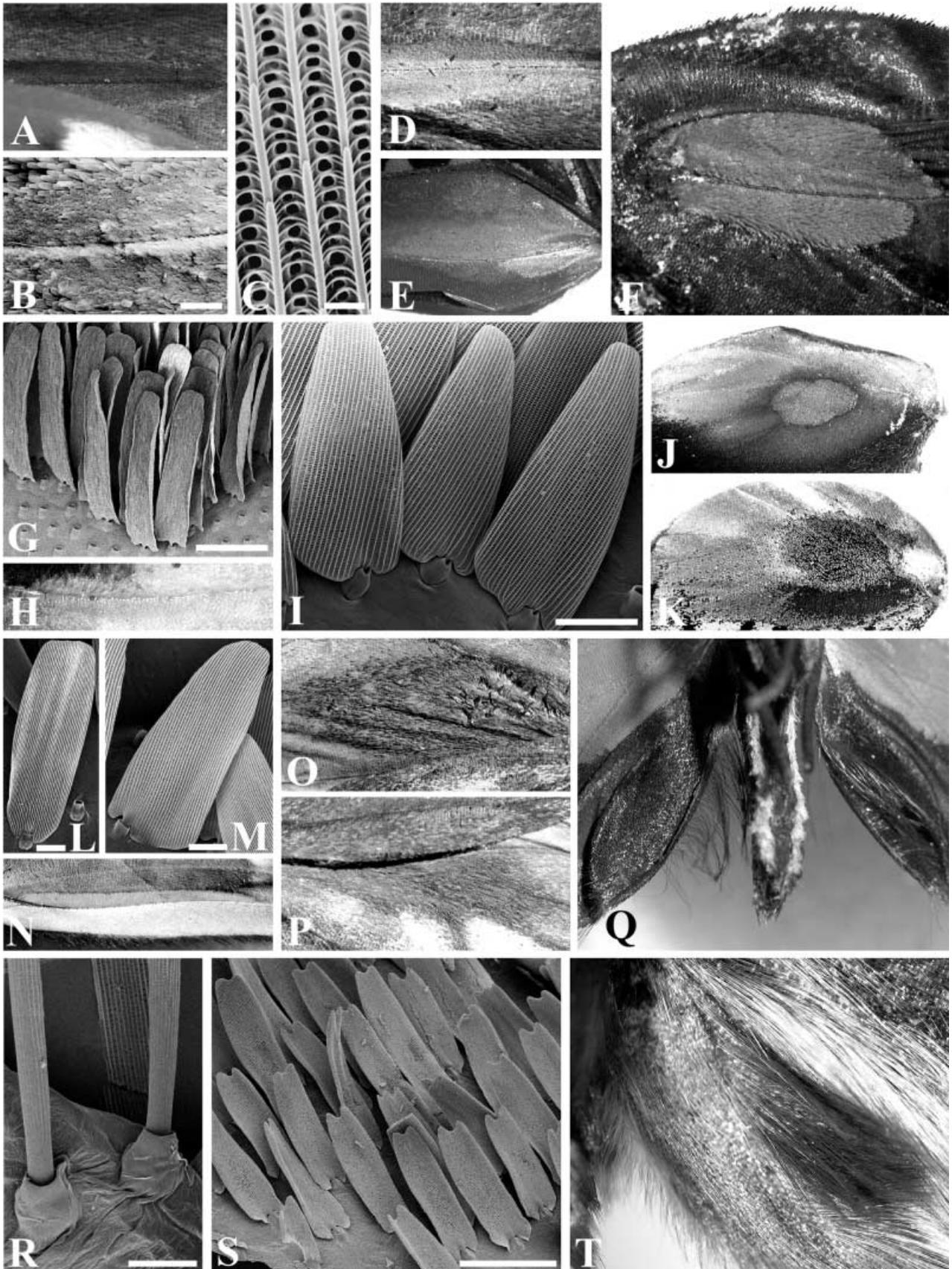


Figure 3. Alar androconia: Nemeobiinae & Riordininae. A, *Dicallaneura pulchra* (Guérin-Ménéville), androconial scales along vein 2A at anal margin of VFW; B, C, *Praetaxila segecia* (Hewitson), androconial scales along vein 2A at anal margin of VFW (B) and androconial scales magnified (C); D, *Taxila haquinus* (Fabricius), androconial scales along vein 2A at anal margin of VFW; E–G, *Paralaxita damajanti* (C. & R. Felder), androconial scales along vein 2A at anal margin of VFW (E) and at costa of DHW (F) and androconial scales of DHW magnified (G); H–I, *Stiboges nymphidia* Butler, androconial scales along vein 2A at anal margin of VFW (H) and androconial scales magnified (I); J, *Mesosemia nesti* Hewitson, androconial patch at costa of DHW; K, *Semomesia marisa* (Hewitson), androconial patch at costa of DHW; L, *Semomesia macaris* (Hewitson), single scale from androconial patch on DHW magnified; M, *Eurybia lycisca* Westwood, single scale from androconial patch along vein 2A at anal margin of VFW magnified; N, *Eurybia nicaeus* (Fabricius), androconial scales along vein 2A at anal margin of VFW; O, P, *Eucorna sanarita* (Schaus), androconial patches at base of VFW (O) and costa of DHW (P); Q–S, *Cartea vitula* (Hewitson), androconial patches at anal margin of VFW with marginal setae erect on left and covering patch on right (Q) and base of setae (R), and androconial scales magnified (S); T, *Anteros renaldus* (Stoll), setal tuft at anal margin of DHW. Scale bars: B, G, S, 100 µm; C, 1 µm; I, L, M, R, 20 µm.

10% potassium hydroxide (KOH) solution for approximately 5 min, and the resulting material stored in glycerol after examination. Light microscopy examination was conducted using an Olympus SZH (magnification up to $\times 128$) and digital images taken using a Nikon HC-300Zi attached to a Wild M400 microscope. Scanning electron microscopy was conducted using a Leica Stereoscan 440 (Smithsonian), a Hitachi S4000 (University of Florida; Fig. 5D,F only) and an ISI Super IIIA (University of Texas; Figs 5J, 6D–L, 7A–E only) with material mounted on aluminium stubs using carbon tape and sputter coated with gold/palladium. Material that was stored in glycerol was rinsed with 70% ethanol and air dried before mounting. The terminology for male and female genital and abdominal structures follows Klots (1956) and Eliot (1973), while nomenclature for venation follows Comstock & Needham (1918).

RESULTS

Several systems of classification have been proposed for lepidopteran androconia (Illig, 1902; Barth, 1958; McColl, 1969), but for clarity and ease of information access, we report their occurrence based on bodily position. Riordinids possess androconial organs associated with the wings, abdomen and appendages.

ALAR ANDROCONIA

Nemeobiinae

Alar androconia are widespread in the tribes Zemerini and Abisarini, but absent in the tribe Nemeobiini (= Hamearini of Harvey, 1987) (see Table 1). In most genera these take the form of pale narrow patches around vein 2A on the ventral forewing (Figs 2A,B,E, 3A,B,D,H) (Harvey, 1987). These scales are slightly smaller, more triangular and densely packed than surrounding ones and their sockets are medially constricted (Figs 2C, 3I), suggesting the shaft can be locked into a more erect position. Nemeobiine alar androconia are most elaborate in the African *talantus*

group of *Abisara* C. & R. Felder, 1860 (Fig. 2K–P), and the Oriental genus *Paralaxita* Eliot, 1978 (Fig. 3E–G), which have a prominent, raised androconial patch at the base of the dorsal hindwing covered by a markedly bulbous forewing anal margin that has a smaller overlapping androconial patch on its ventral surface. *Abisara tantalus* Hewitson, 1866, is the only riordinid to have a setal tuft in the discal cell of the hindwing (Fig. 2P), and *Abisara rutherfordii* Hewitson, 1874, is the only riordinid to have a prominent androconial patch on the dorsal forewing (Fig. 2K). The androconial scales of *Paralaxita* are uniquely medially grooved (Fig. 3G).

Euselasiinae

No members of the subfamily Euselasiinae [within which we include *Styx* Staudinger, 1876, and *Corrachia* Schaus, 1913, as the tribe Corrachini (Hall & Harvey, unpubl. data)] possess alar androconia. Those cited by d'Abrera (1994) for a specimen of *Euselasia ella* Seitz, 1916, are the result of wing damage.

Riordininae

Alar androconia are sparsely distributed throughout all the tribes of the Riordininae, except the four forewing radial veined (FRV) *incertae sedis* section of Harvey (1987) (he recognized two paraphyletic groups of species with unknown affinities to the established tribes, one with 5 FRV and the other with 4 FRV) (see Table 2). These fall into two groups: scale patches and setal tufts. The most well developed scale patches occur in the mesosemiine genus *Semomesia* Westwood, [1851], which has overlapping patches at the costal margin of the hindwing (Fig. 3K) and anal margin of the forewing. *Eucorna sanarita* (Schaus, 1902) (Fig. 3O,P), *Pandemos pasiphae* (Cramer, [1775]) (Fig. 4I,J) and *Adelotypa chaessa* (Stichel, 1910) have a similar pattern of androconial patches, but the scales are generally less highly modified. All such scales tend to

Table 1. Distribution of alar androconia in the subfamily Nemeobiinae

Tribe/genus	Species	Description	Figure
Zemerini:			
<i>Zemerus</i>	all species	VFW with narrow pale androconial patch surrounding basal two-thirds of vein 2A composed of slightly smaller, more densely packed and tightly appressed scales than adjacent ones	2A
<i>Dodona</i>	all species	VFW with narrow pale androconial patch surrounding middle half of vein 2A composed of substantially smaller, more densely packed, triangular and tightly appressed scales than adjacent ones	2B,C
Abisarini:			
<i>Saribia</i>	all species	DHW with pale androconial patch covering base of cell R1 and surrounding veins composed of substantially smaller, more densely packed, rounded and tightly appressed scales than adjacent ones; same type of partially overlapping scales around basal half of vein 2A on VFW	2D-G
<i>Abisara</i>	<i>gerontes</i> gr.	DHW costa with brown or black androconial patch in upper portion of discal cell and base of cells R5 and R1 composed of similar scales to rest of wing, covered by convex anal margin of forewing; VFW with overlapping brown or black androconial patch at base of cell 2A and Cu2 composed of broader, more rounded, densely packed and upwardly directed (pointing to costa and apex) scales than adjacent ones	2H-J
	<i>talantus</i> gr.	DHW with large black medially divided androconial patch at end of discal cell and base of cells M2-R5 composed of long, slightly twisted and upwardly directed scales (<i>rutherfordii</i> only); DHW with dense tuft of long erectile androconial setae in discal cell (sockets at cell base) and sparse patch of setae along base of cell Cu2 (<i>talantus</i> only) or black androconial patch in upper portion of discal cell and base of cells R5 and R1 composed of long, roundly bulbous, markedly upwardly directed scales (i.e. a raised area) (<i>talantus</i> & <i>rutherfordii</i>) with additional brown patch immediately to right in <i>rutherfordii</i> composed of scales intermediate between those of black patch and rest of wing, all androconia at HW costa covered by pronouncedly convex anal margin of forewing; VFW with silvery brown nacreous scales in basal two-thirds of cells 2A and Cu2, overlapping small brown androconial patch of more densely packed scales around or below middle of vein 2A (<i>talantus</i> & <i>rutherfordii</i>)	2K-P
Dicallaneura	many spp.	VFW with narrow pale androconial patch surrounding basal one-third to two-thirds of vein 2A composed of smaller, more pointed and slightly more densely packed scales than adjacent ones	3A
<i>Praetaxila</i>	many spp.	Same as above but patch surrounds basal one-third of vein 2A	3A,B
<i>Taxila</i>	<i>haquinus</i>	Same as above but patch surrounds basal half of vein 2A	3D
<i>Paralaxita</i>	all species	DHW with medially divided white androconial patch set within silvery brown nacreous scales in upper portion of discal cell and base of cell R1 composed of medially concave, longer, more rounded, upwardly directed (i.e. creating a raised area) and densely packed scales than adjacent ones, covered by convex anal margin of forewing; VFW with overlapping ovoid brown patch around middle of vein 2A composed of slightly larger and more upwardly directed scales than adjacent ones	3E-G
<i>Stiboges</i>	<i>nymphidia</i>	VFW with narrow pale androconial patch surrounding basal one-third of vein 2A composed of smaller, more pointed and slightly more densely packed scales than adjacent ones	3H-I

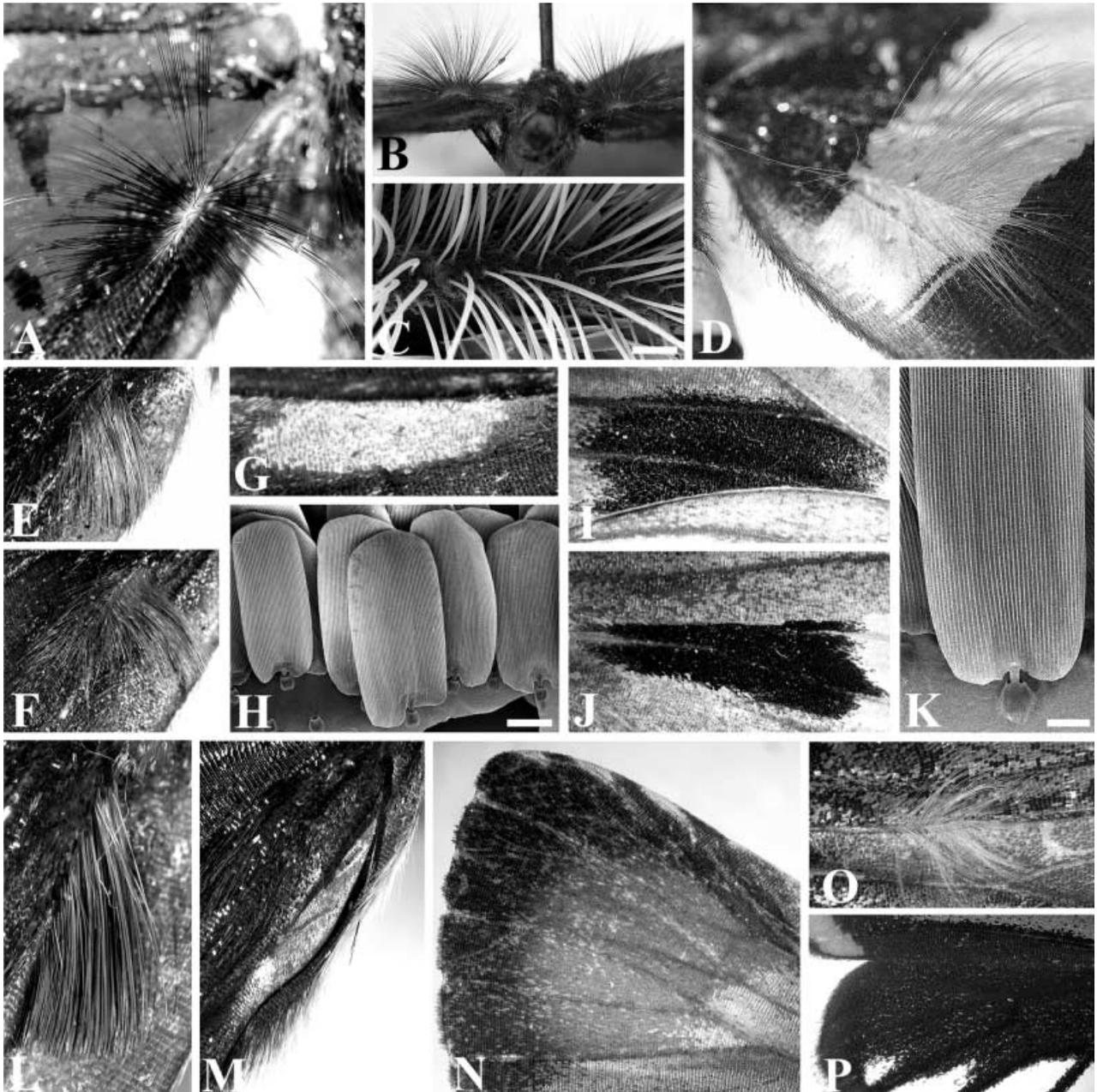


Figure 4. Alar androconia: Riodininae. A–C *Symmachia leena* Hewitson, erect setal tuft(s) in cell Cu2 of DHW in dorsal (A) and lateral views (B), and base of scales magnified (C); D, *Pirascca tyriotes* (Godman & Salvin), erect setal tuft in cell Cu2 of DHW; E, *Pterographium sicora* (Hewitson), setal tuft in cell Cu2 of DHW; F, *Panaropsis elegans* (Schaus), setal tuft in cell Cu2 of DHW; G, H, '*Adelotypa lampros* (Bates), androconial patch at costa of DHW (G) and androconial scales magnified (H); I–K, *Pandemos pasiphae* (Cramer), androconial patches at base of VFW (I) and costa of DHW (J), and single androconial scale from DHW magnified (K); L, *Menander menander* (Stoll), setal tuft in cell 2A of DHW with base within pouch; M, *Menander coruscans* (Butler), androconial pouch along cell 2A of DHW containing long setae (two protruding); N, *Theope aureonitens* Bates, pale androconial postdiscal patch on DFW; O, *Theope comosa* Stichel, setal tuft originating on VFW showing through at costa of DHW; P, *Stalachtis phaedusa zephyritis* (Dalman), androconial scales along costa of DHW. Scale bars: C, H, K, 50 μ m.

Table 2. Distribution of alar androconia in the subfamily Riordininae. Species groups in *Eurybia* are *sensu* Hanner (1997), in *Symmachia sensu* Hall & Willmott (1996) (see also Table 3), and in *Theope sensu* Hall (1999a)

Tribe/Genus	Species	Description	Figure
Mesosemiini:			
<i>Mesosemia</i>	<i>nesti</i>	DHW costa with small black androconial patch set among nacreous white scales in upper portion of discal cell and base of cells M2 and M1 composed of slightly more elongate, more densely packed and upwardly directed scales than adjacent ones	3J
<i>Semomesia</i>	all species	DHW costa with one or two (<i>marisa</i>) variably sized black androconial patch(es) set among nacreous white scales in upper portion of discal cell and base of cells M1 to R1 composed of slightly more elongate, more densely packed and upwardly directed scales (black or mixture of black and brown) than adjacent ones [note: no 'brushes' as per d'Aberra (1994)], covered by convex anal margin of forewing; similar arrangement of overlapping scales at base of VFW, nacreous white scales reduced	3K,L
Eurybiini:			
<i>Eurybia</i>	all species except <i>dardus</i> & <i>juturna</i> grs.	VFW with narrow pale androconial patch immediately above basal one-third to three-quarters of vein 2A composed of smaller, more pointed, densely packed and apically directed scales than adjacent ones, with asymmetrical bases	3M,N
Incertae sedis (5 FRV):			
<i>Eucoma</i>	<i>sanarita</i>	DHW with large brown androconial patch in upper portion of discal cell and base of cells M1 to Sc+R1 composed of larger and longer scales than on adjacent ones, with more rounded tips	3O,P
Riordinini:			
<i>Cartea</i>	<i>vitula</i>	VHW with an elongate black androconial patch set in shallowly concave pouch in cell 2A and part of cell Cu2 composed of more elongate, rounded, densely packed and upwardly directed scales than adjacent ones; long androconial setae along anal fringe of HW are either erect to contact abdomen or cover androconial pouch – forms dual system with dorsal androconial scales on abdomen	3Q–S
Helicopini:			
<i>Anteros</i>	<i>renaldus</i>	dense tuft of short black androconial setae at base of DHW cell 2A	3T

Symmachiini:					
<i>Symmachia</i>	<i>leona</i> gr., <i>hippodice</i> & <i>satana</i> all species	Dense orange or black patch of short erectile androconial setae along medially raised ridge at base of DHW cell Cu2 – forms dual system with concealed abdominal androconial scales same as above but patch always dense	4A–C		
<i>Pirascia</i>	<i>sicora</i> all species	same as above but patch always black same as above but patch dense or sparse	4D 4E 4F		
Nymphidiini:					
' <i>Adelotypa</i> '	<i>charessa</i>	Ill-defined dark brown androconial patch along costa of DHW and anal margin of VFW (ultrastructure of unique type not examined)	none		
	<i>lampros</i>	DHW with small yellow androconial patch in upper portion of discal cell and base of cells R5 and R1 composed of slightly larger and more distally rounded and densely packed scales (mixture of yellow and brown) than adjacent ones	4G,H		
<i>Pandemos</i>	<i>pasiphae</i>	DHW costa with large black androconial patch in upper portion of discal cell and base of cells M1 to R1 composed of more densely packed scales than adjacent ones; similar overlapping patch towards base of cell Cu2 on VFW	4I–K		
<i>Menander</i>	<i>menander</i> & <i>nitida</i>	Dense tuft of short black androconial setae towards base of DHW cell 2A with bases within medial pouch, pouch forms a visible bulge on VHW	4L		
	<i>coruscans</i>	Same as above but setae and pouch extend along nearly entire length of DHW cell 2A, setae can be entirely retracted within pouch	4M		
<i>Theope</i>	some <i>sericea</i> gr. species & <i>terambus</i> gr. <i>galionicus</i> & <i>comosa</i>	DFW with round area of pale brown scales in end of discal cell and base of cells Cu1 to M1, no apparent differences with adjacent scales DHW with ovoid area of small rounded tightly appressed scales in upper portion of discal cell and cell R1; VFW with small tuft of downwardly directed short androconial setae at middle of vein 2A that overlaps with element on DHW	4N 4O		
Stalachtini:					
<i>Stalachtis</i>	<i>phaedusa</i>	DHW with large black androconial patch in costal half of wing composed of more elongate, rounded, densely packed and upwardly directed scales than adjacent ones	4P		

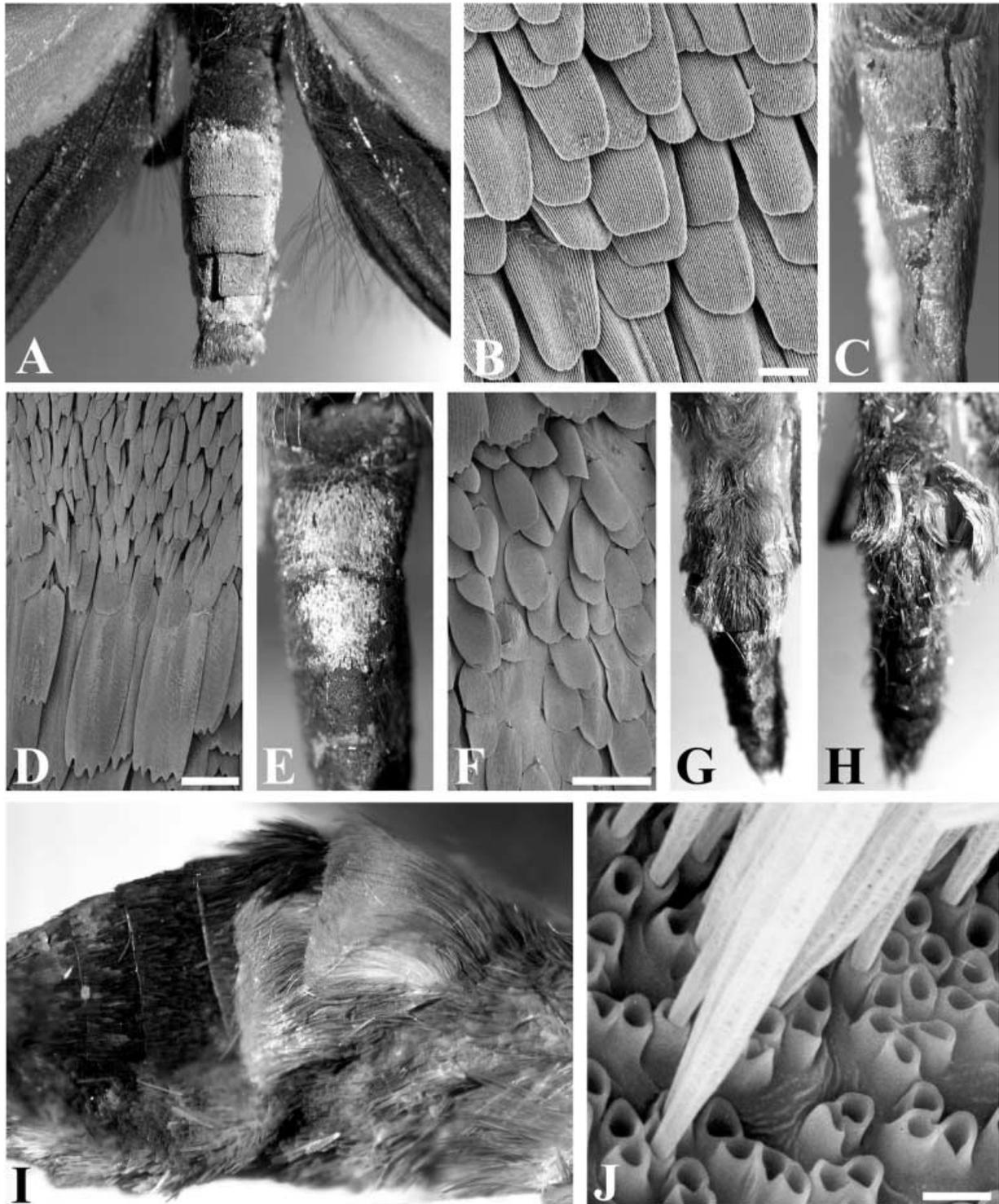


Figure 5. External abdominal androconia. A, B, *Cartea vitula* (Hewitson), pale brown dorsal abdominal androconial scales and adjacent setae on hindwing (A) and androconial scales magnified (B); C, D, *Theope eudocia* Westwood, small dark dorsal square of androconial abdominal scales (A) and transitional area of scales magnified [androconial scales at top] (D); E, F, *Theope sobrina* Bates, pale dorsal abdominal androconial patches (E) and transitional area of scales magnified [androconial scales at bottom] (F); G–J, *Eunogyra satyrus* Westwood, dorsal (G [intact], H [scales on right lifted]) and lateral (I) views of dense basal abdominal setal clumps, and sockets of same scales magnified (J). Scale bars: B, 20 μm ; D, F, 50 μm ; J, 5 μm .

be slightly more elongate, more densely packed and upwardly directed than surrounding ones (Figs 3L, 4K). *Cartea vitula* (Hewitson, [1853]) is the only rioidinid to have androconial scales on the ventral hindwing. These are confined to an ovoid patch along the anal margin (Fig. 3Q) and appear to form part of a complex dual system involving external dorsal abdominal androconial scales and long setae along the hindwing anal margin (Figs 3Q,R, 5A).

The presence of a pale narrow patch of androconial scales around vein 2A on the ventral forewing is common in the Nemeobiinae, but within the Rioidininae is restricted to the genus *Eurybia* Illiger, 1807 (Eurybiini) (Fig. 3N). It occurs in all species except *E. donna* C. & R. Felder, 1862, the *dardus* group (except *latifasciata* Hewitson and *jemima* Hewitson) and the *juturna* group (*sensu* Hanner, 1997). This potentially important character for helping to generate a phylogenetic hypothesis for *Eurybia* was omitted by Hanner (1997). Those species without the patch clustered near the base of his cladogram, but those with it did not form a monophyletic group.

The most prevalent type of setal tuft is that found on the anal hindwing margin of several symmachiine genera (Fig. 4A–F), *Menander menander* group species (Fig. 4L,M) and *Anteros renaldus* (Stoll, 1790) (Fig. 3T). They are positioned either at the base of cell 2A (*A. renaldus* and *Menander* Hemming, 1939) or along a raised medial ridge in cell Cu2 (Symmachiini), and those of the *Menander menander* group can be partially (*menander* Stoll, [1780] and *nitida* Butler, 1867) or fully (*coruscans* Butler, 1867) retracted within a folded pouch (Fig. 4M) whose outline is clearly visible on the ventral hindwing. These setae may lie flat against the wing (e.g. Fig. 4L) or become erect to create a semicircular fan (Fig. 4B). In the case of the symmachiine genera and *Menander* this presumably allows the more effective dissemination of sex pheromones transferred from the concealed abdominal androconia (see below). However, no such abdominal androconia appear to exist in *A. renaldus*, although the abdominal intersegmental membrane opposite the tuft is roughened and the scale sockets are unusually long, and the function of its setal tuft is unclear. In two species of *Theope* Doubleday, 1847, small setal tufts occur at the middle of vein 2A on the ventral forewing and are often visible protruding into a modified area of scales at the costa of the dorsal hindwing (Fig. 3O) (Hall 1999a).

ABDOMINAL ANDROCONIA

External androconial scales

Three unrelated genera have external androconial patches dorsally and laterally on the abdomen. *Cartea vitula* (Hewitson, [1853]) (Rioidinini) possesses a broad

dorsal region of modified scales on tergites three to six that are similar to those at the anal margin of the ventral hindwing (Fig. 5A) (see above and Table 2). They are narrower, more elongate and densely packed than scales on neighbouring segments and conspicuously pale brown instead of black (Fig. 5B). It seems likely that the fringe of long setae along the hindwing anal margin aids the dissemination of pheromones originating from both the abdomen and wings. Most species of the *Theope pedias* and *T. eudocia* groups (Fig. 5C,D), and a few in the *T. theritas* group (Fig. 5E,F) (Nymphidiini), possess similar patches positioned dorsally on one or more medial abdominal tergites, but they are smaller and consist of considerably smaller and more rounded scales than on neighbouring segments (Hall, 1999a).

Both species of *Eunogyra* Westwood, [1851] (5 FRV *incertae sedis* section of Harvey 1987), *satyrus* Westwood, [1851] and *curupira* Bates, 1868, are unique in having dense clumps of external androconial setae at the base of the abdomen (Fig. 5G–I). They have a tightly packed clump of fine pale brown setae lying flat laterally either side of segments two and three with a smaller, sparser area of long dark brown setae dorsally. The sockets of the lateral setae are densely packed raised tubes (Fig. 5J). Clues as to their use during courtship come from the observations that they very readily come loose from their sockets, and, at least when in water, exude a sticky substance. It is unclear whether these setae are used in conjunction with the abdominal coremata during courtship (see below).

Concealed androconial scales

Androconial scales along the anterior margins of abdominal tergites four to seven, concealed beneath the posterior margins of the preceding segments, have evolved independently at least three times in disparate groups of rioidinids. These highly modified scales were first reported by Harvey (1987) for the nymphidiine genera *Periplacis* Geyer, 1837 (Figs 7F–K, 8A–C) and *Menander* (Fig. 8D–J), and as a defining synapomorphy for his redefined tribe Symmachiini (Figs 6A–L, 7A–E). Those in *Calydna* Doubleday, 1847 (4 FRV *incertae sedis* section of Harvey 1987) were recently reported by Hall (2002a) (Fig. 8K–N).

All 13 genera in the Symmachiini possess such narrow patches of androconial scales on abdominal segments four to seven, although only very rarely on segment seven (Fig. 6A,B). Their dorsal surface is markedly convex and covered with longitudinal ribs with an uneven column of perforations between each rib, while the ventral surface is smoother (Figs 6C–L, 7A–E). Glandular material can be seen underlying these scales suggesting they function as pheromone

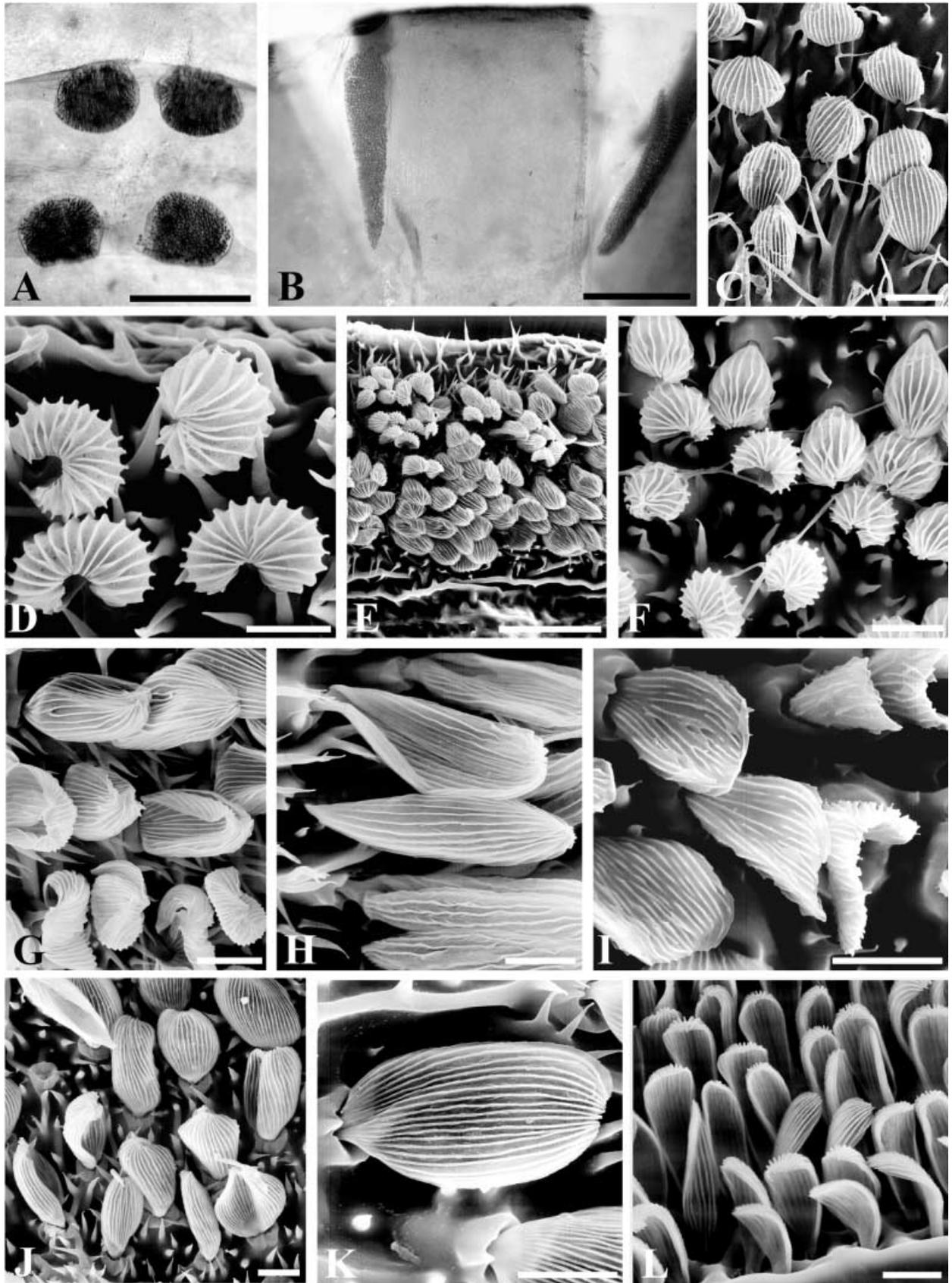


Figure 6. Concealed abdominal androconia: Symmachiini. Magnified scales from anterior margin of tergite unless otherwise stated. A, *Mesene velda* Stichel, ventral view of paired round androconial patches on tergites 4 and 5; B, *Symmachia virgatula* Stichel, lateral view of elongate androconial patches on tergites 4 and 5; C, *Phaenochitonia cingulus* (Stoll); D, *Mesene phareus* (Cramer); E, *Chimastrum argentea* (Bates); F, *Symmachia probetor* (Stoll); G, *Stichelia bocchoris* (Hewitson); H, *Xynias lithosina* Bates; I, *Xenandra helius* (Cramer); J, K, *Mesenopsis bryaxis* (Hewitson), overview (J) and one scale magnified (K); L, *Pirascia sagaris* (Cramer). Scale bars: A, B, 0.5 mm; C, D, F–L, 10 µm; E, 50 µm.

disseminators. Having examined the ultrastructure of these scales using the SEM for representatives of each genus, structural variation is clearly apparent, but without examining more species it is not clear whether these represent interspecific or intergeneric differences. Examining these scales for representatives from each species group may well provide the key to creating a natural generic classification for this tribe of almost entirely mimetic species. The segmental distribution of these scales and whether they extend around the entire margin of the tergite or are medially divided certainly provides good species-group and generic-level characters and this information is given for 91% of species in Table 3 (no males are known for many of the remaining species).

Similar scales occur in *Periplacis* and *Menander*, although they lack longitudinal ribs and well differentiated dorsal and ventral surfaces, and acanthae (acellular projections) between the scales are absent (Figs 7G, 8E–J). In *Menander* they also occur along the anterior margins of segments, but only on tergites six and seven, and the patches are always continuous (Fig. 8D). All species have this arrangement except *M. pretus* (Cramer, 1777), which has them restricted to segment seven. The report of additional scales on segment five in *M. menander* by Harvey (1987) was incorrect. Examination of the ultrastructure of these scales using the SEM for all 13 species, as part of a revision of this genus (Hall, in prep.), revealed the existence of two scale types. Most species have an intricate raised lattice-work of ribs around the tip of each scale (Fig. 8E–H), but in *menander* group species the scales are evenly fluted from base to tip (Fig. 8I, J). Due to the presence of this latter scale type in males of the taxa *lyncestes* Hewitson, 1874 and *apotheta* Bates, 1868, as well as male genitalia typical of *Menander*, we transfer the two species from *Calospila* Geyer, 1832, to the *menander* group of *Menander* (combs. n.). In *Periplacis*, the androconial scales are confined to paired, dorso-lateral invaginated sacs along the anterior margins of tergites six and seven (Figs 7F, 8A). Although the genus is considered monotypic by Callaghan & Lamas (2002), the existence of two distinct androconial scale types suggests two parapatric species should be recognized, the widespread *P. splendida* (Butler, 1867) and *P. glaucoma* Geyer, 1837, confined to southeastern Brazil (Hall, in

prep.). In *P. splendida*, the scales are long, narrow and taper to a point (Fig. 7G), whereas in *P. glaucoma* they are short and round (Fig. 8B). In both cases, the scales have very large surface areas, but in *P. splendida* they are entirely covered with tightly shingled toothed elements (Fig. 7H, I), whereas in *P. glaucoma* they are covered with a broken series of longitudinal ribs (Fig. 8B, C). The sockets of both scale types extend through the sac membrane and form external 'button'-shaped bases (Fig. 7J, K) which connect to glandular tissue. Although the abdominal sacs of *Periplacis* are unique within the Riodinidae, similar organs occur in the nymphalid genera *Vila* Kirby, 1871 (Munroe, 1949) and *Biblis* Fabricius, 1807 (Müller, 1877a) on segments four to six, and five and six, respectively. However, at least in *Biblis*, there are black sacs which occur in both sexes and additional smaller white sacs which occur in males only that are believed to be used in defence and courtship, respectively (Müller, 1877a).

In most species of *Calydna*, the anterior margins of tergites five to seven contain a continuous densely shingled clump of black fan-shaped scales, often with long pedicels (Fig. 8K–N). They are not as highly modified as androconial scales in the aforementioned groups, being more two-dimensional and lacking such an extensive surface area. Such scales occur in all *Calydna* species except the three members of the most basal *caicta* group, which includes *C. caicta* Hewitson, 1854, *C. calamisa* Hewitson, 1854 and *C. charila* Hewitson, 1854 (Hall, 2002a). In the *C. thersander* group the scales are distributed on segments five to seven, and in the *C. hiria* group they are distributed on segments five and six only (Fig. 8K) (Hall, 2002a). The ultrastructure of the scales in the two groups appears not to differ significantly.

In the case of all those species that possess androconial scales along the anterior margins of abdominal segments, the perching adult males are assumed to disseminate the pheromones by telescoping out the abdomen to reveal the androconial patches and, if hindwing brushes are also present (see above), passing pheromones to them to further enhance dissemination. This behaviour was once observed in *Menander hebrus* (Cramer, [1775]) in Ecuador, with the male resting on fully extended legs with the wings angled sharply downwards to touch the leaf surface and the telescoped abdomen curled over its thorax (Hall

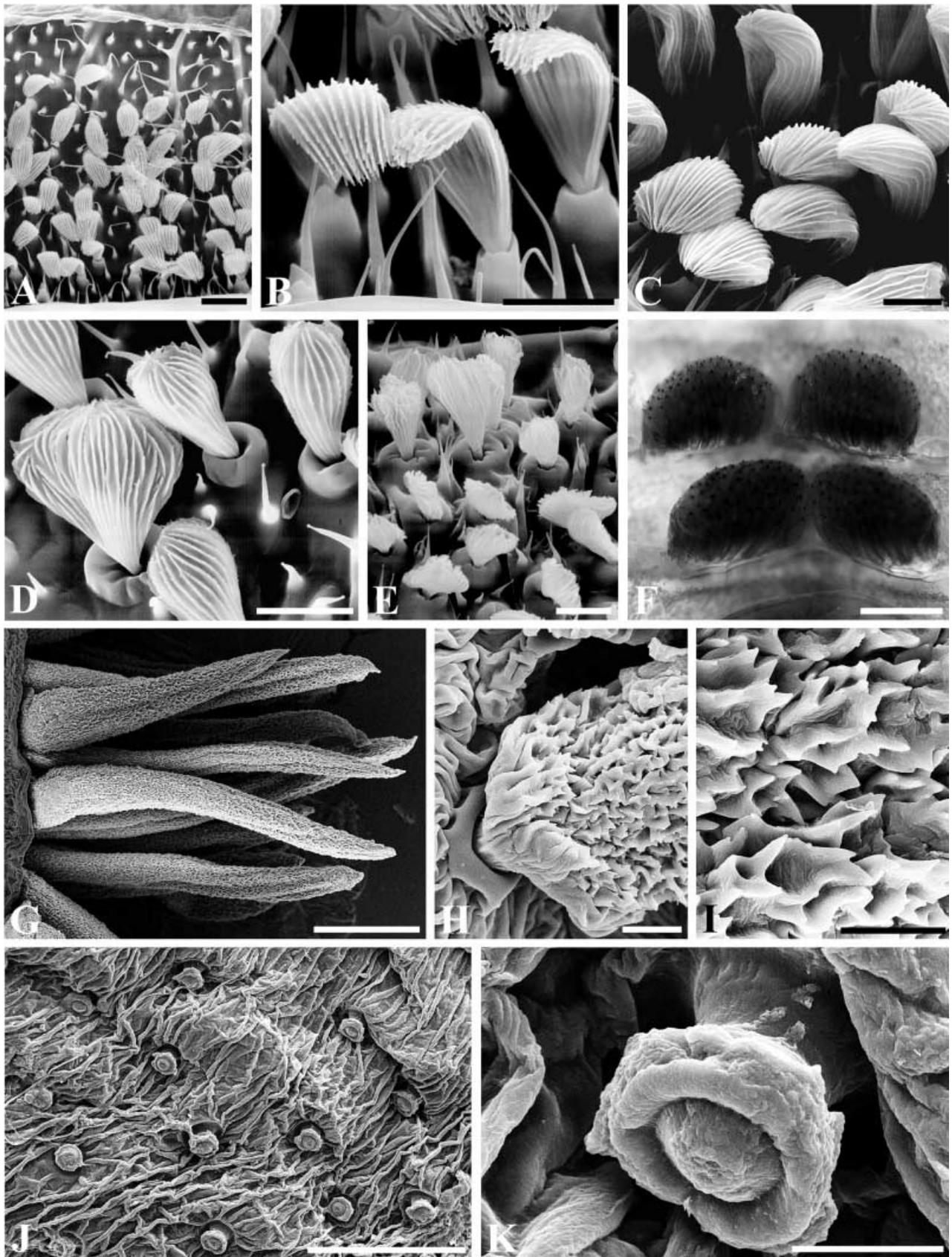


Figure 7. Concealed abdominal androconia: Symmachiini & Nymphidiini. A–E, magnified scales from anterior margin of tergite. A, B, *Pterographium sicora* (Hewitson), overview (A) and one scale magnified (B); C, *Panaropsis elegans* (Schaus); D, *Esthemopsis alicia* Bates; E, *Lucillella camissa* (Hewitson); F–K, *Periplacis splendida* Butler, ventral view of paired invaginated sacs on tergites 6 and 7 [scale sockets at top] (F), cluster of androconial scales in lateral view magnified (G), base of scale magnified (H, I), outer margin of sac in (F) showing external scale sockets (J) and single socket magnified (K). Scale bars: A, 20 µm; B–E, H, I, K, 10 µm; F, 0.5 mm; G, J, 100 µm.

& Willmott, pers. obs.) (see Fig. 1). In the case of *Periplacis*, the presence of partially everted sacs in some dissected specimens indicates that the sacs are everted to the outside and turned inside-out to expose the androconial scales.

Brush organs

Two riodinid genera in the tribe Nymphidiini have brush organs or tufts of androconial setae associated with the male genitalia. The existence of long androconial setae on the last abdominal segment in males of *Nymphidium* was first noted by Callaghan (1983). These are actually inserted medially in the intersegmental membrane between the eighth tergite and the male genitalia, and form a pair of long setal tufts (Fig. 9A–C). They occur only in a group of species comprising the most derived half of the genus, and in two presumed sister species, *N. haematostictum* (Godman & Salvin, 1878) and *N. acherois* (Boisduval, 1836), they are substantially reduced in length (Hall, in prep.). Callaghan (1983) reports that “these scent hairs can be extended and retracted much like the hair pencils of certain Danainae”, however, this is not strictly accurate, as there is no pouch into which they can be retracted. When the genitalia are retracted within the abdomen, the setal tufts project forwards, but when the genitalia are extruded from the tip of the abdomen, the setal tufts splay outwards in a semicircular fan. Such setae have been erroneously reported for *Synargis* Hübner, [1819] and *Audre* Hemming, 1934 (Callaghan, 1983).

All species of *Juditha* Hemming, 1964, possess long setae on an unsclerotized region between the pedicel and the base of the valvae in the genitalia (Fig. 9D,E) (Stichel, 1910–11), which becomes a better defined and broader pad with more setal sockets in the more derived species (Hall & Harvey, 2001). This pad is sparsely covered with very small spines and the sockets form large round indentations (Fig. 9F); the setae are highly ‘sponge-like’ inside (Fig. 9G). Such setae have been erroneously reported for *Thysanota* Stichel, 1910; and *Theope* (Penz & DeVries, 1999) (see Hall & Harvey, 2001).

Coremata

The two species of *Eunogyra* are unique within the Riodinidae in possessing a pair of eversible membra-

nous tubes or coremata (*sensu* Janse, 1932) in the posterior section of the abdomen (Fig. 10A,B). When withdrawn, these tubes extend diagonally and anteriorly upwards from their opening in the eighth segment near the base of the genital valvae as far as segment six, and appear black upon soaking the abdomen in KOH because of the densely packed setal hairs within. The tube is lined with densely packed, heavily ribbed and bifurcate scales, which are presumably pheromone releasers (Fig. 10D). When everted by haemolymph pressure, the rounded tubes appear pale with very long black setae around the tip and shorter setae along the shaft (Fig. 10B). A cross-section of a single seta shows it to be filled with spongy trabeculae (Fig. 10C), suggesting it is efficient at storage and dissemination of pheromones.

Similar coremata occur in several moth families (e.g. Arctiidae), but elsewhere in the butterflies only in the nymphalid subfamilies Satyrinae, Danainae and Morphinae (Vane-Wright, 1972b; Ackery & Vane-Wright, 1984), and the Lycaenidae (Eliot, 1973). The coremata of danaines are perhaps the most complex, with setae or hairpencils of different colours, lengths and morphologies positioned only at the tip or evenly along the entire shaft (Boppré & Vane-Wright, 1989). Males of *Eunogyra* perch low to the ground in the forest understorey during the gloom of late afternoon and the everted coremata can just be perceived as tiny pale yellow ventrolateral tubes at the tip of the abdomen; gently squeezing the abdomen of a live individual also has the effect of everting the coremata (Hall & Willmott, pers. obs.). It is not known how or whether the coremata interact with the external abdominal androconia (see above). It seems possible that, as in the Brassoliniinae (Srygley & Penz, 1999), the proliferation of prominent androconial organs in males of *Eunogyra* species is due to their crepuscular courtship behaviour and allows females to locate them despite their low visibility at dusk.

APPENDAGE ANDROCONIA

Twelve species currently placed in the genera *Ithomiola* C. & R. Felder, 1865 (all species), *Napaea* Hübner, [1819] (the majority of *nepos* group species)

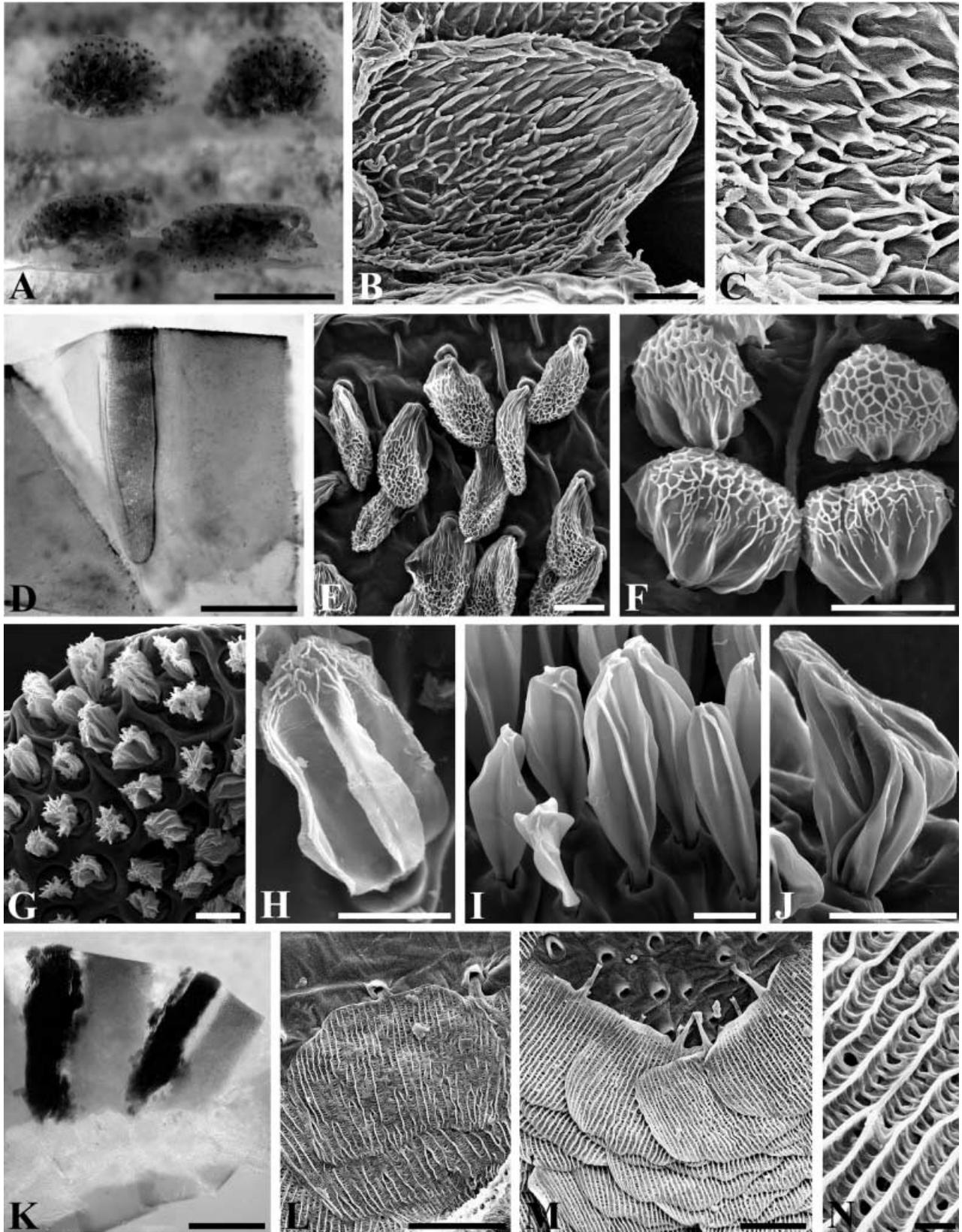


Figure 8. Concealed abdominal androconia: Nymphidiini & *incertae sedis* (4 FRV). E–J and L–N, magnified scales from anterior margin of tergite. A–C, *Periplacis glaucoma* Geyer, ventral view of paired invaginated sacs on tergites 6 and 7 (A), and an androconial scale magnified (B, C); D, *Menander menander* (Stoll), lateral view of elongate androconial patch on tergite 6; E, *Menander clotho* (Stichel); F, *Menander cicuta* (Hewitson); G, *Menander felsina* (Hewitson); H, *Menander aldasi* Hall & Willmott; I, *Menander apotheta* (Bates); J, *Menander coruscans* (Butler); K, *Calydna cea* Hewitson, lateral view of dense black androconial scales on tergites 5 and 6; L, *Calydna lusca* (Geyer); M, N, *Calydna cabira* Hewitson. Scale bars: A, D, K, 0.5 mm; B, C, L, M, 20 μ m; E–J, 10 μ m; N, 2 μ m.

(Fig. 11E,F), *Cremna* Doubleday, 1847 (*alector* Geyer, 1837 and *thasus* Stoll, [1780]) (Fig. 11C,D,G), and *Hermathena* Hewitson, 1874 (all species) (5 FRV *incertae sedis* section of Harvey 1987) (Fig. 11A,B,H–L) possess long androconial setae on the hindleg. These are inserted at the inner distal tip of a shortened tibia (Fig. 11F,G) and lie within a pouch along the inner edge of a lengthened first tarsal segment (Fig. 11E,F). The correlation between the presence of hairpencils and a tibia that is considerably shorter instead of

longer than the first tarsal segment is perfect in the Riodinidae except for certain *N. nepos* group species and *Mesosemia acuta* Hewitson, 1873, which possess the abnormal tibia to first tarsal segment ratio but no hairpencils. The pouch occupies about one-third of the lumen of the tarsal segment (Fig. 11J,K) and is lined with sparsely distributed oval, ribbed and presumably pheromone-releasing scales (Fig. 11H,I). The hairpencil sockets are medially constricted (Fig. 11G), suggesting the shaft can be kept in repose or erect, and

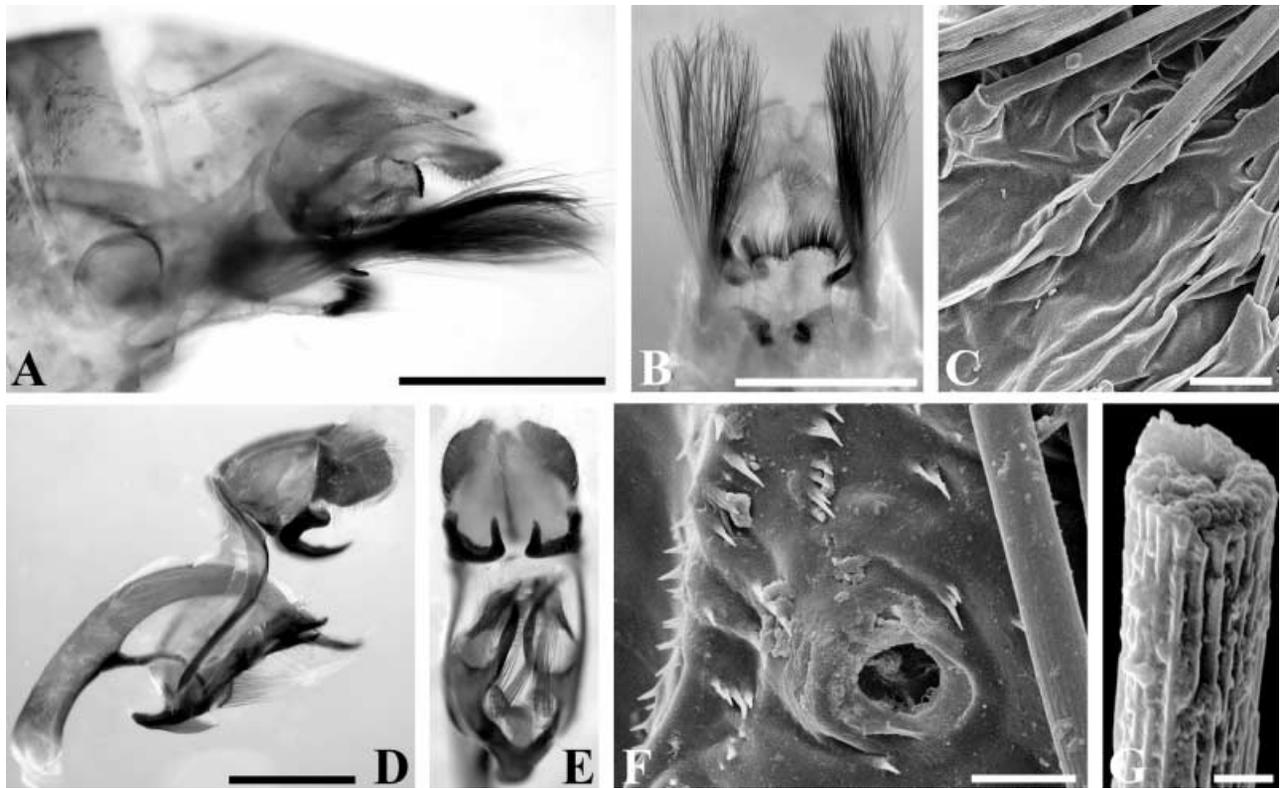


Figure 9. Abdominal brush organs. A–C, *Nymphidium caricae* (Linnaeus), lateral view of last two abdominal segments illustrating position of lateral brushes relative to *in situ* genitalia (A), ventral view of last abdominal segment with brushes laterally, uncus at top and last sternite and valvae at bottom (B), and sockets of brush setae magnified (C); *Juditha azan* (Westwood), lateral (D) and ventral (E) view of genitalia illustrating setal brush between base of valvae and pedicel, and socket and spiny surface of setal pad (F) and setal tip (G) magnified. Scale bars: A, B, D, E, 1 mm; C, 20 μ m; F, 10 μ m; G, 2 μ m.

Table 3. Distribution of concealed androconial scales on the anterior margins of abdominal tergites in males of 129 species in the tribe Symmachiini (out of 141). Solid bars at the left-hand margin are used to preliminarily identify monophyletic groups, based on male and female genitalia, distribution and structure of abdominal androconia, and external facies. Androconial patches on segments 4–7 were either absent (0), a continuous patch (1), or dorsally divided into two patches (2). References: (a) Harvey (1987); (b) Willmott & Hall (1994); (c) Hall & Willmott (1995); (d) Hall & Willmott (1996); (e) Hall & Furtado (1999); (f) Callaghan & Salazar (1999); (g) Hall & Lamas (2001); (h) Hall & Willmott (2002); (i) Hall & Harvey (2002); (j) this study. See Appendix 1 for footnotes

Taxon	Abdominal segment number				Ref
	4	5	6	7	
<i>Phaenochitonina fuliginea</i> (Bates, 1868)	1	1	0	0	d
<i>Phaenochitonina ignipicta</i> Schaus, 1913	1	1	0	0	j
<i>Phaenochitonina pseudodebilis</i> Hall & Willmott, 1996	1	1	0	0	d
<i>Phaenochitonina pyrsoles</i> (Bates, 1868)	1	1	0	0	d
<i>Phaenochitonina cingulus</i> (Stoll, [1790])	1	1	0	0	a
<i>Phaenochitonina gallardi</i> Hall & Willmott, 1996	1	1	0	0	d
<i>Mesene florus</i> (Fabricius, 1793)	1	1	0	0	j
<i>Mesene veleda</i> Stichel, 1923 ¹	2	2	0	0	j
<i>Mesene philonis</i> Hewitson, 1874	1	1	1	0	j
<i>Mesene phareus</i> (Cramer, 1777)	1	1	1	0	a
<i>Mesene leucophrys</i> Bates, 1868	1	1	1	0	j
<i>Mesene martha</i> Schaus, 1902 ²	1	1	1	0	a
<i>Mesene mygdon</i> Schaus, 1913	1	1	1	0	j
<i>Mesene fenestrella</i> Bates, 1868	1	1	1	0	j
<i>Mesene epaphus</i> (Stoll, [1780]) ³	1	1	1	0	j
<i>Mesene ingrumaensis</i> Callaghan & Salazar, 1999	1	1	1	0	f
<i>Mesene sardonix</i> Stichel, 1910	1	1	1	0	j
<i>Mesene bigemmis</i> Stichel, 1925 ⁴	1	1	1	0	j
<i>Mesene pyrippe</i> Hewitson, 1874	1	1	1	0	j
<i>Mesene silaris</i> Godman & Salvin, 1878	1	1	1	0	a
<i>Mesene leucopus</i> Godman & Salvin, 1886	1	1	1	0	j
<i>Mesene babosa</i> Hall & Willmott, 1995	1	1	1	0	d
<i>Mesene cyneas</i> (Hewitson, 1874)	1	1	1	0	c
<i>Mesene citrinella</i> Hall & Willmott, 1995	1	1	1	0	d
<i>Mesene croceella</i> Bates, 1865	1	1	1	0	d
<i>Mesene simplex</i> Bates, 1868	1	1	1	0	j
<i>Mesene nepticula</i> Möschler, 1877	1	1	1	0	j
<i>Mesene patawa</i> Brévignon, 1995	1	1	1	0	j
<i>Mesene monostigma</i> (Erichson, [1849]) ⁵	1	1	1	0	a
<i>Mesene hyale</i> C. & R. Felder, 1865	1	1	1	0	j
<i>Mesene nola</i> Herrich-Schäffer, [1853] ⁶	1	1	1	0	d
<i>Mesene margaretta</i> (White, 1843) ⁷	1	1	1	1	e
<i>Chimastrum argentea</i> (Bates, 1866)	1	1	1	0	a
<i>Chimastrum celina</i> (Bates, 1868) ⁸	1	1	1	0	d
<i>Symmachia stigmatissima</i> Stichel, 1910	1	1	0	0	j
<i>Symmachia arion</i> (C. & R. Felder, 1865)	2	2	0	0	j
<i>Symmachia mielke</i> (Hall & Furtado, 1999)	2	2	0	0	e
<i>Symmachia hippodice</i> Godman, 1903	2	2	0	0	j
<i>Symmachia satana</i> Hall & Harvey, 2002	2	2	0	0	i
<i>Symmachia virgatula</i> Stichel, 1910	2	2	0	0	j
<i>Symmachia fulvicauda</i> Stichel, 1924	1	1	0	0	j
<i>Symmachia fassli</i> Hall & Willmott, 1995 ⁹	1	1	0	0	d
<i>Symmachia virgaurea</i> Stichel, 1910	1	1	0	0	j
<i>Symmachia phaedra</i> (Bates, 1868)	2	2	0	0	d
<i>Symmachia xypete</i> (Hewitson, 1870)	2	2	0	0	a
<i>Symmachia rubrica</i> (Stichel, 1929)	2	2	0	0	b
<i>Symmachia batesi</i> (Staudinger, [1887])	1	1	0	0	d
<i>Symmachia hippea</i> Herrich-Schäffer, [1853]	1	1	0	0	j
<i>Symmachia calligrapha</i> Hewitson, 1867	1	1	0	0	d
<i>Symmachia probetor</i> (Stoll, 1782) ¹⁰	1	1	0	0	a
<i>Symmachia falcistriga</i> Stichel, 1910	1	1	0	0	j
<i>Symmachia praxila</i> Westwood, [1851]	1	1	0	0	i
<i>Symmachia accusatrix</i> Westwood, [1851]	1	1	0	0	a
<i>Symmachia threissa</i> Hewitson, 1870	0	2	0	0	j
<i>Symmachia miron</i> Grose-Smith, 1898	1	1	0	0	j
<i>Symmachia jugurtha</i> Staudinger, [1887]	1	1	0	0	d
<i>Symmachia titiana</i> Hewitson, 1870	1	1	0	0	d
<i>Symmachia aconia</i> Hewitson, 1876	0	1	0	0	j
<i>Symmachia leena</i> Hewitson, 1870	0	1	0	0	d
<i>Symmachia pardalia</i> Stichel, 1924	0	1	0	0	j
<i>Symmachia busbyi</i> Hall & Willmott, 2002	1	1	0	0	h
<i>Symmachia juratrix</i> Westwood, [1851]	1	1	0	0	j
<i>Symmachia calliste</i> Hewitson, 1867	1	1	0	0	j
<i>Symmachia multesima</i> Stichel, 1910	1	1	0	0	j

Table 3. Continued

Taxon	Abdominal segment number				Ref
	4	5	6	7	
<i>Symmachia menetas</i> (Drury, 1782)	1	1	0	0	j
<i>Symmachia technema</i> Stichel, 1910	1	1	0	0	j
<i>Symmachia maeonius</i> Staudinger, 1888 ¹¹	1	1	0	0	d
<i>Symmachia rubina</i> Bates, 1866	1	1	0	0	a
<i>Symmachia suevia</i> Hewitson, 1877	1	1	0	0	d
<i>Symmachia tricolor</i> Hewitson, 1867	1	1	0	0	a
<i>Symmachia triangularis</i> (Thieme, 1907)	1	1	0	0	d
<i>Symmachia basilissa</i> (Bates, 1868)	1	1	0	0	d
<i>Symmachia calderoni</i> Hall & Lamas, 2001	1	1	0	0	g
<i>Symmachia elinas</i> (Rebillard, 1958) ¹²	1	1	0	0	j
<i>Symmachia eraste</i> (Bates, 1868)	1	1	0	0	j
<i>Symmachia hetaerina</i> Hewitson, 1867	1	1	0	0	j
<i>Symmachia emeralda</i> Hall & Willmott, 2002	1	1	0	0	h
<i>Symmachia hazelana</i> Hall & Willmott, 1996	1	1	0	0	d
<i>Symmachia rita</i> Staudinger, [1887]	1	1	0	0	j
<i>Symmachia sepyra</i> ¹³ (Hewitson, 1877)	1	1	0	0	j
<i>Symmachia hypochloris</i> (Bates, 1868)	1	0	0	0	h
<i>Stichelia pelotensis</i> Biezanko <i>et al.</i> , 1978	2	2	0	0	d
<i>Stichelia dukinfieldia</i> (Schaus, 1902)	2	2	0	0	j
<i>Stichelia bocchoris</i> (Hewitson, 1876)	2	2	0	0	a
<i>Stichelia almeidai</i> (Zikán, 1946)	2	2	0	0	j
<i>Xynias lithosina</i> (Bates, 1868) ¹⁴	1	1	0	0	a
<i>Xenandra poliotactis</i> (Stichel, 1910) ¹⁵	2	2	0	0	j
<i>Xenandra ahrenholzi</i> Hall & Willmott, 2002	2	2	0	0	h
<i>Xenandra vulcanalis</i> Stichel, 1910	1	1	0	0	j
<i>Xenandra desora</i> Schaus, 1928	1	1	0	0	a
<i>Xenandra nigrivenata</i> Schaus, 1913	1	1	0	0	j
<i>Xenandra agria</i> (Hewitson, [1853])	1	1	0	0	a
<i>Xenandra helius</i> (Cramer, [1779])	1	1	0	0	a
<i>Xenandra pelopia</i> (Druce, 1890)	1	1	1	1	j
<i>Mesenopsis albivitta</i> (Lathy, 1904)	1	1	0	0	j
<i>Mesenopsis briseis</i> Godman & Salvin, 1886	1	1	0	0	a
<i>Mesenopsis bryaxis</i> (Hewitson, 1870)	1	1	0	0	a
<i>Mesenopsis melanochlora</i> (Godman & Salvin, 1878)	1	1	0	0	j
<i>Mesenopsis pulchella</i> Godman, 1903	1	1	0	0	e
<i>Pirascia patriciae</i> Hall & Willmott, 2002	1	0	0	0	h
<i>Pirascia arbuscula</i> (Möschler, 1883)	1	1	0	0	d
<i>Pirascia phoenicura</i> (Godman & Salvin, 1886)	1	1	0	0	d
<i>Pirascia suapure</i> (Weeks, 1906)	1	1	0	0	j
<i>Pirascia pluto</i> (Stichel, 1911)	1	1	0	0	j
<i>Pirascia crocostigma</i> (Bates, 1868)	1	1	0	0	d
<i>Pirascia sticheli</i> (Lathy, 1932)	1	1	0	0	j
<i>Pirascia polemistes</i> Hall & Willmott, 1996	1	1	0	0	d
<i>Pirascia tyriotes</i> (Godman & Salvin, 1878)	1	1	0	0	d
<i>Pirascia interrupta</i> (Lathy, 1932)	1	1	0	0	d
<i>Pirascia iasis</i> (Godman, 1903)	1	1	0	0	d
<i>Pirascia sagaris</i> (Cramer, [1775])	1	1	0	0	a
<i>Pterographium sicora</i> (Hewitson, 1875)	2	1	0	0	j
<i>Panaropsis semiota</i> (Bates, 1868)	2	2	0	0	j
<i>Panaropsis elegans</i> (Schaus, 1920)	2	2	0	0	a
<i>Panaropsis inaria</i> (Westwood, [1851])	2	2	0	0	a
<i>Panaropsis thyatira</i> (Hewitson, [1853])	2	2	0	0	j
<i>Esthemopsis crystallina</i> Brévignon & Gallard, 1992	1	1	1	0	j
<i>Esthemopsis pherephatte</i> (Godart, [1824]) ¹⁶	2	2	2	0	a
<i>Esthemopsis jesse</i> (Butler, 1870)	2	2	2	0	j
<i>Esthemopsis talamanca</i> Hall & Harvey, 2002	2	2	2	0	i
<i>Esthemopsis sericina</i> (Bates, 1867)	2	2	2	0	a
<i>Esthemopsis colaxes</i> (Hewitson, 1870)	2	2	2	0	d
<i>Esthemopsis clonia</i> C. & R. Felder	2	2	2	0	a
<i>Esthemopsis alicia</i> (Bates, 1865)	2	2	2	0	a
<i>Lucillella aterra</i> (Grose-Smith, 1898)	2	2	2	0	j
<i>Lucillella pomposa</i> (Stichel, 1910)	2	2	2	0	j
<i>Lucillella camissa</i> (Hewitson, 1870)	2	2	2	0	a
<i>Lucillella splendida</i> Hall & Harvey, 2002	2	2	2	0	i
<i>Lucillella suberra</i> (Hewitson, 1877)	2	2	2	0	j

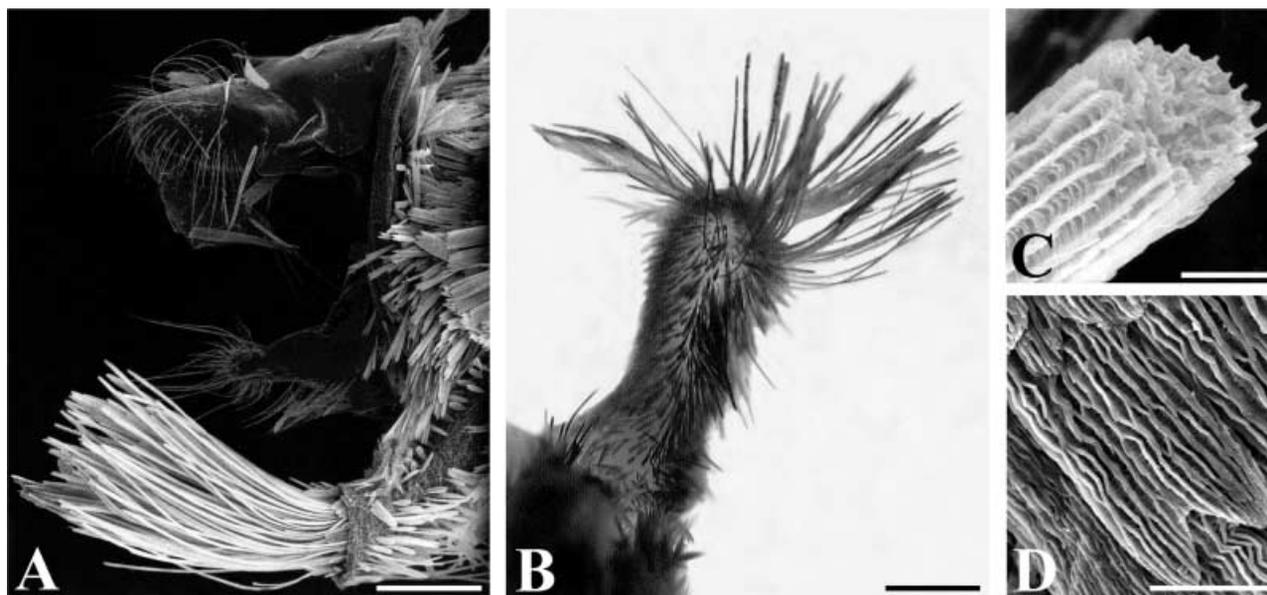


Figure 10. Abdominal coremata. A–D, *Eunogyra satyrus* Westwood, lateral view of abdominal tip with uncus at top, valvae at middle and partially everted coremata at bottom (A), everted coremata (B) and tip of coremata seta (C), and scales lining surface of coremata (D) magnified. Scale bars: A, B, 200 μm ; C, D, 5 μm .

Table 4. Percentage of riordinid species with androconial organs broken down into biogeographic zone and bodily position of organ

Biogeographic zone	% of spp. with wing androconia	% of spp. with abdominal androconia	% of spp. with appendage androconia	Total % of spp. with androconia
Neotropical	6	17	1	21
Ethiopian	100	0	0	100
Oriental	71	0	0	71
All zones	10	16	1	25

the shafts are ribbed in cross-section and filled with spongy trabeculae (Fig. 11L), suggesting efficient storage and dissemination of pheromones.

Leg hairpencils are widespread in a number of moth groups (e.g. Geometridae, Noctuoidea, Pyraloidea, Tortricidae – Kristensen, 1999) and also occur, more rarely, in certain hesperiid genera of the Pyrginae and Coeliadinae (Müller, 1877c; Evans, 1949), but in this case the setae originate on the proximal end of the tibia and typically insert into a metathoracic pouch (e.g. see Burns, 1998). This is the first report of leg hairpencils occurring in the Papilionoidea. One lycaenid species, *Janthecla rocena* (Hewitson, 1867), has a bulbous patch of elongate, putatively androconial scales at the distal tip of an elongate femur (Robbins & Venables, 1991), and many pierids have tibial scale brushes, although it is unclear whether

these are androconial organs or are used for antennal cleaning (Robbins, 1989). The 5 FRV *incertae sedis* section of Harvey (1987) is currently under revision by the authors, and the systematic distribution of these leg androconia, even if they do not define a monophyletic group, provides clear evidence, as supported by other morphological characters, that a revised generic classification is needed for this group.

DISCUSSION

Although the Riordinidae have never been discussed in overviews of androconial organs in the Lepidoptera, we report here that at least 25% of riordinid species possess a wide morphological array of them, with 10% having alar organs, 16% having abdominal organs and 1% having appendage organs (Table 4). Several new

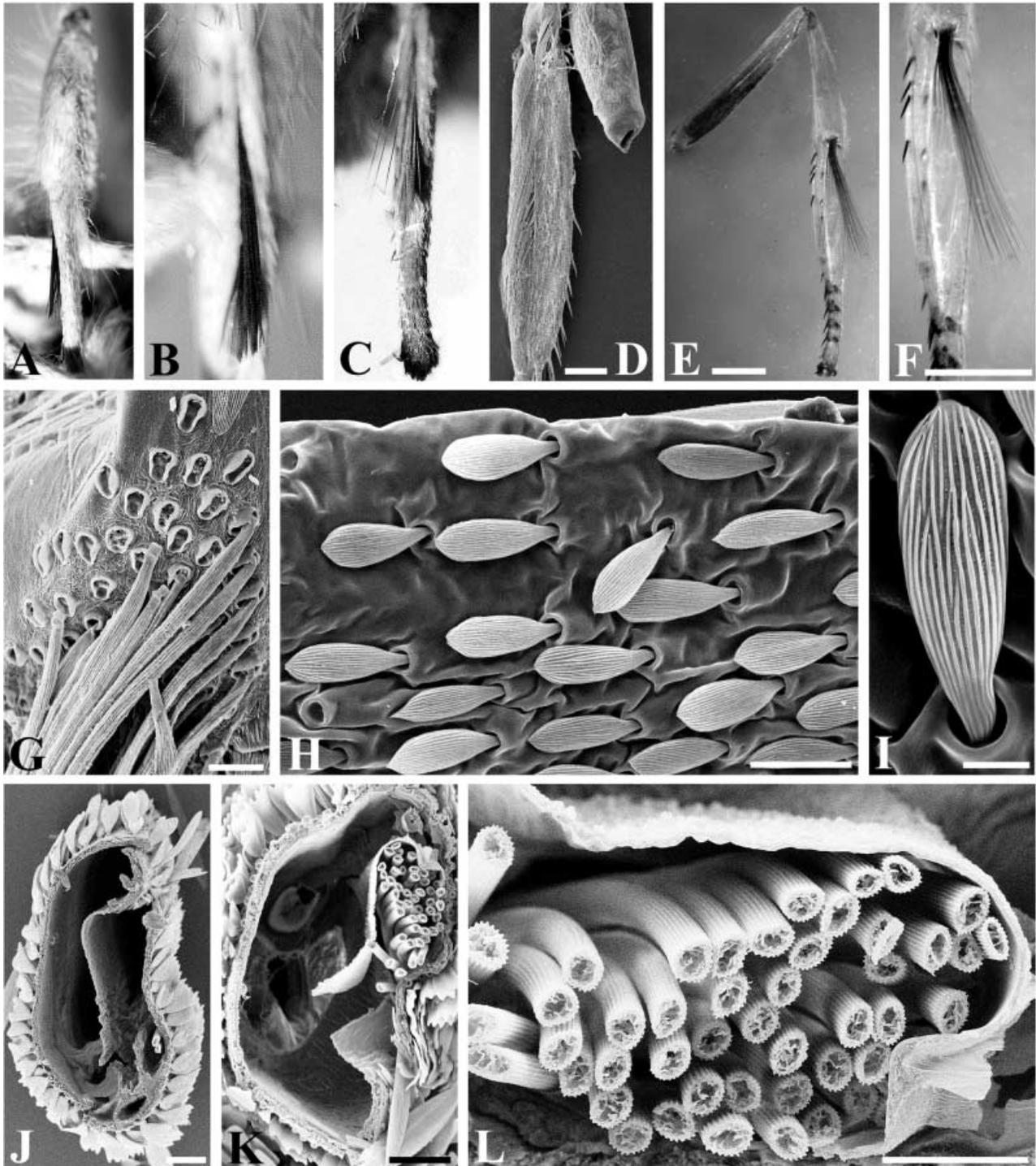


Figure 11. Hindleg hairpencils. A–F, overview of whole or part of hindleg. A, B, *Hermathena candidata* Hewitson, lateral (A) and ventral (B) views; C, D, *Cremna thasus* (Stoll), dried specimen (C) and SEM specimen (D); E, F, *Napaea neildi* Hall & Willmott; G, *Cremna thasus*, medially constricted setal sockets on tibia; H–L, *Hermathena candidata*, androconial scales lining tarsal setal pouch (H, I), and cross-sections of tarsal pouch (J, K) with setae magnified (L). Scale bars: D, 200 μ m; E, F, 0.5 mm; E, H, L, 20 μ m; I, 5 μ m; J, K, 50 μ m.

abdominal organs are described here, including the first report for the butterflies outside the Nymphalidae of coremata and dual androconial organs (*sensu* Boppré & Vane-Wright, 1989), involving the probable transfer of pheromones from concealed abdominal scales to hindwing brushes. Androconial hairpencils on the legs are reported for the first time in the Papilionoidea or true butterflies. The Riodinidae can thus reasonably be described as exhibiting among the

greatest morphological diversity of androconial organs in the butterflies.

Although androconia are well known to be evolutionarily labile, they frequently provide good systematic characters at various hierarchical levels in the Riodinidae, from distinguishing sibling species (*Periplacis*), to defining genera (*Eunogyra*, *Menander*) and tribes (Symmachiini). Once an androconial character is derived in a riodinid clade it seems to be rarely

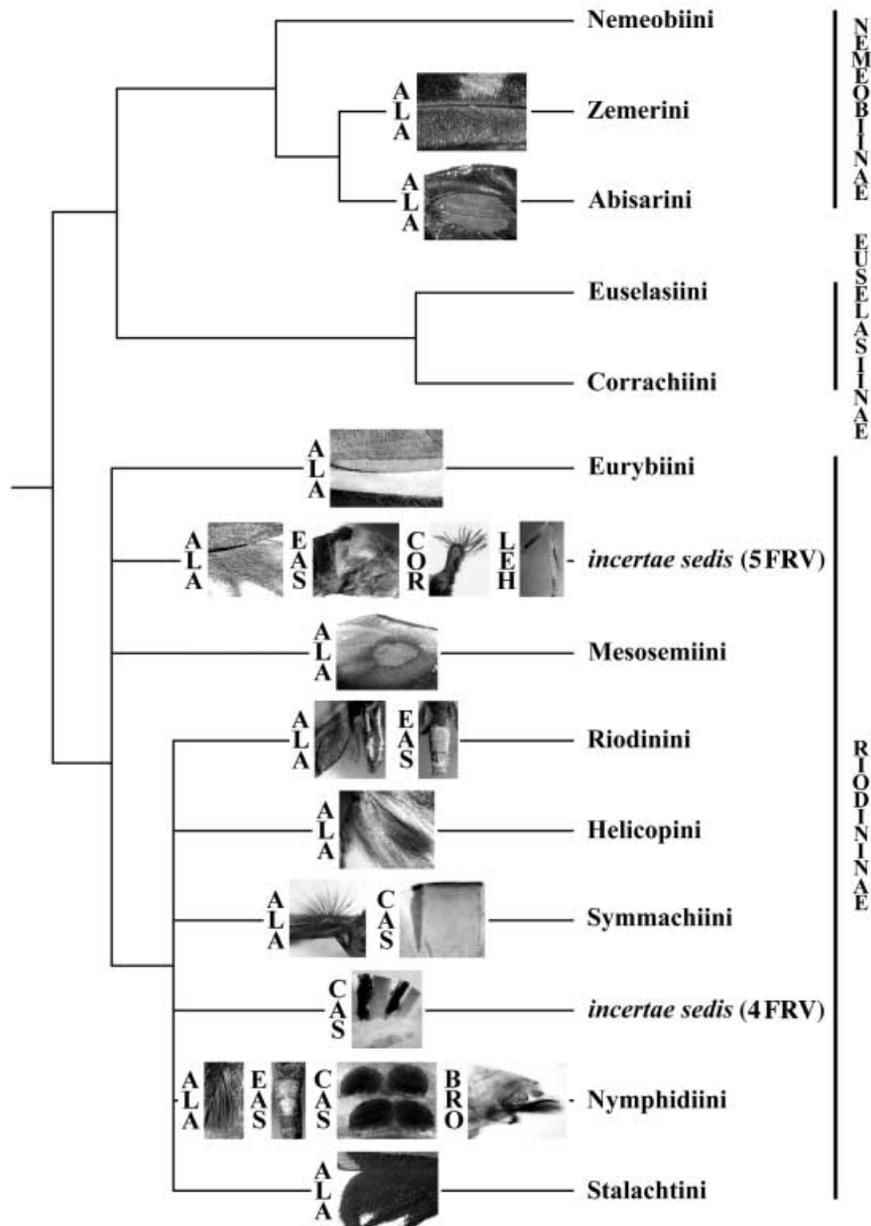


Figure 12. Phylogenetic distribution of androconial types in the Riodinidae. The cladogram is a conservative consensus of the current state of knowledge based on Harvey (1987), Campbell (1998) and Hall & Harvey (unpubl. data). Codes: ALA = alar androconia; EAS = external abdominal scales; COR = coremata; LEH = leg hairpencils; CAS = concealed abdominal scales; BRO = brush organ.

lost. The largest available comprehensive species-level phylogeny for the Riodinidae is that for the nymphidine subtribe Theopina (75 species) (Hall, 1999b, 2002b). Of the six out of 13 *Theope* species groups in which androconia are present, half contain species that all have androconia and there is not a single unambiguous instance of androconia being lost. Species-level phylogenetic studies for *Juditha* (Hall & Harvey, 2001) and *Nymphidium* (Hall, unpubl. data) also show that once their abdominal androconia are evolved, they are modified but never lost. Androconial organs clearly have the potential to provide a wealth of characters useful for generating phylogenetic hypotheses in the Riodinidae. Unlike in the androconial systems of the Danainae (Boppré & Vane-Wright, 1989), there appears to be no correlation between the morphological complexity of androconial organs and how derived the species or genera are that possess them. In fact the only group which possesses all three general androconial types (i.e. alar, abdominal and appendage) is the 5 FRV *incertae sedis* section of Harvey (1987), which is believed to be relatively basal within the Riodininae (Harvey, 1987; Campbell, 1998; Campbell *et al.*, 2000). The distribution of androconial types within the family is illustrated in Fig. 12.

It is presumably only a phylogenetic artifact that such a high percentage of Afrotropical and Oriental riodinids (all belonging to the Nemeobiinae) have androconial organs (100% and 71%, respectively) compared to Neotropical riodinids (21%). However, the low percentage for Neotropical species is unexpected given the very diverse radiations of closely related taxa there and the often apparent complete overlap of perching niches (Callaghan, 1983; Hall, 1998, 1999a). Much like mimetic butterflies (Brower, 1963; Boppré, 1978; Vane-Wright & Boppré, 1993), male riodinids which are externally nearly indistinguishable and perch in close proximity, would be expected to possess androconial organs and use chemical communication to allow females to more readily locate them for mating.

The obvious answer to this puzzle is that we have somehow underestimated the number of species with androconia. Firstly, the physiological function of many scale types is still very uncertain (Downey & Allyn, 1975; Scoble, 1992), and it is possible that scales which do not appear to be functional androconia in fact are. More detailed histological studies are needed to ascertain which scales have underlying glandular tissue. Secondly, it is possible that some thoracic and abdominal androconial organs are sufficiently fragile as to be damaged or destroyed during traditional dissection techniques involving soaking of material in hot potassium hydroxide. For example, DeVries (1997) and C. Jiggins (pers. comm.) report observing coloured 'finger-like' protrusions from the thorax of *Chorinea* Gray, 1832, and the abdomen of *Helicopsis* Fabricius,

1807, respectively. However, despite careful dissection of dried material we could find no such potential structures. It seems likely that more such androconial organs will be discovered through patient field observations such as those by Müller in Brazil during the last century, and by dissecting fresh material. The thorax in particular has been poorly investigated for the presence of androconial scales in the riodinids and butterflies in general (but, e.g. see de Jong, 1982).

To the list of fascinating aspects of riodinid biology (e.g. see DeVries, 1997; Hall, 1999a; Hall & Willmott, 2000) can certainly be added androconial organs and courtship. While we have aimed here to fill the gap in knowledge on the morphology of riodinid androconial organs, by providing a comprehensive survey of their occurrence in the family, still very little is known about how most of these organs function during courtship, and the chemical composition of riodinid sex pheromones remains completely unknown.

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APPENDIX 1

Footnotes for Table 3. The catalogue of Callaghan & Lamas (2002) is the reference upon which we base our nomenclatural changes.

1. *Mesene boyi* Stichel, 1925 and *M. veleda* were described from and have remained known only from males and females, respectively. Having collected both phenotypes sympatrically in Ecuador (JPWH), and given the matching pattern

- of red/orange on the hindwing, we believe these names refer to different sexes of the same species. As the junior name, *boyi* is synonymized with *veleda* (**syn. n.**).
2. Callaghan & Lamas (2002) synonymize *Mesene martha* with *M. leucophrys*. Without a revisionary study of the *phareus* group, it does not seem possible to conclude whether these two names represent two phenotypes of a single dimorphic species or distinct species. We therefore tentatively continue to use *M. martha* as a full species in this Table, although it may actually be conspecific with *M. phareus*. In Ecuador, different male lekking groups have always been one phenotype or the other (*martha* or *leucophrys*) (JPWH).
 3. The taxon *pyrrha* Bates, 1868, is returned to a subspecies of *Mesene epaphus* (**stat. rev.**). Since there are some intergrades between specimens with an entirely red forewing apex (*epaphus*) and those with no red in the forewing apex, it is possible that no subspecies should be recognized in *M. epaphus*.
 4. An intermediate specimen from east Ecuador between nominotypical *Mesene fissurata* Stichel, 1929, from Colombia, and the type of *M. bigemmis* from Santarém, Brazil, suggests *M. fissurata* is conspecific with *M. bigemmis*. The hindwing of the Ecuadorian specimen is as in *fissurata* and the forewing is a mixture of the two species, with the white markings in cells M2 and M1 merged, as in *bigemmis*, but the white mark in cell M3 elongate and touching the basal red, as in *fissurata*. Given that only a handful of specimens exist and the extent of within population variation is unknown, and the male genitalia do not differ, we choose to synonymize *fissurata* with *bigemmis* (**syn. n.**).
 5. Since there are some intergrades between *Mesene discolor* Stichel, 1929 and *M. monostigma* along the base of the eastern Andes, we downgrade the former to a subspecies of the latter (**stat. n.**).
 6. The taxon *nydia* Bates, 1868 (= *mulleola* Stichel 1910), differs from the highly variable *Mesene nola* by having reduced rays at the distal margin of the hindwing and a narrow black costal and distal margin on the forewing. However, since this phenotype occupies only a small region of western Brazil, within the range of *M. nola*, and the male genitalia of the two phenotypes do not differ, we believe *nydia* to be a local geographical form of *M. nola* and thus synonymize it with that species (**syn. n.**).
 7. *Mesene margaretta* is perhaps the most geographically variable species in the genus. This cluster of parapatric (and often recurring) phenotypes which range throughout the western Andes and more rarely along the eastern Andes all have the same genitalia and the same unusual pattern of abdominal androconia (found elsewhere only in *Xenandra pelopia*). We therefore return the north Venezuelan *oriens* Butler, 1870, to a subspecies of *M. margaretta* (**stat. rev.**).
 8. The taxon *celina* was described in and has always been treated in *Esthemopsis*, but we transfer it to *Chimastrum* (**comb. n.**) because of great similarities with the only member of that genus, *argentea*, in male and female genitalia, overall wing pattern, and the presence in both of yellow scaling on the frons, palpi, legs and ventral wing bases. The taxon *aeolia* Bates, 1868 (Guianas, lower Amazon) differs from *C. celina* (upper Amazon) only by having separated instead of fused forewing subapical white pattern elements (the genitalia are the same), and we place it as a subspecies of *celina* (**stat. rev.**), also transferring it from *Esthemopsis* (**comb. n.**).
 9. The taxon *aurigera* Weeks, 1902, described from a unique female, has been treated as a synonym of *Lucillella camissa* (Stichel 1930–31) or as a full species in that genus (Callaghan & Lamas, 2002), however, it actually belongs in *Symmachia*. It is either the female of *S. fassli* (similar sympatric females are known from Ecuador) or *S. virgaurea* Stichel, 1910 (no females are known with certainty but they are expected to be very similar to those of *fassli*), which occur on the east and west slopes of the Andes, respectively. However, since *aurigera* was described from 'Bogotá, Colombia', a general labelling centre that encompasses localities from all three cordilleras, it is currently not possible to definitively place it with either *fassli* or *virgaurea*. Since *aurigera* is the oldest of the three names, the nomenclatural stability of this group is threatened and an application to the ICZN should probably be made to suppress the name *aurigera*.
 10. In their annotated checklist of French Guianan riodinids, Brévignon & Gallard (1998) recognized two "probetor-like" species, *Symmachia probetor* and *S. astiama* Seitz, 1914, giving no explanation for raising the latter to species status, but pointing out apparent male genital differences in illustrations. This position was followed by Callaghan & Lamas (2002), who used the name *belti* Godman & Salvin, 1886, with *astiama* as a synonym. Having examined the male genitalia of five 'S. probetor' specimens covering the geographical range and wing pattern variation of the species, we conclude those differences highlighted by Brévignon & Gallard (1998) to be intraspecific and we resynonymize *belti* with *probetor* (**syn. rev.**). We suggest the female illustrated by Brévignon & Gallard (1998) as *S. astiama* is *S. falcistriga*.

11. The taxon *maeonius* was described as and has always been regarded as a species, but Callaghan & Lamas (2002) synonymized it with *Symmachia menetas*. However, the male genitalia of *S. technema* are more similar to those of *S. menetas*. These three allopatric species could be regarded as a single superspecies, but given the consistent wing pattern differences between them (the genital differences are very minor) we prefer to treat them as three distinct species. We return *maeonius* to species rank (**stat. rev.**).
12. The taxon *elinas* was described by Rebillard (1958) in the riordinine genus *Metacharis* Butler, 1867, and subsequently transferred to *Cariomothis* Stichel, 1910; by Callaghan (1995). However, the presence of concealed abdominal androconial scales in the male places it in the Symmachiini. Due to overall similarities with *S. eraste* and *S. emeralda*, we place *elinas* in *Symmachia* (**comb. n.**).
13. The taxon *sepyra* has long been treated in either *Ancyluris* Hübner, [1819] or *Necyria* Westwood, [1851] (Riordinini). However, the presence of concealed abdominal androconial scales in the male places it in the Symmachiini. Unsurprisingly, given its unique phenotype, the male genitalia are unlike those of any other species in the tribe and we can only place it for now in what has become the 'catch-all' genus *Symmachia* (**comb. n.**).
14. The taxon *lithosina* was described in and has always been treated in *Esthemopsis*, yet does not differ in any regard from the type species of *Xynias*, *cynosema* (although the species were described from different sexes). We thus transfer *lithosina* to *Xynias* (**comb. n.**), and synonymize *cynosema* with *lithosina* (**syn. n.**). The type of *christalla* Grose-Smith, 1902, differs from *X. lithosina* only slightly in the shape of the forewing apical band, a character that is variable within populations, and we also synonymize it with *lithosina* (**syn. n.**). Note that although d'Abrera (1994) synonymized *Xynias* with *Esthemopsis*, their morphology is quite distinct.
15. The taxon *poliotactis* was described in and has always been treated in *Esthemopsis*, but its male genital morphology indicates it more appropriately belongs in *Xenandra* (**comb. n.**).
16. The taxa *teras* Stichel 1910 and *pallida* Lathy, 1932, are treated by Callaghan & Lamas (2002) in the riordinine genus *Pheles* Herrich-Schäffer, [1853], as full species, but since their types do not significantly differ we synonymize the latter with the former (**syn. n.**). The presence of concealed abdominal androconial scales in male *teras* places it in the Symmachiini, and since it differs from *Esthemopsis pherephatte* only by having a white instead of yellow forewing subapical band (the male genitalia are the same) and occurs allopatrically (around the eastern periphery of South America), we place *teras* as a subspecies of *E. pherephatte* (**stat. n.**). Note, *E. pherephatte* has been known until recently under the name *caeruleata* Godman & Salvin, 1878.
17. The following taxa lack concealed abdominal androconia and are removed from the tribe Symmachiini: *pulcherrima* Herrich-Schäffer, [1853], is transferred from *Xenandra* to *Themone* Westwood, [1851], in the tribe Riordinini (**comb. n.**), and on the basis of similarities in the male genitalia, wing pattern, wing shape and pattern of white fringe elements it appears to be most closely related to *T. poecila* Bates, 1868; *fenella* Grose-Smith, 1902, is transferred from *Esthemopsis* to *Pheles* in the Riordinini (**comb. n.**), where we place it as a synonym of *P. strigosa* (Staudinger, 1876) (**syn. n.**) [note this taxon should in turn probably be regarded as a subspecies of *P. melanchroia* (C. & R. Felder, 1865)].
18. The following twelve symmachiine species were not included in Table 3 because they were unavailable to us (NM signifies no male is known for this species): *Pirascca apolecta* (Bates, 1868), *S. arcuata* Hewitson, 1867 (NM), *S. cuneifascia* (Zikán, 1946), *S. exigua* (Bates, 1868) (**comb. n.**) (NM) (long placed in *Metacharis* and currently placed in *Comphotis* Stichel 1910; *exigua* can be placed in the Symmachiini, as a close relative of *S. batesi* and *S. calligrapha*, on the basis of wing pattern alone), *S. leopardina* (C. & R. Felder, 1865), *S. nemesis* Le Cerf, 1958, *S. norina* Hewitson, 1867 (NM), *S. pardalis* Hewitson, 1867 (NM), *S. splendida* (Salazar & Constantino, 1993), *S. tigrina* Hewitson, 1867 (NM), *Xynias lilacina* Lathy, 1932, and *Esthemopsis macara* (Grose-Smith, 1902) (**stat. rev.**) (this taxon is currently placed as a subspecies of *E. alicia*, which occurs from Mexico to Guatemala, but since the probable sister species of *E. alicia*, *E. clonia*, replaces it in the remainder of Central America, the phenotypically distinct Colombian taxon *macara* must be regarded as a full species).