

## *Miriamica*, a New Genus of Milkweed Butterflies with Unique Androconial Organs (Lepidoptera: Nymphalidae)

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**Abstract.** Results of microscopical (SEM) investigations of the androconial organs of *Parantica sita* and *P. weiskei* are presented. Such is the structural novelty of the patch scales in *P. weiskei* that, in combination with other morphological characters, it is proposed that a new genus *Miriamica* is established to accommodate this species, together with a second species, *M. thalassina*, until now regarded as a subspecies of *weiskei*, separate from *Parantica* and other members of the subtribe Amaurina.

**Key words.** Danainae, Amaurina, *Parantica*, *Amauris*, *Ideopsis*, *weiskei*, *thalassina*, taxonomy, pheromone-transfer-particles, wing scales.

### 1. INTRODUCTION

The milkweed butterflies (Nymphalidae: Danainae), which include the remarkable migratory monarch (*Danaus plexippus plexippus* (Linnaeus, 1758): MALCOLM & ZALUCKI 1993), various mimicry rings (e.g. within the genus *Euploea* Fabricius, 1807: CARPENTER 1953), and elaborate male sex-pheromone systems (e.g. in the genus *Amauris* Hübner, 1816: SCHULZ et al. 1993), are amongst the best-known and biologically most interesting of all insects. ACKERY & VANE-WRIGHT (1984), in their global review of the subfamily, recognised 11 genera, including 38 species in the Indo-Pacific genus *Parantica* Moore, 1880, to which *Parantica fuscela* Parsons, 1989, from New Britain (Papua New Guinea), *P. noeli* Treadaway & Nuyda, 1993, from Mindoro (Philippines), and *P. swinhoei* (Moore, 1883) (see KOIWAYA & NISHIMURA 1997) from north-east India, northern Indo-China, China and Taiwan must now be added. Amongst these 41 species, one stands out as distinct. First described by Walter ROTHSCHILD (1901) as *Danaus weiskei*, this New Guinea endemic differs markedly from all other *Parantica* in a number of characters, including the androconia – the specialised glandular scales that form the major structural components of the courtship

pheromone systems of male Lepidoptera (BOPPRÉ 1984). The fine structure of both the alar and abdominal androconial organs of *D. weiskei*, reported below for the first time, reveals unique features. Compared to other danaine genera, the synapomorphies for *Parantica* to include *D. weiskei* have been acknowledged to be weak (ACKERY & VANE-WRIGHT 1984: 28). Consequently, we now consider separate generic status for *D. weiskei* to be justified, and here propose a new genus to receive it. With the exclusion of *D. weiskei*, the 40 species remaining in *Parantica* form a very homogeneous and evidently monophyletic group.

### 2. MATERIAL AND METHODS

Specimens investigated by using scanning electron microscopy (SEM) came from The Natural History Museum, London (BMNH), and from private collections (see Acknowledgements). In addition, newly hatched males of *Parantica sita* (Kollar, 1844) were examined for comparison.

For SEM, alar organs and hairpencils were dissected, gold-coated and investigated with a Zeiss DSM 940A. Images were taken electronically and processed using Adobe Photoshop 6.0® and Adobe PageMaker 7.0®.

For histological studies, androconial organs of freshly killed specimens were immersed either in Dalton's  $K_2Cr_2O_7$ - $OsO_4$  mixture or in 2%  $OsO_4$  in Zetterquist buffer (cf. GLAUERT 1974), then dehydrated in graded ethanols and embedded in Durcupan AMC (Fluka). For light microscopy (LM), 0.5–2.0  $\mu m$  sections were made with a 2050 Supercut (Reichert-Jung), stained with azur II-methylenblue after RICHARDSON et al. (1960) and evaluated with a Zeiss Axioscope.

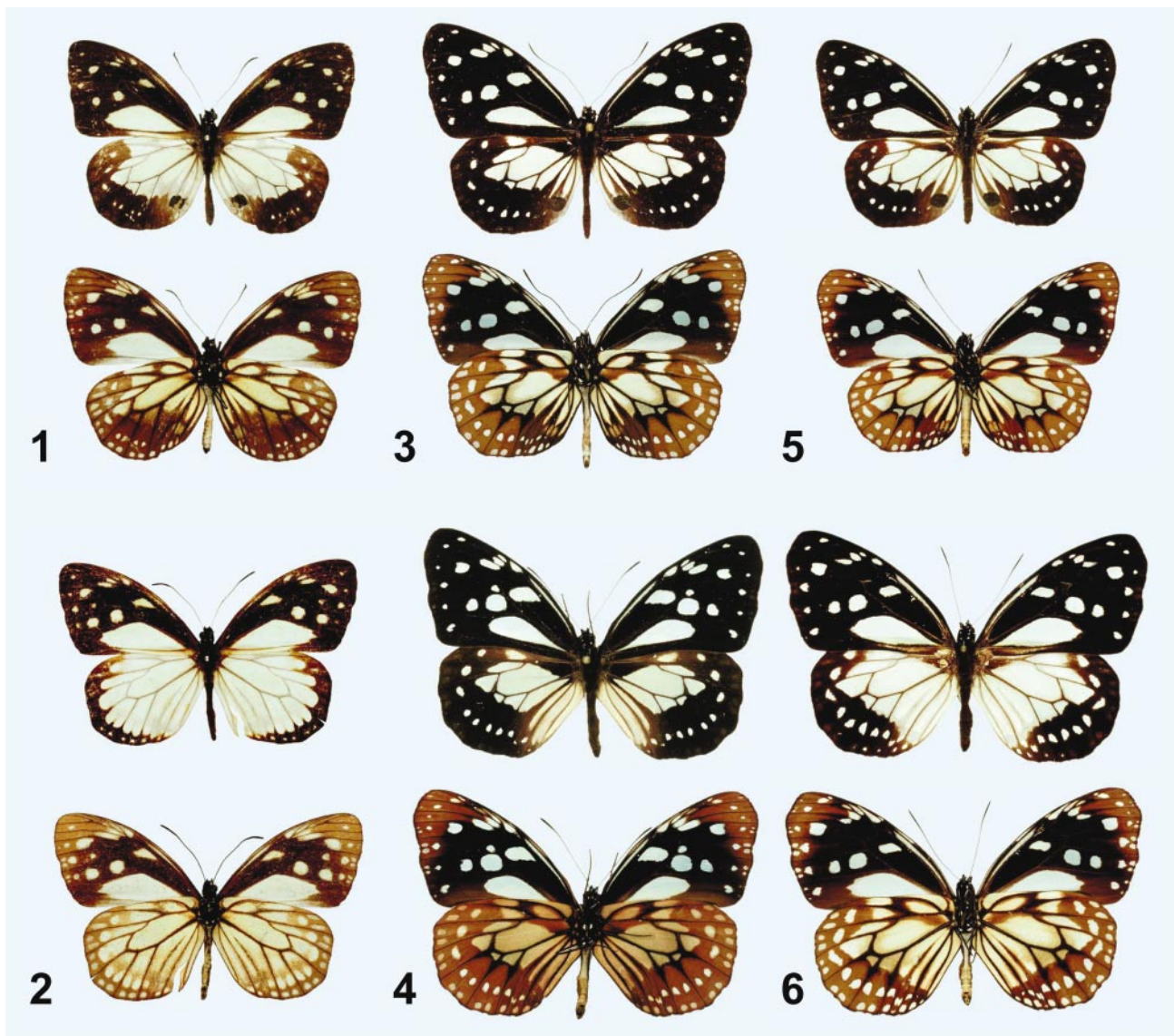
### 3. RESULTS

#### 3.1. Taxonomy

**3.1.1. Genus *Miriamica* gen. nov.** (Nymphalidae, Danainae, Danaini, Amaurina)

**Type-species:** *Danaus weiskei* Rothschild, 1901, here designated.

**Included species** (Figs. 1–6).



**Figs. 1–6.** *Miriamica* butterflies, uppersides above, undersides below. **1, 2** *M. thalassina* (Joicey & Noakes). **1** male syntype, [Indonesia, Irian Jaya], Angi Lakes, Arfak Mts, 6000ft., North N. Guinea, Jan–Feb, 1914. A, C, & F. Pratt. **2** female syntype, [Indonesia, Irian Jaya], Angi Lakes, Arkak Mts, 6000ft., North N. Guinea, Jan–Feb, 1914. A, C, & F. Pratt. Brit. Mus. 1931–291. **3, 4** *M. weiskei* (Rothschild), 'dark form'; **3** male, Indonesia, Irian Jaya, Pass Valley, R. Suwagi Km 48. Leg. H. van Mastrigt. BMNH(E) 1999-244; **4** female, [Indonesia, Irian Jaya], Ilaga. 10. viii. 1988. Henk van Mastrigt. [Held on deposit, BMNH]. **5, 6** *M. weiskei* (Rothschild), typical or 'pale form'. **5** male holotype, [Papua New Guinea], Aroa R., Brit. N. G., Weiske. B. M. 1939-1. **6** female, [Papua New Guinea], Owgarra, Upp. Aroa R., Brit. N. Guinea, Febr. 1905, A. S. Meek. B. M. 1939-1.

*Miriamica weiskei* (Rothschild), **comb. nov.**, from *Danaus weiskei* Rothschild, 1901: 218, pl. 10, fig. 1. Holotype, male, Papua New Guinea, Aroa River [BMNH: examined].

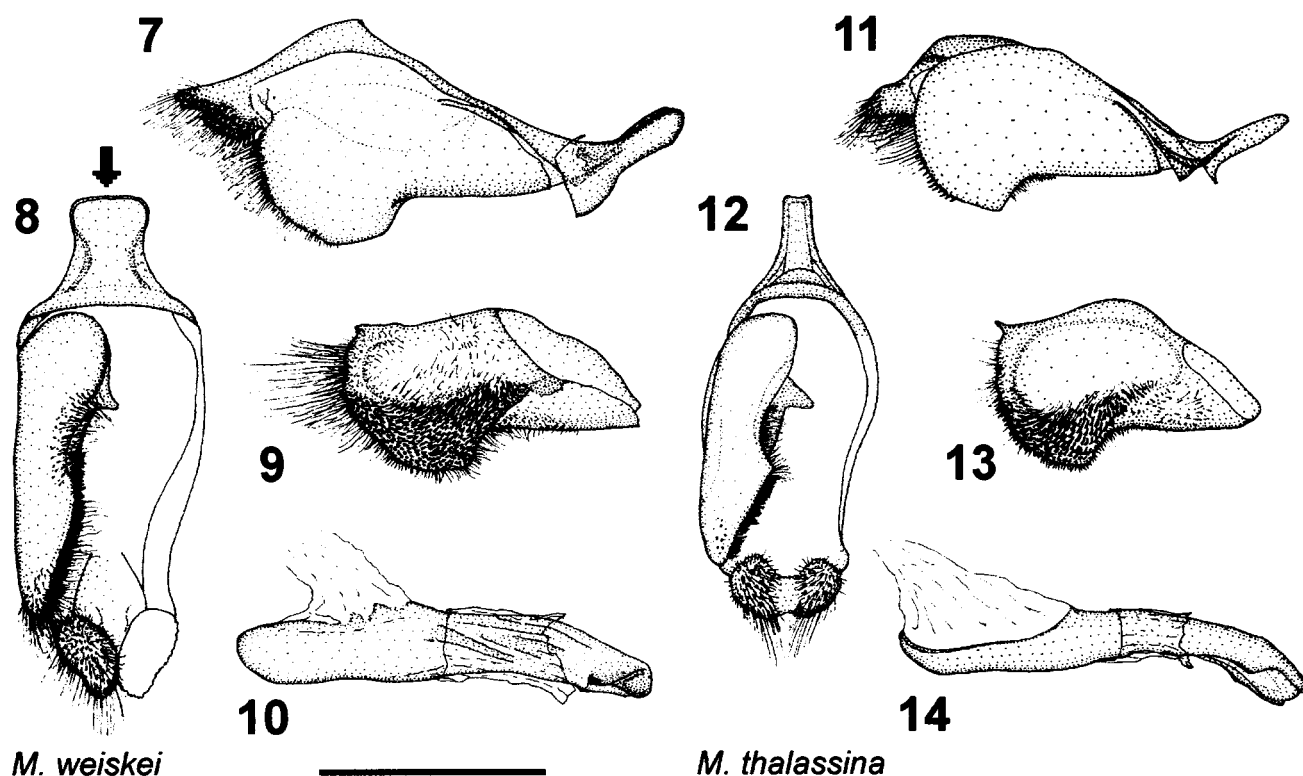
*Miriamica thalassina* (Joicey & Noakes), **comb. nov.**, **stat. nov.**, from *Danaida weiskei thalassina* Joicey & Noakes, 1916: 364, pl. 55, figs. 3,4. Syntypes (5 male, 2 female), Irian Jaya, Arfak Mts, 6000 ft. [BMNH: examined]. [= *Parantica weiskei barbarus* Tsukada & Nishiyama, 1979: 5, 21, figs. 6, 7. Described from Sulawesi apparently in error; currently regarded as a subjective synonym of *thalassina*; type-material not examined.]

In the section that follows, numbers in parentheses refer to characters listed and discussed by ACKERY & VANE-WRIGHT (1984); likewise the classification follows these authors.

Amongst the Danainae, *Miriamica* has a unique suite of features. The hindwing cubital veins are hairy on the upperside (54). In addition, the socii of the male genitalia are fused (56 – although a comparable condition occurs in *Amauris* – 15; cf. figs. 41, 42 in ACKERY &

VANE-WRIGHT 1984), and the wing membrane is bare in the forewing discal cell beneath (11 – but this condition occurs in some *Parantica* species). The androconial organs, which are also unique in certain features, notably the modified patch scales of the hindwing, are described in detail below. The male genitalia of *Miriamica* also differ from other Danaini in the form of the tegumen and the annellus (Figs. 7–14).

The type species, *Miriamica weiskei* (Rothschild, 1901), is restricted to New Guinea, where it occurs in two diagnosable forms: dark *M. weiskei* (Figs. 3, 4, 15) in the mountains of eastern Irian Jaya, and pale or typical *M. weiskei* in the mountains of Papua New Guinea (Figs. 5, 6, 15). A second species, *M. thalassina* (Joicey & Noakes, 1916) (Figs. 1, 2, 15) occurs in the Arfak Mountains of the Vogelkop, western Irian Jaya. *M. thalassina* differs primarily in the saccus (not broadened as in *weiskei* (Figs. 7–14) – character 55 in ACKERY & VANE-WRIGHT 1984), and its relatively elongate hindwing discal cell, in which  $m_2$ – $m_3$  is also more oblique, as well as smaller size and a number of constant colour pattern differences (summarised in



**Figs. 7–14.** Male genitalia of (left) *Miriamica weiskei* (7–10) and (right) *M. thalassina* (11–14). 7, 11: external genitalia, right lateral view; 8, 12: ventral view, left valve removed (note far greater breadth of saccus in *M. weiskei*; arrow). 9, 13: excised left valve, internal lateral view; 10, 14: aedeagus, left lateral view. Provenance of *M. weiskei*: Indonesia, Irian Jaya, Pasa Valley, R. Suwagi km 48, 22–26. i. 1998 (BMNH dissection vial Rhop. 5473). Provenance of *M. thalassina*: Indonesia, Irian Jaya, Arfak Mts, Anggi Lakes (BMNH dissection vial Rhop. 5480). Scale bar: 2 mm.

Tab. 1). We have examined over 80 specimens of *M. weiskei*, and 8 of *M. thalassina*, and they exhibit an interesting geographical counter-shift in coloration: the western *M. thalassina* has a far more extensive pale hindwing pattern especially in the females than the eastern *M. weiskei*, while the latter has more extensive, sharply-defined whitish-blue forewing markings compared to *M. thalassina*, in which the forewing pale spots are small and dyslegnic (edges soft and diffuse: POULTON 1916). Fresh material of *M. weiskei* clearly has blue membrane pigment underlying all pale wing areas, a feature well known in *Tirumala* Moore, 1880, and *Ideopsis*, but as yet uncertainly recorded for some *Parantica* species.

Judging by the specimens we have seen, material from the three areas can be identified by phenotype alone (Figs. 1–6), probably with 100% accuracy. This raises the question, should the dark form of *M. weiskei* be described as a new subspecies, or even species? Given the degree to which New Guinea taxa often exhibit complex patterns of replacing exo-phenotypic variations and stepped clines, with gene flow in montane groups potentially restricted but not necessarily wholly cut off by steep valleys and low passes, we prefer here simply to draw attention to the difference, without proposing an additional formal taxon. This view is reinforced by some preliminary biometric work on the length of the pale basal element in upperside hindwing cell  $R_5$ , which suggests a (possibly stepped) cline from shortest to longest on going from west to east, the assessment of which is affected by an apparent gap in distribution in the border region between Irian Jaya and PNG. This gap lies either side of the major Strickland River valley, close to the dividing line between watersheds flowing east and those flowing west (Fig. 15), and which could act as a partial barrier to *Miriamica*. Thus we propose to refer to the eastern Irian Jaya population simply as “dark *weiskei*”. Tab. 1 summaris-

es the differences between the three formal and informal taxa.

*Miriamica* belongs to the Nymphalidae (tri-carinate antennae, and reduced, non-ambulatory prothoracic legs in both sexes of the adult). Like all members of the Danainae, *Miriamica* has paired eversible abdominal hairpencils in the adult male, and clubbed, ankylosed foretarsi in the adult female. Amongst the Danainae it belongs to the tribe Danaini, the members of which have legs with very small pulvilli and paronychialia (1), straight tarsal claws (2), and hindwing vein  $1A + 2A$  usually with a swollen section (3) (although in *Miriamica* this swelling, if it occurs at all, is very slight). Within the Danaini, *Miriamica* is considered to belong to the subtribe Amaurina – members of which typically have the margin of the male eighth sternite armed with spines (6). However, although the eighth sternite is modified in *Miriamica*, it is not clear that true spines are present and, in light of the new findings presented here, its membership of the Amaurina must be open to some doubt (see Section 4.1.). Within the Amaurina, *Miriamica* differs from *Amauris* by having hairpencils that lack black ‘contact hairs’ (16). With both *Ideopsis* Horsfield, 1858, and *Parantica*, *Miriamica* shares two peculiarities which, however, are homoplasious: forewing cell  $M_3$  with a single centrally located submarginal spot (12), and female reproductive system with a double corpus bursae (14). The latter appears to be universal in the three genera, and absent in other Danaini, but recurs in some Itunina, and also some Ithomiinae. *Miriamica* lacks characteristic features of *Ideopsis*: the folded, downwardly-directed process of the male genital clasper (18), androconia distributed along the entire length of hindwing vein  $1A+2A$  (19), and the anastomosis of forewing veins  $R_1$  and  $Sc$  (20). Like *Parantica*, *Miriamica* has an angle between hindwing veins  $m_1-m_2$  and  $m_2-m_3$  (17), rather than the rectilinear arrangement seen in other Danaini, but the

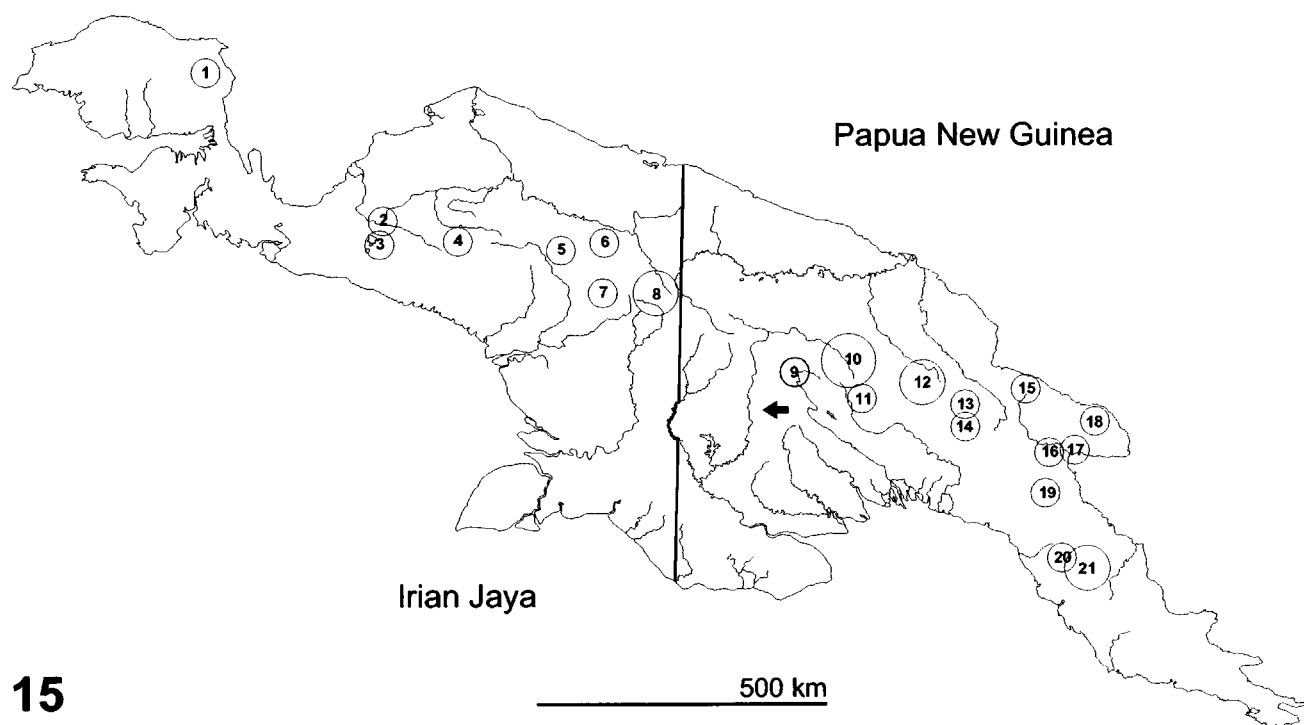
**Tab. 1.** Summary of characters separating the two *Miriamica* species, including both geographical forms of *M. weiskei*. **fw** forewing; **fwl** forewing length to tip of  $R_4$ ; **hw** hindwing. See also text.

	<i>thalassina</i>	dark <i>weiskei</i>	typical <i>weiskei</i>
range male fwl (mm)	30–33	32–40	32–37
mean male fwl (mm)	31.8	35.0	34.3
range female fwl (mm)	32–34	33–43	33–39
pre-apical fw spots	indistinct	sharp	sharp
basal spot fw $R_4$	absent	distinct	distinct
pale basal spot hw $R_5$ (mm)	6.0–8.0	0–5.0	3.5–8.0
base of hw discal cell	pale	dark	intermediate
hw CuP in pale wing area	all pale	all black	base pale
sexual dimorphism	strong	weak	intermediate
hw discal cell length/width (mm)	long, >2.86	short, <2.86	short, <2.86
saccus	narrow	broad	broad

hindwing cross-vein  $m_2$ – $m_3$  is long, not short (58) as in *Parantica* as redefined below.

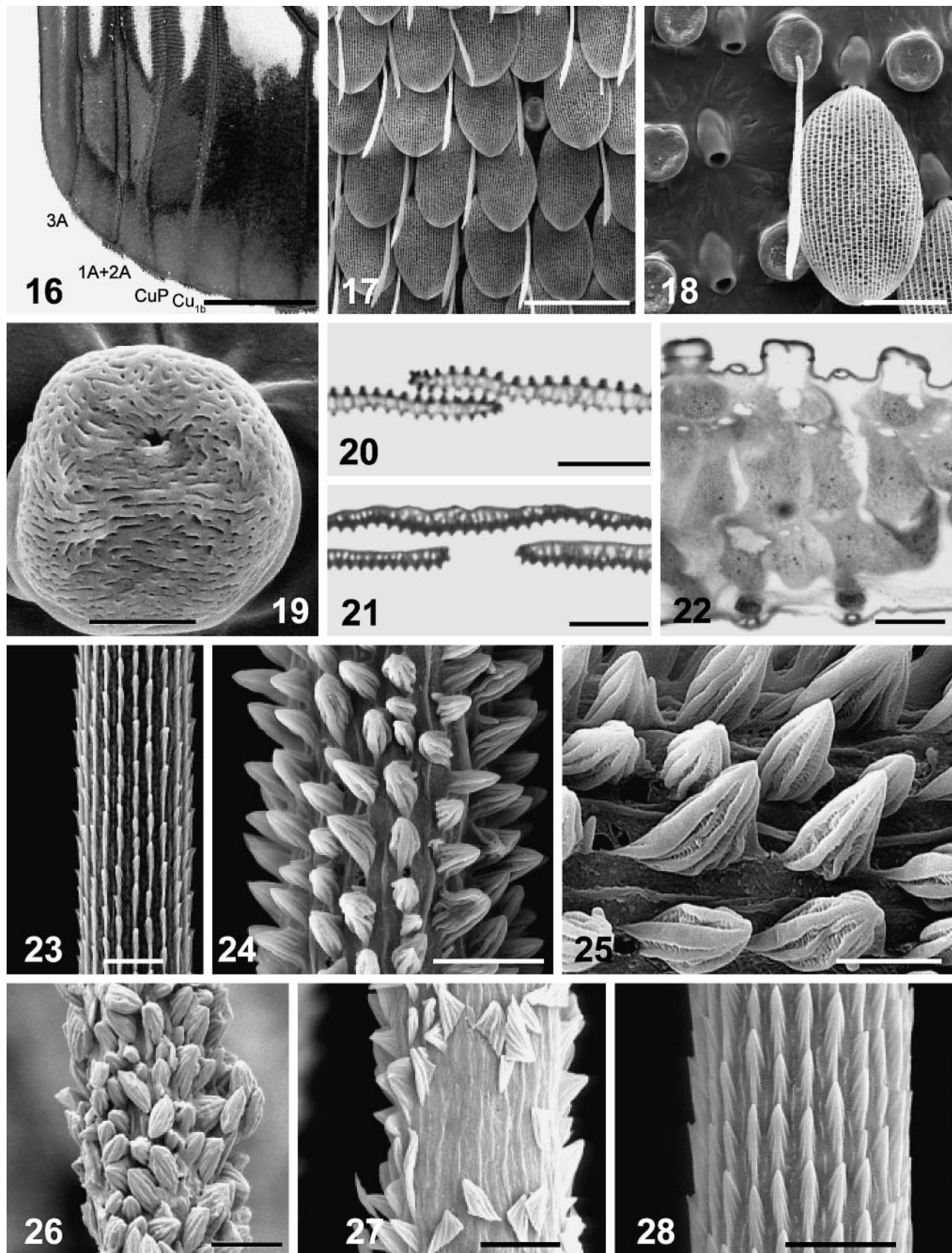
**Bionomics.** According to ACKERY & VANE-WRIGHT (1984: 174) *M. weiskei* occurs in open country and scrub vegetation but, as PARSONS (1991, 1999) indicates, mid to upper-montane primary and secondary forest is the correct biotope. CHEESMAN found *M. weiskei* at puddles on a road at Mt Tafa, and gives illustrations of the “upper mossy forest” biotope (CHEESMAN 1935: figs. 12–15). PARSONS (1991) describes the butterfly as rare on Mt Kaindi (Bulolo-Wau valley), but notes numerous specimens obtained from localities in Eastern Highlands Province of PNG. According to Bernard TURLIN, Andresy, France (in litt. 2000), who came across dark *M. weiskei* in 1997 in forests near Abmisibil (Irian Jaya, close to the PNG border), it is fairly common but usually encountered

singly, flying slowly along rivers, where it settles on wet rocks or even on the water to drink. TURLIN, who did not see it visiting flowers, notes that it can be captured by hand, and is only active from 09.00–13.00 hrs, not flying later in the day. Philip SAWYER, Sunbury, Victoria, Australia (in litt. 1997) confirms that, in PNG, he encountered typical *M. weiskei* “in sunny openings during the morning in primary high altitude rainforest ... I never noticed them visit flowers ...”. Specimens have been collected in all months of the year, at altitudes of 1400–2800 m. Ernst MAYR (1930) collected *M. thalassina* in June 1928 at or near the village of Dohunsehik [Irian Jaya] on the upper Issim river, at 1400 m, which he described as “wonderfully situated in the middle of the mountain forest”, in the vicinity of the Angi Lakes. The type-series of *M. thalassina* was collected by A. C. & F. PRATT at 1800 m, in



**Fig. 15.** Distribution of the genus *Miriamica*, endemic to the island of New Guinea). 1: *M. thalassina* [mountains of Vogelkop, Irian Jaya]; 2–8, ‘dark’ *M. weiskei* [Central Range mountains, Irian Jaya]; 9–21, ‘pale’ or typical *M. weiskei* [mountains of Papua New Guinea]. Bold line: political boundary between Irian Jaya and Papua New Guinea. Arrow: the Strickland River, which may form a natural divide between ‘dark’ and ‘pale’ *weiskei* (see text). The numbers refer to known single (small circles) or grouped localities (larger circles): 1 Hing, Angi Lakes; 2 Dawagu; 3 Enarotali; 4 Sinak, Ilaga; 5 Pass Valley; 6 Pass Valley, Mt Yarken; 7 Langda; 8 Abmisibil Village, Sabin, Sterren Mts; 9 Koroba; 10 Mt Nose, Kandep, Wabag, Porgera, Mariamanda, Enga; 11 Mt Giluwe; 12 Mt Hagen, Kerowagi, Mt Wilhelm; 13 Goroka District; 14 Mt Michael; 15 Finisterre Range; 16 Herzog Mts; 17 Rawlinson Mts; 18 Komba; 19 Mt Kaindi; 20 Loloipa River; 21 Kerau, Kosipe, Mt Tafa, Angabunga River. Data from material in BM(NH) London, NNM Leiden, UM Oxford, Allyn Museum Florida, CSIRO Canberra, Bishop Museum Hawaii, Hyogo Prefectural Museum Japan, Tochigi Prefectural Museum Japan; private collections of B. TURLIN, H. VAN MASTRIGT, S. HASHIMOTO, M. OKANO, P. SAWYER, and the late E. N. ARCHER; information received from H. VAN MASTRIGT, K. MORISHITA, B. TURLIN, C. DAVENPORT, P. SAWYER, and J. TENNENT (all pers. comm.); and published records in GRES-SITT & NADKARNI (1978), ROTHSCHILD (1901), JOICEY & NOAKES (1916), MILLER & MILLER (1978), and PARSONS (1991, 1999). [Map is modified from MapArt® by CARTESIA Software (1994).]





the Arfak Mountains, January–March 1914. The early stages and larval hosts (expected to be Asclepiadaceae or Apocynaceae), as well as any adult attractants, remain unknown.

**Etymology.** *Miriamica* is named in honour of The Honourable Dame Miriam ROTHSCILD, FRS, our dear friend and mentor, to whom we are indebted, both personally and for her profound contributions to biological science. The type-species was originally described by her uncle, Lord Walter ROTHSCILD.

### 3.1.2. Genus *Parantica* Moore, 1880 (Nymphalidae, Danainae, Danaini, Amaurina).

*Parantica* Moore, [1880]

Type-species: *Papilio aglea* Stoll, [1782], by original designation. Details for the generic synonyms *Chittira* Moore, [1880]; *Lintorata* Moore, 1883; *Caduga* Moore, 1883; *Ravadeba* Moore, 1883; *Phirdana* Moore, 1883; *Bahora* Moore, 1883; *Asthipa* Moore, 1883; *Mangalisa* Moore, 1883; *Badacara* Moore, [1890]; *Chlorochropsis* Rothschild, 1892, are given by ACKERY & VANE-WRIGHT (1984: 174).

*Parantica* species (which collectively occur from Pakistan east to Japan and Vanuatu, thus being found throughout most of the Indo-Australian tropics) share all features described above for *Miriamica* except those listed as unique to the latter, including a spinoid eighth sternite, and angled formation of hindwing cross-veins  $m_1$ – $m_2$  and  $m_2$ – $m_3$ . Most male *Parantica* have a distinctly swollen section of vein 1A+2A. The genus *Parantica*, as restricted here, differs from *Miriamica* in having  $m_2$ – $m_3$  short, equal to half or even less than half the length of  $m_1$ – $m_2$  (in *Miriamica*, as in all other Danaini,  $m_2$ – $m_3$  is longer, almost subequal in length to  $m_1$ – $m_2$ ). The androconial organs of *Parantica sita* are described in detail below.

The male genitalia of *Parantica* species differ from *Miriamica* in having the socii well separated. The tegumen is relatively short, and partly projects forward or anterior to the annellus, whereas in *Miriamica* the dorsal part of the annellus is contiguous with the anterior margin of the tegumen.

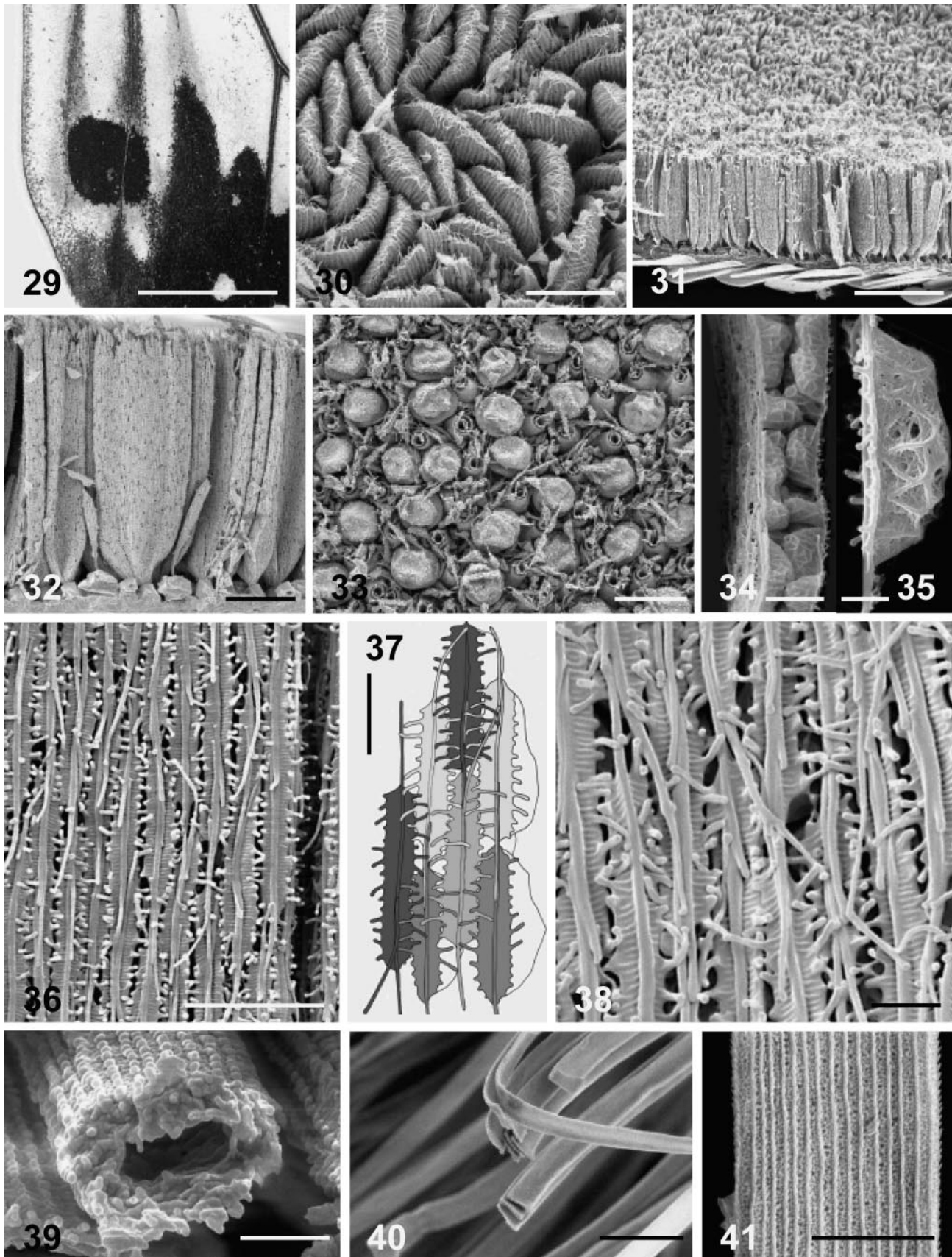
Bionomics: *Parantica* species are found in forested and more open areas, including secondary vegetation and even the margins of cultivated fields; in Hong

Kong one of us observed *P. aglea* (Stoll, 1782) apparently “at home” in an overgrown rubbish dump. Some are lowland species (e.g. *P. vitrina* (Felder & Felder, 1861) in the Philippines), and others range widely from shore lines to mountains (e.g. *P. agleoides* (Felder & Felder, 1860)), but most are typically montane, occurring at lower to middle altitudes in the range 800–2500 m, sometimes as high as 3000 m. Adults visit water, mud and salt, and are frequent at flowers. In Malaysia RIV-W observed male *P. melaneus* (Cramer, 1775) and *P. sita* on *Ageratum* flowers almost throughout the day, presumably sequestering pyrrolizidine alkaloids. In Japan, *P. sita* populations are known to make migrations at the onset of winter, flying 1000 km and more to the south-west. The flight of most *Parantica* species is generally slow and steady, usually within a few metres of the ground, but some apparently fly faster (e.g. *P. albata* Zinken, 1831) and others higher (*P. crowleyi* (Jenner Weir, 1894)). In northern Sulawesi RIV-W noted that the beautiful primrose-yellow mid-montane endemic *P. kuekenthali* (Pagenstecher, 1896) has an unusual “skipping” flight, being observed flying at about 0.5–1 m. above the ground both in coffee forest and in more undisturbed areas. All recorded hostplants belong to the Asclepiadaceae. The known larvae have tubercles on post-cephalic segments 2 and 11 only, and usually bear patterns of yellow and white spots.

### 3.2. Morphology of androconial organs

As *M. weiskei* has until now been included within *Parantica*, and as relatively few detailed investigations of the androconial organs of *Parantica* have been made, we considered it prudent to examine a variety of *Parantica* species. We used SEM to compare representatives of major groups of *Parantica* recognised in the current classification (clades 1111–211, 2121, 2122, 2211, 2212, 2213, 2221, and 2222 of ACKERY & VANE-WRIGHT 1984). We found them all to have a consistent, even monotonous structure, differing microscopically only in minor details of size and shape, and macroscopically in extent of the alar organs. For the purpose of comparison with *Miriamica* and *Amauris*, it is sufficient to record here details of just a single species,

**Figs. 16–28.** Androconia of *Parantica sita*. **16** Hindwing showing androconial patch. **17** SEM of androconial patch of a freshly hatched male showing ‘patch scales’ and ‘cushion scales’. **18** SEM of androconial patch artificially denuded of scales in part, showing a ‘patch scale’, a ‘cushion scale’ several ‘cushions’ and bases of patch scales. **19** SEM of a cushion. **20** LM showing ‘double lattice’ structure of cushion scales. **21** LM of ordinary wing scales. **22** LM of cross section of androconial patch showing glandular origin of cushions. **23–28** SEMs of abdominal hairpencil hairs. **23** ‘marginal hair’; **24–28** ‘particle-budding hairs’. For details see text. Scale bars: 16: 5 mm. 17: 50  $\mu$ m. 18, 22: 20  $\mu$ m. 19, 24, 26–28: 5  $\mu$ m. 20, 21: 10  $\mu$ m. 23: 100  $\mu$ m. 25: 2  $\mu$ m.





*Parantica sita* and to contrast it with *M. weiskei*. In the following, the descriptions of danaine scent organs by BOPPRÉ & VANE-WRIGHT (1989) and their terminology are followed.

### 3.2.1. Morphology of *Parantica sita* androconial organs

**Alar organs.** While readily visible to the naked eye as two 'textured' zones on the upperside hindwing, one to either side of vein 1A+2A, closer examination reveals that the special scales that make up this area extend anteriorly right up to vein  $Cu_{1b}$  and a little beyond, into a very small region of cell  $Cu_{1a}$  (Fig. 16). Along the entire length of the alar organ, vein 1A+2A is greatly thickened, being up to five times the diameter in cross section of a 'normal' wing vein. At the posterior edge of the patch, vein 3A is likewise thickened but less so, being up to three times the diameter of a typical vein, and expanded towards the anterior, alar-organ side only. In the walls of these thickened veins large cells are conspicuous in histological cross sections, suggestive of a glandular or transport function. The track of obsolete vein  $CuP$  passes through the patch and, while there is no vein to be thickened, its path is clearly visible under SEM as a narrow strip devoid of "double-lattice scales" and glandular "cushions" (see below), as is also the case for the surface of veins 3A, 1A+2A and  $Cu_{1b}$  as they cross the alar organ. Unlike 3A and 1A+2A, however, where vein  $Cu_{1b}$  runs adjacent to or through the most anterior part of the organ, it is not noticeably expanded. The overall thickness of the wing membrane is also greatly increased across the whole patch, from about three times the thickness of the normal wing membrane in the anterior section between  $CuP$  and  $Cu_{1b}$ , to nearly 15 times normal thickness between  $CuP$  and 1A+2A, and between 1A+2A and 3A, where it is up to 85  $\mu m$  thick.

Under SEM, viewed from above, all parts of the entire alar organ area look identical, and are extremely similar to *A. niavius* (Linnaeus, 1758) and *A. tartarea* Mabille, 1876. The wing membrane is covered by 'patch scales' and, in fresh specimens only, regular rows of cushion hairs are also evident (Fig. 17). The latter arise from cushions (Figs. 18, 19), and are in general largely or entirely missing from older specimens –

apparently, as in *Amauris*, due to abrasion during contact behaviour (see below). The patch scales arise from ordinary scale sockets, while the cushion hairs arise from the cushions, the two sorts of scales being arrayed in regularly alternating rows (Fig. 18). Overall, these alar organ scales are far more densely packed per unit area than the normal wing-covering scales. In fine structure the patch scales are of the double lattice type, with longitudinal ridges on both upper- and under-surfaces (Fig. 19), typical of the alar organs of most Danaini, and unlike normal wing-covering scales, which have flat, non-ridged under-surfaces (Fig. 20).

Histological investigation of the alar organ in cross-section reveals glandular cells with large nuclei underneath the glandular plates (Fig. 22). In addition, there is a second type of cell, larger than the first one. It might also be glandular, however this could not be fully established with the limited material available.

As in *Amauris*, various species of *Parantica* differ in the dimensions and extent of their alar organs, the size and density of the patch scales, and the length of the cushion hairs. Thus in *P. sita* the patch scales overlap, so that no wing membrane is visible between them, and the cushion hairs exceed the patch scales in length. The minor differences observed (at least in *Amauris*: ACKERY & VANE-WRIGHT 1984) can provide useful taxonomic characters, but it is unknown if they have any functional significance.

**Hairpencils.** While the alar organs of *P. sita* greatly resemble those found in *Amauris* species, the abdominal hairpencils resemble those of *Danaus Kluk*, 1802. The hairpencils are made up by about 1000 hairs, are some 5 mm in total length, and are composed of just two hair types, with the marginal hairs (Fig. 23) surrounding the particle-budding hairs (Figs. 24–28). The particles are inserted on the particle-budding hairs as longitudinal rows of outgrowths, about 16–20 rows per hair, and appear to be elaborated between a corresponding number of low and indistinct longitudinal ribs (Fig. 24). Each particle forms a discrete but contiguous, roughly asymmetrical triangle (reminiscent of a shark tooth in outline), and is lenticular in cross-section, with about five coarse ribs running up from the base on each side, all of which converge and fuse at the

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**Figs. 29–41.** Androconia of *Miriamica weiskei*. **29** Hindwing showing androconial patch. **30** SEM of undisturbed patch from above. **31–32** SEMs of androconial patch cut through to show 'cushions' (c), 'cushion scales' (sc), and 'patch scales' (ps). **33** SEM of patch artificially denuded of scales to show cushions, sockets of patch scales, and fragmented patch scales. **34** SEM of longitudinal section of a patch scale showing alignment of particles. **35** SEM of individual particle. **36, 38** SEMs of patch scales and a sketch to illustrate entanglement of particles in an undisturbed scale (**37**). **38** SEM of broken hairpencil hair at basal part. **39** SEM of flattened hairs. **40** SEM of surface of hair. Scale bars: 29: 5 mm. 30, 33: 20  $\mu m$ . 31: 100  $\mu m$ . 32, 36–39, 41: 5  $\mu m$ . 34, 35: 2.5  $\mu m$ . 40: 50  $\mu m$ .

tip. Between these converging longitudinal ribs, fine cross scutes are visible, other than at the tip zone (Fig. 25). These particles appear to snap off laterally, to leave a smooth surface (Fig. 27). Near the base, as in *Danaus*, detachable particles are not produced (Fig. 28), and here the particle-budding hairs look quite similar to marginal hairs.

### 3.2.2. Morphology of *Miriamica androconial* organs

The descriptions given here are based exclusively on material of *M. weiskei*; superficial examination of *M. thalassina* suggest that it is similar in all respects.

**Alar organs.** On the hindwing upperside, extending from vein 3A to cell  $Cu_{1b}$  (but not reaching  $CuP$ ), there is a deep black, felt-like, roughly circular patch about 3 mm in diameter (Fig. 29). Where this patch crosses 1A+2A, the vein is perhaps very slightly swollen. This alar organ is characterized by its densely packed (Fig. 30), upright scales, standing 100  $\mu$ m above the wing surface (Fig. 31). In comparison to the other genera of subtribe Amaurina, the patch is located in a grossly similar position to the alar organs of *Amauris* and *Parantica* (cf. Fig. 16), but *Ideopsis* lacks such a discrete patch and has, instead, a diffuse androconial zone extending over the entire anal area of the wing (ACKERY & VANE-WRIGHT 1984)

The fine structure of the alar organ of *M. weiskei* resembles *Amauris* and *Parantica* insofar as the zone is clothed in patch and cushion scales, arising from typical scale sockets and cushions, respectively. While the individual cushions and cushion scales (Figs. 32, 33) are essentially the same as in *Amauris* and *Parantica*, atypically they do not form a regular, alternate array with the patch scales, even though both scale types occur in roughly equal numbers (Fig. 33). However, it is the patch scales which differ so markedly and make this alar organ unique. Each patch scale has a long, wide and flat blade (Fig. 32). The lateral surface (Fig. 34), on both sides, presents an unusual pattern of interrupted, flanged, longitudinal ribs interconnected by short side stalks, representing modified longitudinal ridges and transverse crossribs, respectively, of the basic lepidopteran scale (DOWNEY & ALLYN 1975; GHIRADELLA 1998). The flanges bear fine microribs or flutes (Fig. 38) typical of longitudinal ridges. Adjacent rows of crossribs interlock like a zip-fastener (Fig. 37). At some places one or more crossribs, instead of interlocking with ribs opposite, hook over the lamella running along the crest of an adjacent longitudinal ridge ("scute" in the nomenclature of DOWNEY & ALLYN 1975: 19). These crossrib connections are readily disengaged, permitting the entire scale to break up into very numerous fusiform particles, each of which typi-

cally retains a piece of the ridge-lamella projecting from each end, rather like a stick, as well as some crossribs (Figs. 35, 37). The lateral and lower surfaces of each particle show a rough lattice of polygonal ridges with numerous holes, to give a sponge-like appearance (Fig. 35).

From cross and longitudinal sections, it is evident that the particles are bulbous outgrowths that arise from beneath the longitudinal ridges on both sides of each scale, packing the entire lumen closely, even if somewhat irregularly, to form a double layer (Fig. 34). Possibly the particles represent modified trabeculae of the typical scale. Despite the fact that patch scales are readily abraded to form flocculent masses of particles, in practically all material examined the alar patches are entire. In a few specimens the patch scales have been disturbed, but in all such cases most plausibly due to post-mortem damage (e.g., abrasion during setting).

**Hairpencils.** The hairpencils of *M. weiskei*, which are about 5 mm in total length, differ from other Danainae by the inclusion of extremely flattened hairs in addition to 'ordinary' round ones. The latter form a central bundle (made of about 450 hairs) arising near the hair-pencil base, while those of the flattened type arise further up the sheath and surround the round hairs. In contrast to other Danainae, the hairpencils of *Miriamica* are difficult to study from dried specimens. The outer, flattened scales at their bases are also thick-walled and rounded (Fig. 39), with a normal ridged and punctured surface (Fig. 40). Only beyond the base do they become flattened, but the surface structure remains much the same (Fig. 41). Unlike other hairpencils, these ribbon-like hairs appear to be pliable, and probably insufficiently rigid to abrade or sweep-up particles from the alar organs, were they applied to them. The fact that all of the numerous male *Miriamica* so far investigated have their alar organs entire, with the „particles“ undisturbed, suggests that they are not subject to any form of interaction from the hairpencils – or that, if they are, it serves a different function to that seen in *Tirumala*.

## 4. DISCUSSION

### 4.1. Classification of *Miriamica* within the Danainae

We believe that separation of *M. weiskei* and *M. thalassina* from *Parantica* is justified, to form a twelfth genus of the Danainae. ACKERY & VANE-WRIGHT (1985) and KITCHING et al. (1993) indicated that, although interrelationships remained uncertain, the eleven genera of Danainae then recognised were

almost certainly monophyletic groups. Even so, inclusion of *M. weiskei* within *Parantica* rendered this the least secure genus. Exclusion of *M. weiskei* and *M. thalassina* makes *Parantica* homogeneous with respect to its main distinguishing features, including those of the androconial system. Even if *Parantica* and *Miriamica* continue to be treated as sister groups, this distinction would remain valid.

However, it may not be correct to assume that *Miriamica* and *Parantica* have a sister-group relationship. As noted by ACKERY & VANE-WRIGHT (1984), *Miriamica* shares some weak characters with *Ideopsis* (such as a broad saccus in *M. weiskei* – but this is not a feature of *M. thalassina*), and perhaps other features with *Amauris* (e.g. fused socii). The different relative lengths of hindwing cross-veins  $m_1$ – $m_2$  and  $m_2$ – $m_3$  in *Parantica* and *Miriamica* could indicate that the peculiarity of their angled configuration may only be an analogous, not homologous condition in the two genera. *Miriamica* might ultimately prove to have a wholly novel relationship, such as sister to (*Parantica* + *Ideopsis*) for example, or even *Amauris*. The similar form of the tegumen/annellus in *Parantica* and *Ideopsis*, in sharp contrast to *Miriamica*, suggests, for example, that a sister relationship between the first two is quite plausible. The generic interrelationships of the Danainae could now usefully be pursued using molecular sequencing techniques. Only an unlikely result, such as *M. weiskei* clustering within *Parantica* or *Ideopsis*, would question the generic status of *Miriamica*. At present we consider it most reasonable to place *Miriamica*, *Ideopsis* and *Parantica* in an unresolved trichotomy, as the sister-group to *Amauris*. However, even the grouping of *Miriamica* with these three genera to form the Amaurina must be open to some doubt, as this putative grouping is currently based on a single apomorphy, the spinoid male eighth sternite. Contra ACKERY & VANE-WRIGHT (1984), this character is not clearly seen in *Miriamica* (see 3.1.1 above). An additional synapomorphy could be the position of the male hindwing alar organs, posterior to the cubital veins. This location is unique to all four genera, but it seems unlikely that the alar organs of *Ideopsis*, *Parantica*, *Amauris* and *Miriamica* are all homologous.

#### 4.2. Peculiarities of *Miriamica* androconial organs

Existing knowledge of danaine morphology and biology might suggest that the patch scales of *Miriamica* produce pheromone-transfer-particles (PTPs) in a previously unknown manner. According to BOPPRÉ & VANE-WRIGHT (1989), PTPs in Danainae are made by abdominal hairpencils in three different ways: as outgrowths of longitudinal ridges in *Danaus* hairpencil

hairs, through disintegration of ‘long white hairs’ in *Amauris* subgenus *Amaura*, and by longitudinal fracturing of ‘particle-producing hairs’ in *Amauris* subgenus *Amauris*. In *Tirumala*, PTPs are produced by another, fourth method, through fragmentation of alar cushion scales. The fragmentation of alar patch scales in *Miriamica* would then represent a fifth mode, comparable to *Tirumala* in being produced on the wings rather than in the abdominal hairpencils, although their non-homology seems certain: modification of cushion scales in *Tirumala* versus modification of double-lattice patch scales in *Miriamica*, and the striking differences in particle ultrastructure. Moreover, while in *Miriamica* the particle-forming scales occur on an open patch, the PTPs of *Tirumala* are formed and stored inside a cubital pouch forming a protective reservoir for the PTPs, potentially enabling a male to recharge his hairpencils on a number of occasions. In *Danaus*, *Amauris* and *Parantica*, in which PTPs are produced in the hairpencils, males presumably are more at risk of losing all or most of their PTPs in their first bout of courtship, and this may be evident in the fact that male *Tirumala* and *Euploea* (the latter do not employ particles at all) readily exert their hairpencils when handled (likely as a predator-alerting signal), whereas *Danaus*, *Amauris*, *Parantica*, and *Miriamica* seem unwilling to do so. For *Miriamica*, Bernard TURLIN, Andresy, France (in litt. 2000) recalls that “... *weiskei* does not extrude hairpencils when seized by fingers.”

A great puzzle lies in the ‘contact behaviour’, i.e. the mechanical contacts made between abdominal and alar organs, and which is well known for *Danaus*, *Tirumala* and *Amauris* (BOPPRÉ & VANE-WRIGHT 1989). For *Parantica agleoides* (Felder & Felder, 1860), a single report is available: LAMBORN (1922) observed a male passing the unexpanded hairpencils over the patches at about a rate of twenty strokes per minute, after curving the abdomen to bring the hairpencils in line with the patches. If this singular record is typical for *Parantica*, it reflects a fundamental difference to the contact behaviour of *Amauris*, in which a special hair type (“lateral hair”) is fanned out and rubbed over the patches. Indeed, in *P. sita* we found no such specialized hair but an arrangement as seen in *Danaus*, which inserts its hairpencils unexpanded into the alar pockets. In addition, the loss of cushion scales observed in field-caught *Parantica* is explicable from LAMBORN’S observation.

According to our present understanding of PTP-use in Danaini, they are distributed by the male hairpencils onto the female antennae during courtship. In *Tirumala*, before this can happen, the wing-produced PTPs must be transferred to the hairpencils by contact behaviour, involving pre-courtship insertion of the

everted but still unexpanded hairpencils directly into the wing pouch cavities in which the PTPs are generated (cf. above). What of *Miriamica* with regard to use of their apparently abundant particles? Unfortunately the scant available observations of the living insects offer no insights. However, it is difficult to imagine how the abdominal hairpencils of *Miriamica* could effectively and efficiently take up the particles that have first to be abraded from the open wing patch. The fact that the patches of all 80 field-caught males that we could check appear 'untouched' suggests that the particles of *Miriamica* are unlikely to be functionally comparable to the PTPs of other danaines, i.e. deposited on the female antennae. Conceivably the known glandular nature of the cushions, which are outwardly identical in *Miriamica* to other Danaini, coupled with the massive adsorptive volume offered by the patch scales, indicates that the alar organs are a primary source of male pheromones in *Miriamica*, perhaps produced during development in the pupa and stored in the patch scales? Then, this massive sponge could release pheromonal signals more or less continuously. Only such an interpretation, while entirely speculative (and thus in the best tradition of our mentor), might explain the intact condition of the alar organs in so many museum specimens.

## 5. CONCLUSIONS

The modifications of the androconial organs of *Miriamica* are unique. However, the unknown function of the peculiar *Miriamica* patch scales, as well the flattened hairpencil hairs, simply serve to remind us that the function of the patches in *Amauris* and *Euploea* Fabricius, 1807, are equally not understood, any more than they are in *Parantica*. Contact behaviour between the alar organs and hairpencils in *Danaus* and *Tirumala* is at least known to be essential for dihydropyrolizine synthesis in 'normal' amounts (BOPPRÉ et al. 1978; and unpublished), and in *Tirumala* it is evident that there is the additional function to gather PTPs from the wing organs for later distribution (see above). More detailed studies would be rewarding, but it must be appreciated that obtaining and maintaining suitable living material for laboratory investigations is not easy. The diversity of androconial organs within the Danainae remains a great challenge for chemical and behavioural ecology. Thus another New Guinea region danainae genus, *Tiradelphe* Ackery & Vane-Wright, 1984, remains a complete mystery regarding its complement of male scent organs. Still only known from two females collected on Guadalcanal in the Solomon Islands (see TENNENT 1998), it is anticipated that discovery of the male will not only offer insight into the

evolution of chemical communication within these butterflies, but will also provide extremely valuable information for systematics and higher classification (VANE-WRIGHT & BOPPRÉ 1984). In the present case, our studies of the androconial organs of *weiskei* have convinced us that this species, and its close relative *thalassina*, require erection of a new genus to receive them, separate from *Parantica*. Indeed, in carrying this investigation through, it has become apparent that the classification of *Miriamica*, in relation to all other members of the Amaurina or even the Danaini, remains open to further re-investigation.

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