Reconsideration of the taxonomy of the *Ropalidia malayana*complex (Hymenoptera: Vespidae: Polistinae)

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Key words: Hymenoptera; Polistinae; Vespidae; Ropalidia malayana; Southeast Asia.

The taxonomy of the *Ropalidia malayana*-complex is reconsidered after studying mainly the specimens examined by van der Vecht (1941, 1962) and housed in the Nationaal Natuurhistorisch Museum, Leiden. The complex is shown to consist of three species: *R. malayana* (Cameron, 1903) [= *R. parvimaculata* (Cameron, 1907), = *R. delicata* Dover, 1931], *R. erythrospila* (Cameron, 1908) and *R. pseudomalayana* spec. nov. The last species is described from Borneo.

Introduction

The Ropalidia malayana-complex, or R. malayana (Cameron, 1903) and its closely allied "species", is of potential interest in the studies on the evolution of social behaviour in paper wasps because they are among a small number of social wasp species that make unenveloped nests in open spaces and are suggested to found a colony by a swarm of wasps (van der Vecht, 1962): most swarm-founding species make enveloped nests or nest in preformed cavities, preventing us from observation of wasp behaviour. However, the taxonomy of the R. malayana-complex is not yet established sufficiently, as shown below, to provide a taxonomic basis for studies of the social behaviour or social structure.

The Ropalidia malayana-complex comprises four "species" so far described (van der Vecht, 1941): Icaria malayana Cameron, 1903, I. parvimaculata Cameron, 1907, I. erythrospila Cameron, 1908, and Ropalidia delicata Dover, 1931. Their distributions are confined to Southeast Asia. Van der Vecht (1941: 174) synonymized R. delicata with R. malayana and treated the remaining two "species" of Cameron as varieties of R. malayana (van der Vecht, 1941: 176). He confirmed this view in his 1962 paper (van der Vecht, 1962: 34) stating that "although the inhabitants of a single nest appear to be rather uniformly coloured, additional material of this species confirms the previously expressed view, that the colour phases are not sharply separated." He also recorded specimens showing transitional colourations.

Richards (1978: 57), in his list of *Ropalidia* species, regarded *R. erythrospila* as a valid species, although he treated it as a subspecies of *R. malayana* in the note on nests in the same paper (1978: 54). Kojima & Yamane (1984: 104), following the view of Richards (1978: 57), treated *erythrospila* as a valid species when they described the larvae. Kojima & Yamane (1990: 36) pointed out the possibility that *R. malayana* in the sense of van der Vecht (1941, 1962) comprises more than one species, but tentatively treated *parvimaculata* as a variety of *R. malayana*. On the other hand, Gusenleitner

(1996: 18) treated *parvimaculata* as a subspecies of *R. malayana* when he compared it with his new species, *R. vietnama* Gusenleitner, 1996.

The grounds for these changes in taxonomy, however, were not mentioned by any of these authors except van der Vecht (1941, 1962).

In the course of the taxonomic and phylogenetic studies on Asian and Papua-Australian species of *Ropalidia*, I reached a taxonomic conclusion different from that of either van der Vecht (1941, 1962) or Richards (1978: 57) as described below.

Specimens examined in this study are housed in the Nationaal Natuurhistorisch Museum, Leiden (indicated as "RMNH" for type material) unless otherwise noted. Other institutions where specimens are harboured are abbreviated as follows: BISH, Bernice P. Bishop Museum, Honolulu; BMNH, the Natural History Museum, London; IUNH, Natural History Laboratory, Ibaraki University, Mito; SAM, South Australian Museum, Adelaide; ZMA, Zoologisch Museum, Amsterdam.

Characters defining the Ropalidia malayana-complex

According to the key and descriptions by van der Vecht (1941), the Ropalidia malayana-complex is defined by the following characters as far as the species in the subgenus "Anthreneida" sensu van der Vecht (1962) are considered: (1) the mesepisternum with a raised carina bordering the coarsely punctured posterodorsal area and unpunctured, smooth anteroventral area, (2) the first metasomal tergum in profile gradually swollen posteriorly, (3) the first metasomal segment short, and wider than long, and (4) the second metasomal segment rather coarsely and rugosely punctured. Adding the presence of three submarginal cells to the characters mentioned above, the R. malayana-complex may be defined even if all the Ropalidia species are taken into consideration. Another character that should be added to define the R. malayanacomplex in the phylogenetic sense is the twisted mandibles. That is, the mandibles are twisted so that all teeth are in the same plane as that of the clypeus when the mandibles are opened (figs 1, 8-13, 18). Van der Vecht's (1941: 174) description that the "lower margin of the mandible [is] slightly emarginate at the base" seems to correspond to this state. Dover (1931) described it as "mandibles long and very sharply pointed". Although neither van der Vecht (1941, 1962) nor Richards (1978) referred to it, the twisted mandibles are found also in two other Oriental species, R. binghami van der Vecht, 1941 and R. pilosa (Smith, 1858), and in several Papua-Australian species in the subgenera "Icarielia Dalla Torre, 1904" and "Icariela Dalla Torre, 1904" sensu Richards (1978), such as R. ("Icarielia") festina (Smith, 1865), R. ("Icarielia") bensoni Richards, 1978, R. ("Icariola") mackayensis Richards, 1978, and R. ("Icariola") kurandae Richards, 1978. Although R. binghami + R. pilosa and the Papua-Australian species each seem to form a natural group, it is not yet clear whether they form together with the R. malayana-complex a larger natural group or not.

Descriptions

Ropalidia malayana (Cameron, 1903) (figs 1-2, 5, 7-9, 14-15, 18-19, 21, 26-27)

Icaria malayana Cameron, 1903: 171.

Ropalidia malayana typical form; van der Vecht, 1941: 174-176 [partim]; 1962: 34. Icaria parvimaculata Cameron, 1907: 25. Syn. nov. Ropalidia malayana var. parvimaculata; van der Vecht, 1941: 176; 1962: 34. Ropalidia delicata Dover, 1931: 257. Syn. by van der Vecht (1941: 104).

Material (specimens listed under "R. malayana typical form" and "R. malayana var. parvimaculata" by van der Vecht are indicated with asterisks and double-asterisks, respectively).--- Borneo: holotype of Icaria malayana Cameron, 9 (BMNH), labelled "Type" [circled with orange], "Lungga Nov. 1897.99", "Icaria malayana Cam. Type, Borneo" [in Cameron's handwriting], "P. Cameron coll. 1914-110", "Ropalidia malayana Cam.", "J. S. B. A. Soc. p.171-2, 1903", and "B. M. Type HYM 18.842"; holotype of Icaria paroimaculata Cameron, Q (BMNH), labelled "Type" [circled with red], "Marup JH, May 1906", "Icaria parvimaculata Cam. Type, Borneo" [in Cameron's handwriting], "P. Cameron coll. 1914-110", and "B. M. Type HYM 18.844"; 1 9 (BISH), Tawau Residency, Kalabakan R., Tawau 30 mi west, 9-18.xi.1958, L.W. Quate; 19, SE Sabah nr. Danum Valley, Field C, Malaise trap 10, c. 150 m, 15-19.iii.1987, C. v.Achterberg; 19, same data but 20-22.xi.1987; 399, same data but Malaise trap 6; **19, Sarawak, foot of Mt. Dulit, Janction of rives Tinjar & Lejok, 22.viii.1932, Oxford Univ. Exp. B.M. Hoby & A.W. Moore; **1 9, same data but 11.x.1932; **1 9, same data but 9.x.1932; **1 9, Sarawak, R. Kapah Trib., of R. Tinjah, 9.x.1932, Oxford Univ. Exp. B.M. Hoby & A.W. Moore; *1 9, Palawan Besar, vi.1937, M.E. Walsh; 19, same data but v.1937; **19, Bettotan nr. Sandakan, 26.vii.1927; **19, same data but 16.viii.1927; **1 9, same data but 19.viii.1927; 69 9, Sibau I., 6.vii.1894, Butlikoper; **1 9, Pajan River, xi.1925, Eric Mjaberg; *1 º, Pemantas Sampis Riv., alt. 100 m, vii.1953, M.A. Lieftinck; 1 º, Tabang, Bengen River, 20.viii.1956, A.M.R. Wegner; **29 9, Balikpapan, Mentawir River, x.[19]50, A.M.R. Wegner. Peninsular Malaysia: holotype of Ropalidia delicata Dover, 9 (BMNH), labelled "Type" [circled with red], "Malay Penin.: Pahang, F. M. S. Kuala Lipis, Bencha Forest Res. May 28th 1926, H. M. Pendlebury", "Ropalidia delicata Dover, Holotype 9 1926", "Ropalidia malayana var. delicata Dover", and "B.M.Type HYM 18.843"; 19, S. Kedah, Bading, Badenoch Estate, 21.ii.1963, M.A. Lieftinck; **19, Selangor, Bukit Kutu, 3300 ft. 28.ix.[19]30, H.M. Pendlebury; *19, Perak, Larut Hills, 3700-4000 ft. 10.ii.1932, H.M. Pendlebury; *1º, Kelantan. Sumatra: 1º, Padangpanjang, 800 m, 0°30'S, 10°26'E, 1.v.1988, R. Hensen; *2 & &, Toba-meer, B. Hagen; *1 &, Sibolangit, 8.x.1925, Fulmek & Karny.

Female.— Head in front nearly 1.2 times as wide as high (fig. 1), distinctly wider than mesosoma including tegulae; in dorsal view broadly emarginate posteriorly, with lateral sides behind eyes rather strongly convex and strongly converging in posterior half (fig. 5). Gena in profile nearly as wide as eye (figs 2, 41). Occipital carina complete, fine; in profile running down obliquely in nearly straight line below the level of one-fourth of eye from below. Distance between inner eye margins about 1.1 times wider at level of vertex than at level of clypeus (fig. 1). Ocelli arranged in nearly equilateral triangle, posterior ocelli about 2.5 times further from inner margin of eye than each other, the latter distance about 1.5 times as large as the diameter of posterior ocellus; distance between posterior ocellus and inner eye margin about the same as that from posterior ocellus to occiput (or to occipital carina). Clypeus convex, with rather acute apex, transverse, about 1.5 times as wide (measured as a distance between the uppermost points where clypeus touches eyes) as high (measured from the bottom of dorsal emargination to the apex), touching eye for a length about equal to diameter of antennal socket. Mandible twisted, all teeth nearly flat, hardly curved inwards (figs 8-9); ventral tooth elongate, about 1.5 times as long as the third. Antenna short, swollen apically (fig. 7); third segment about twice as long as wide at apex, nearly as long as fourth and fifth segments combined; fourth segment rectangle in outline; fifth wider than long; each of sixth to eleventh segments distinctly wider than long, tenth segment about 1.5 times as wide as long; terminal segment bullet shaped, about as long as wide at base.



Figs 1-17, characters of \mathfrak{P} of the *Ropalidia malayana*-complex. Fig. 1-6, head in front (1), profile (2-4) and dorsal view (5-6); fig. 7, right antenna; figs 8-13, left mandible in front (8, 10, 12) and ventral view (9, 11, 13); figs 14-17, first and second metasomal segments in lateral view. Figs 1-2, 5, 7-9, 14-15, R. malayana (Cameron); figs 3, 10-11, 16, *R. erythrospila* (Cameron); figs 4, 6, 12-13, 17, *R. pseudomalayana* spec. nov.

Mesosoma in dorsal view about 1.5 times as long as wide. Pronotum in dorsal view broadly rounded anteriorly, with lateral sides slighty convex and weakly diverging posteriorly; pronotal carina complete, sharply raised, reaching close to the ventral corner of pronotum, hardly sinuate laterally. Scutum weakly convex, wider than long. Disk of scutellum trapezoid, convex, with ill-defined median depressed

line. Disk of metanotum margined laterally with sharp truncation. Propodeum in dorsal view with lateral sides broadly rounded; in profile its posterior face slightly convex; median concavity rather deep, nearly oval in outline; propodeal valvula small, rounded triangle in outline, in profile hardly covering propodeal tooth; propodeal orifice rounded above, hardly narrowed dorsally, about twice as long as wide. Wing venation rather variable, but vein 3r-m as a rule not strongly sinuate proximally in its posterior half; basal angle of second submarginal cell slightly larger than 90° (cf. figs 24-25).

Metasoma short (figs 14-15); first segment short, wider (measured at the posterior margin) than long (measured as a distance between the posterior end of reception of propodeal muscle and posterodorsal end of the tergum in profile); in profile dorsal face of tergum gradually rising from the posterior end of reception of propodeal muscle, then evenly curved (fig. 26); in dorsal view, strongly widening after a short basal parallel-sided part, the maximum width about three times as wide as its basal parallel-sided part (fig. 27); ventral margins of tergum beneath only slightly approching each other before they diverge posteriorly; posterior flattened triangle of first sternum wider than long, deeply emerginate posteriorly. Second segment wider than long, and wider than high; tergum slightly swollen near the posterior margin, so that the dorsal surface in profile looks to be slightly concave near the posterior margin (figs 14-15); apical lamella strongly depressed; articulation of tergum margined posteriorly by prominent truncation, truncation sharper laterally than medially; suture between tergum and sternum fine, almost disappearing posteriorly.

Body, except clypeus, covered with appressed, fine, silvary tomentum; suberect setae less densely covering body, setae rather long on clypeus, propodeum and first metasomal tergum; eye bare. Clypeus polished, and with scattered, superficial punctures. Frons, vertex, pronotum, scutum, scutellum with dense, well defined punctures, each of which possesses a central postule; punctures on gena less dense than those on vertex. Anterior part of metanotum with punctures similar to those on scutellum, posterior part unpunctured and polished. Posterior part of mesepisternum densely covered with punctures similar to those on pronotum, anterior part unpunctured; border between them sharp, often raised into fine carina. Metapleura with scattered, small, shallow punctures, usually with several striae dorsally. Posterior concavity of propodeum shining, hardly sculptured; outer surface of propodeum with oblique striae and irregular punctures between striae. First metasomal segment with scattered shallow punctures anteriorly; posteriorly with dense punctures similar to those on pronotum. Second segment densely covered with large punctures, each of which is ill-defined in posterior margin; punctures slightly less dense on sternum than on tergum. Following segments with punctures similar to those near posterior margin of first tergum.

Body black; mandible, clypeus, antenna and legs dark brown; scape, tibia and tarsi sometimes brown or ferruginous; pronotum sometimes ferruginous; metasoma sometimes dark ferruginous. Following parts yellow: spot on fore coxa (often absent), small spot at base of mandible, paired lateral spots on clypeus (varying greatly in size and only sometimes absent), short and narrow line at inner orbit (often absent), short and narrow median band on pronotal carina (sometimes absent or much wider to occupy most dorsal part of pronotum), paired spots on scutellum



Figs 18-21, characters of 3 of the *Ropalidia malayana*-complex; figs 22-25, characters of 9 of *R. pseudoma-layana* spec. nov. Fig. 18-20, head in front (18) and profile (19-20); fig. 21 right antenna; fig. 22, propodeal tooth and propodeal valvula, lateral view; fig. 23, propodeal orifice; figs 24-25, part of left fore wing, showing submarginal cells. Figs 18-19, 21, *R. malayana* (Cameron); fig. 20, *R. erythrospila* (Cameron).

and metanotum (sometimes absent, but sometimes large and united to form wide anterior bands which are usually associated with posterior parts of these segments coloured ferruginous), paired spots on posterior face of propodeum (varying in size and sometimes absent); apical band on first and second metasomal segment (often absent), apical bands on third to sixth terga (often absent).

Length (of head + mesosoma + first and second metasomal segments) 5.5-6.5 mm.

Male.— Similar to female, but eyes more strongly swollen laterally; inner eye margins more strongly convergent below, distance between them nearly 1.3 times more at vertex than at level of clypeus (fig. 18); clypeus less transverse, about 1.3 times as wide as high; gena relatively narrower, in profile about 0.45 times as wide as

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eye (fig. 19); terminal antennal segment short, as long as wide at base (fig. 21); third to terminal antennal segments with weak tyloids.

Yellow markings generally more developed than in female; spots on clypeus larger, often nearly coalescent at their ventral margins.

Length (of head + mesosoma + first and second metasomal segments) 5.5-6 mm.

Ropalidia erythrospila (Cameron, 1908) (figs 3, 10-11, 16, 20, 29-33)

Icaria erythrospila Cameron, 1908: 563. Ropalidia erythrospila; Dover, 1931: 257. Ropalidia malayana var. erythrospila; van der Vecht, 1941: 176; 1962: 34.

Material.— Borneo: holotype, \Im (BMNH), labelled "Type" [circled with orange], "Kuching, Sep. 06 JH", "*Icaria erythrospila* Cam. Type Borneo" [in Cameron's handwriting], "H.2.0", "P. Cameron coll. 1914-110", and "B. M. Type HYM 18.854"; 1 \Im , Sarawak, 20.ix-5.x.1950, M.A. Lieftinck; 3 \Im \Im , Forest Camp, 19 km N. of Kalabakan, 30.xi.1962, K.J. Kuncheria; 1 \Im , Tabang, Bengen River, 23.viii.1956, A.M.R. Wegner; 1 \Im , Bettotan nr. Sandakan, 15.viii.1927. Thailand: 2 \Im \Im , 27 km SW Hat Yai, Ton Nga Chang N. P., 6°54'N, 100°21'E, 24.vii.1986, R. Hensen. Peninsula Malaysia: 1 \Im , Kuala Lumpur, 24.viii.1933, H.M. Pendlebury; 1 \Im , same data but 10.vii.1932; 1 \Im , same data but 12.vii.1922; 1 \Im , Sel. Museum, nr. L. Gardens, ii.1935, H.M. Pendlebury; 1 \Im , same data but 8.xii.1935; 1 \Im (SAM), Penang, Lea & Party; 1 Υ (ZMA), Penang, Batu Feringghi, 11-24.ii.1984, R.T. Simon Thomas. Sumatra: 1 \Im , Padangpanjang, 800 m, 0°30'S, 100°26'E, i.v.1988, R. Hensen; 1 \Im , Padang, ix.[18]91, E. Jacobson; 7 \Im \Im + 1 \Im , Bengkulen [= Bengkulu], vii.1916, E. Jacobson; 1 \Im , coll. Gribodo; 2 \Im \Im (ZMA), Padang, ix.1918, Leefmans.

Female.— Structurally similar to female of *R. malayana*, but distinguished from the latter as follows: head in dorsal view with lateral sides behind eyes much less convex, converging posteriorly from the posterior margins of eyes; gena proportionally narrower, in profile about 0.75 times as wide as eye (figs 3, 41); mandibular teeth slightly curved inwards (fig. 11), ventral tooth relatively shorter, only slightly longer than the third (fig. 10). Shape of the first metasomal tergum rather variable (figs 29-33), but dorsal face in profile tending to be slightly more convex than in *R. malayana*; second metasomal tergum hardly swollen near the apical margin, thus dorsal face in profile nearly flat in its posterior half (fig. 16).

Body black; mandibles, clypeus and antenna dark brown. Following parts reddish-brown: pronotum (sometimes with median yellow band along posterior margin), scutum usually entirely (but sometimes black anteriorly or entirely black), scutellum and metanotum (sometimes nearly entirely dark yellow, with reddish-brown posterior margins), propodeum (often black on lateral sides or entirely black), scrobal spot (often absent). Yellow markings as follows: spot at base of mandible, paired lateral spots on clypeus, usually confined to ventral half, ventral surface of antennal scape (often reduced or absent), short and narrow line at inner orbit, apical band on first metasomal tergum (usually absent), apical band on second metasomal segment, narrow apical band on third tergum (often absent). Legs ferruginous; tibia and tarsi often yellowish orange; fore coxa sometimes with yellow spot.

Length (of head + mesosoma + first and second metasomal segments) 5-6 mm.

Male.— Structurally similar to male of R. malayana, but gena proportionally nar-



Figs 26-40, first metasomal tergum of \Im of the *R. malayana*-complex. Figs. 26, 29-39, lateral view; figs 27-28, 40, dorsal view (perpendicular to the dorsal face of posterior widened part). Figs 26-27, *R. malayana* (Cameron); figs 28, 34-40, *R. pseudomalayana* spec. nov. (37-40, females from a single nest); figs 29-33, *R. erythrospila* (Cameron).

rower (fig. 20), in profile about 0.4 times as wide as eye; ventral tooth of mandible relatively shorter. Colouration as in the conspecific female, but yellow markings, especially spots on clypeus, more developed.

Length (of head + mesosoma + first and second metasomal segments) 6 mm.

Ropalidia pseudomalayana spec. nov. (figs 4, 6, 12-13, 17, 22-25, 28, 34-40)

Ropalidia malayana; van der Vecht, 1941: 174-176 [partim]; 1962: 34 [partim].

Material (specimens listed under "*R. malayana* typical form" by van der Vecht (1941, 1962) are indicated with asterisks).— **Borneo**: holotype, ♀ (RMNH), labelled "Borneo: Sarawak, Sarikei Dist., Rejang Delta, 15-26.vii.1958" and "Museum Leiden *Ropalidia malayana* (Cam.) det. J. v.d.Vecht 1979" + paratypes, 9♀♀ (RMNH), same data as the holotype; 1♀ (IUNH), same data as the holotype (metasoma

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detached and glued on the label); 1 °, Shelfond Reg., 21.vii.[19]03; *1 °, E. Borneo, Tabang, Bengen River, 125 m, 23.viii.1956, Wegner. **Bangka**: *13 ° °, Troe, 3.xii.1935, J. v.d.Vecht (including 4 ° ° from a single colony, "nest 4").

Female.— Structure very similar to *R. erythrospila*. Shape of first metasomal tergum rather variable even among specimens from the same colony (figs 37-38), but in general proportionally higher (figs 34-38) and wider than in *R. erythrospila*; the latter values almost overlapping between the two species (fig. 42). One female from the colony "nest 4" has an abnormally flattened and widened first metasomal segment (figs 39-40).

Body black; antenna dark ferruginous; scape, second and third antennal segments paler; scutum reddish brown at posterior margin, but sometimes almost entirely reddish-brown or entirely black. Following parts yellow: spot at base of mandible (usually larger than in the former two species), short and narrow line at inner orbit, paired lateral spots on clypeus, antennal scape below (sometimes entirely ferruginous), pronotum (often ferruginous in ventral part), scrobal spot (often absent or sometimes replaced with ferruginous), entire surface of disks of scutellum and metanotum (lateral depressions of these segments usually ferruginous), paired large spots on posterior face of propodeum (space between spots often ferruginous), apical bands on first metasomal tergum and second segment, apical band on third segment (often absent). Legs ferruginous; tibia, basitarsi, tarsi, yellow or yellowish ferruginous; fore coxa sometimes with yellow spot.

Length (of head + mesosoma + first and second metasomal segments) 5.5-6.5 mm. Structural differences between this species and *R. erythrospila* are slight. The grounds for describing *R. pseudomalayana* as a valid species different from *R. erythrospila* are that their distributions overlap and that the differences in colouration appear to be fixed differences which may diagnose these two taxa.

Key to species of the Ropalidia malayana-complex (?)

1. Head in dorsal view with lateral sides behind eyes relatively strongly convex and strongly converging poteriorly in posterior half (fig. 5); gena in profile about as wide as eye (fig. 2); mandibular teeth hardly curved inwards (fig. 9); ventral tooth of mandible elongate, about 1.5 times as long as the third (fig. 8) Head in dorsal view with lateral sides behind eyes only slightly convex, converging posteriorly from the posterior margins of eyes (fig. 6); gena proportionally narrower, in profile about 0.75 times as wide as eye (figs 3-4); mandibular teeth weakly curved inwards (figs 11, 13); ventral tooth only slightly longer than the 2. Pronotum usually entirely reddish-brown, at most with narrow median yellow band along posterior margin; scutellum and metanotum usually entirely reddishbrown, only sometimes dark yellow with reddish-brown posterior margins Pronotum yellow, sometimes coloured ferruginous only in ventral part; entire surface of disks of scutellum and metanotum yellow



Fig. 41, relationships between the eye widths and the genal width in three species of the *Ropalidia* malayana-complex; fig. 42, relationships between the width of scutum and the apical width of the first metasomal tergum in *R. erythrospila* (Cameron) and *R. pseudomalayana* spec. nov.; m, p, d, e, indicate the types of *Icaria malayana* Cameron, *Icaria parvimaculata* Cameron, *Ropalidia delicata* Dover and *Icaria erythrospila* Cameron, respectively.

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