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REVISION OF THE ORIENTAL GENUS *MATAPA* MOORE (LEPIDOPTERA, HESPERIIDAE) WITH DISCUSSION OF ITS PHYLOGENY AND GEOGRAPHIC HISTORY

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With 55 text-figures

ABSTRACT

A revision is given of the Oriental genus *Matapa* Moore. Two species, *M. intermedia* and *M. deprivata*, and one subspecies, *M. intermedia nigrita*, are described as new. A key to the nine species known at present is provided. Figures are given of male and female genitalia, and of forewings of males. The phylogeny of the genus and its geographic history are discussed. It is shown that three monophyletic groups can be distinguished, which all originated in mainland Southeast Asia. The occurrence of one species in India is the result of a geologically speaking recent invasion. There are indications of a double colonization of Celebes from the Philippines.

INTRODUCTION

The genus *Matapa* Moore is a small Oriental group of mostly dull-coloured HesperIIDae. Evans (1949) recognized six species in this genus. Lee (1962) added one species. The discovery of two more species made a more detailed investigation of the genus worthwhile. It turned out that there are enough usable characters to make a phylogenetic reconstruction and a discussion of the geographic history feasible.

The species have interesting habits, probably all being mainly crepuscular. They have red eyes, at least during their life. The combination of red eyes and crepuscular habits is also found in closely related genera (e.g., *Erionota* Mabille and *Gangara* Moore), as well as in quite distantly related genera (e.g., the Neotropical genus *Bungalotis* Watson, belonging to a different subfamily), suggesting that the red colour has some functional meaning.

Another interesting character, found in two species only, is the woolly hair

at the end of the abdomen in females. These hairs are apparently used to conceal the deposited eggs. Below, all available data related to the bionomics of the species are given.

The author is much indebted to Mr. C.G. Treadaway (Frankfurt am Main) for his help with and gift of Philippine material, and to Mr. R.I. Vane-Wright (British Museum, Natural History, London; abbreviated BM, here) for his help and hospitality during several visits to London. The Rijksmuseum van Natuurlijke Historie, Leiden, is abbreviated RMNH in this paper.

Genus *Matapa* Moore

Moore, F., [1881]. Type-species by original designation: *Ismene aria* Moore, [1866].

Diagnosis* — Medium-sized to large species, length of forewing 15.3–26.7 mm. Nudum consisting of 12 to 14 segments. Eyes red, at least as long as the specimens are alive. Wings on upper and underside brown, with or without purple gloss; no spots; fringes of hindwing may be yellow and this colour may extend a little onto the wing. Forewing cell about 5/8 of wing length; origin of vein 3 before or opposite origin of vein 11; origin of vein 4 opposite origin of vein 10; vein 5 more or less decurved at origin. Hindwing cell not reaching beyond middle of wing; origin of vein 6 opposite origin of vein 2 (fig. 2); vein 5 only visible as a fold; discocellular vein between veins 4 and 6 obsolete.

Male with a usually narrow, broken stigma, consisting of two parts placed one over the other in space 1b just before the middle, and a longer oblique one in the basal part of space 2 (one species without a stigma). In the females of two species, tip of abdomen furnished with thick clothing of woolly hairs.

Male genitalia with uncus slightly to deeply indented; gnathos consisting of separate left and right parts, ventrally slender, ending apically with a rather well-defined area spinulosa with very fine spines or papilles; tegumen with a conspicuous, central, spinelike or flaplike, caudad projection from before the middle of the tegumen; saccus variable, very short to long; inner lamella of valva in proximal part usually strongly developed, sclerotized and folded; aedeagus with variably developed cornutus, apex of aedeagus often asymmetrically developed.

Female genitalia with a more or less well-defined antevaginal plate, laterally to centrally furnished with hornlike projections; antrum as long as broad to much longer than broad; bursa elongate, without signum.

* The diagnosis and further remarks in this chapter are based on an investigation of all species except *M. pseudosasivarna* of which I have not been able to study material.

Discussion. — The genus was placed by Evans (1949) in the *Plastingia* group. For the moment, this seems to be a reasonable classification, if only for want of better.

Although the species of *Matapa* are easily recognized as belonging to this genus, it is difficult to point out which characters are unique to the genus. Outside *Matapa*, the complete absence of spots in both sexes is, in the *Plastingia* group, only found in *Pirdana* Distant (except for the brightly coloured genera *Prada* Evans and *Tiacellia* Evans, which are the only genera of the group occurring east of Celebes). The blue or green colour of the underside of the hindwing in *Pirdana* (may be restricted to the veins) never occurs in *Matapa* and is a useful character to distinguish the two genera. From *Pirdana* as well as from other HesperIIDae *Matapa* can be separated by the position of the origin of vein 6 of the hindwing being opposite instead of well beyond the origin of vein 2.

Evans (1949) stated that the nudum of *Matapa* consisted of 14 segments. I found this number only in *M. druna*, in the other species the number was 12 or 13. The diagnostic use of this character is undoubtedly much less than supposed by Evans, who used it widely in his classifications. The number is often variable within a species. In *Matapa* the number has no use for species recognition, as I found 12 nudum segments in all species except *M. druna*, and 13 in three species.

KEY TO THE SPECIES OF *MATAPA**

1. Fringes of hindwing white to cream-coloured. Upper side of wings uniform brown, underside ferruginous (in ♂ darker than in ♀). Male, stigma narrow and dark, inconspicuous. Female with densely packed hairlike scales at tip of abdomen *aria*
Fringes of hindwing yellow 2
2. Male, stigma narrow, the two parts in space 1b much higher than wide, or stigma absent. Female, yellow of fringes of hindwing not extending onto the wing. India to Borneo 3
Male, stigma broad, the two parts in space 1b at least as broad as high. Female, yellow of fringes of hindwing extending onto wing. Celebes, Philippines 6

* For lack of material, *M. pseudosasivarna* could not be included. According to the original description (Lee, 1962) it is very close to *sasivarna*; judged from the photos of the genitalia it could as well be related to *deprivata*.

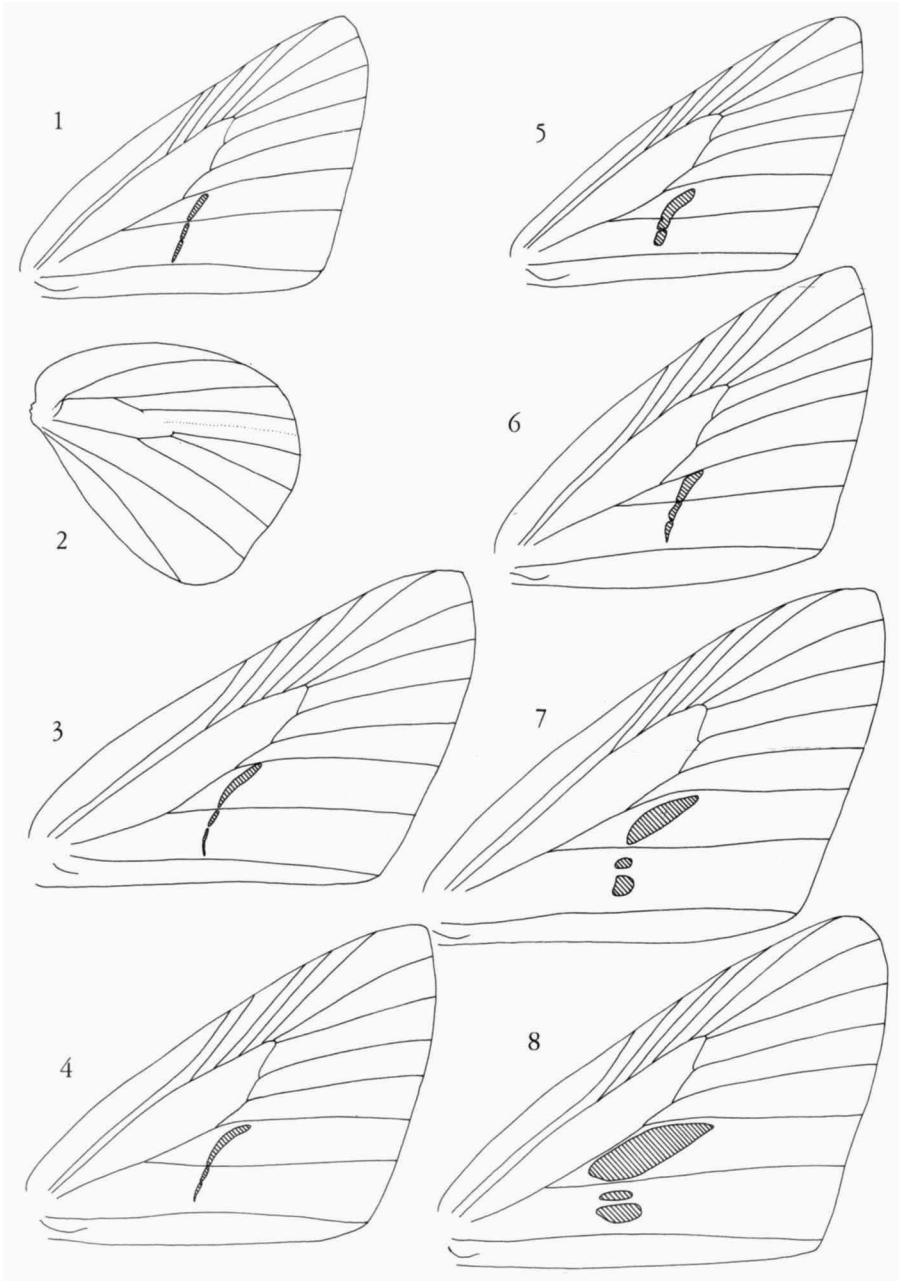
3. Male without stigma. Upper side with strong purple gloss. Female unknown *deprivata*
 Male, stigma grey, conspicuous. Underside of wings ferruginous, or fuliginous with dark veins. Female with or without densely packed hairlike scales at tip of abdomen 4
 Male, stigma black, inconspicuous. Underside of wings grey brown to dark brown, veins not darker than ground colour. Female, no densely packed hairlike scales at tip of abdomen 5
4. Upper side of wings uniform brown, underside ferruginous (in ♂ darker than in ♀). Male, stigma relatively broad and curved. Female, tip of abdomen with densely packed hairlike scales *druna*
 Upper side of wings uniform dark brown, bluish green sheen on thorax and wing bases, underside fuliginous with black veins. Male, stigma narrow and straight. Female, tip of abdomen without densely packed hairlike scales *sasivarna*
5. Underside of wings uniform dark brown. Upper side of wings usually with a strong purple gloss in ♂ *purpurascens*
 Underside of forewing, apical area greyish, distinctly lighter than ground colour. Underside of hindwing, basal area greyish. Upperside of wings usually without purple gloss *cresta*
6. Male, lower part of stigma in space 1b about as high as wide, large part in space 2 not filling most of the basal half of this space. Female unknown *intermedia*
 Male, lower part of stigma in space 1b at least twice as wide as high, large part in space 2 filling most of the basal half of this space *celsina*

DESCRIPTION OF THE SPECIES OF *MATAPA***Matapa aria** (Moore, [1866])

Ismene aria Moore, [1866]: 748. Calcutta. Type (♂) in BM.

Hesperia neglecta Mabille, 1876: 268. Manilla. Type (♀) in BM.

Description. — Length of forewing, ♂ 15.3–20.3 mm, ♀ 16–22.5 mm. Upper side uniform brown, underside ferruginous (female a little paler). Stigma of male (fig. 1) dark grey, straight, inconspicuous. Fringes white to, usual-



Figs. 1–8. Venation of forewing (1, 3–8) and hindwing (2) of *Matapa* species. The hatched areas indicate stigmas. 1–2, *M. aria*; 3, *M. cresta*; 4, *M. purpurascens*; 5, *M. druna*; 6, *M. sasivarna*; 7, *M. intermedia*; 8, *M. celsina*.

ly, cream-coloured. Female, densely packed hairlike scales with broadened tips at end of abdomen.

Male genitalia (figs. 9, 17, 25, 33). Tegumen with broad central flap, 1.5 times as long as broad. Uncus twice as broad as long, apically shallowly indented. Sclerotized fold of inner lamella of valva with serrated edge. Cucullus irregularly serrate. Aedeagus smooth, dorsally weakly sclerotized; apex more strongly developed at the right side; no obvious cornutus. Juxta weakly sclerotized, more or less rectangular, with extended corners.

Female genitalia (fig. 41). Antevaginally a large, central, two-horned plate with inconspicuous microtrichia; horns just reaching beyond the more or less rectangular postvaginal plate, which is densely set with long, conspicuous microtrichia. Ostium wide, antrum parallel-sided, about as long as wide.

Bionomics. — A beautiful colour photo of an egg of *M. aria* in Johnston & Johnston (1980: 88) shows the egg covered with hairs. These hairs undoubtedly come from the tip of the abdomen of the female and probably have a protective function. Remarks on early stages and bionomics can be found in Johnston & Johnston (1980), Piepers & Snellen (1910), Swinhoe (1913), and Woodhouse (1950). The larvae live on bamboo, where they make a refuge by rolling up a blade. They pupate in the tube and if disturbed the chrysalis will rattle itself against the side of its shelter. The adults hatch after eight days; they are active in the early morning and about twilight in the evening.

Distribution (fig. 47). — From Sri Lanka, W and NW India to S China, the Philippines and Sumbawa. It is apparently often a common insect in forested areas. In the Malay Peninsula it occurs in primary and secondary forest below 2500 ft. (Eliot, 1978).

Material examined. — 266 ♂, 170 ♀, from all over the range (BM, RMNH).

Matapa druna (Moore, [1866])

Ismene druna Moore, [1866]: 748. Bengal. Type (♂) in BM.

Hesperia pulla Plötz, 1882: 315. Java. Type probably lost. Evans (1949) synonymized *Hesperia pulla* Plötz with *M. aria*. Plötz indicates, however, clearly in his description that the fringes are yellow, and as the type-locality is Java, the name must relate to the same species described by Moore as *Ismene druna*. Snellen arrived at this conclusion long ago (Piepers & Snellen, 1910).

Matapa shalgrama de Nicéville, 1883: 85. Sikkim. Whereabouts of type not known.

Description. — Length of forewing, ♂ 19.4–23.4 mm, ♀ 21.4–26 mm. Upper side uniform brown, underside ferruginous (female a little paler). Fringes of hindwing yellow. Stigma of male (fig. 5) light grey to beige-coloured, much lighter than ground colour, conspicuous, relatively broad, slightly constricted but not broken at vein 2, curved in space 2. Female, hairlike scales at end of abdomen as in *M. aria*.

Male genitalia (figs. 10, 18, 26, 34). Tegumen with narrow central projection, about ten times as long as wide, reaching to tip of uncus. Uncus broad, 1.5 times as broad as long, apically shallowly indented, laterally with winglike extensions. Sclerotized fold of inner lamella of valva finely serrate only in dorsal part. Cucullus with flattened top, irregularly serrate dorso-distally. Aedeagus with short spines in apical part, more strongly developed at right side; caecum narrowed; cornutus a weakly sclerotized, platelike structure. Juxta a square plate with two large pointed projections with indistinct small bumps at the tips.

Female genitalia (fig. 42). Much like those of *M. aria*. Horns of antevaginal plate a little shorter and more diverging; postvaginal plate more rounded apically.

Bionomics. — The early stages have been described by Piepers & Snellen (1910). The larvae feed on a *Bambusa* species, like those of *M. aria*. As in the latter species the chrysalis rattles in its shelter as soon as it is touched. The adults hatch eight days after pupation.

Distribution (fig. 48). — From Sikkim to North Vietnam, Borneo and Bali. Elwes & Edwards (1897) recorded the species from the Andamans referring to de Roepstorff. It is not clear whether they had seen material from these islands. I have not found any, and I consider it advisable not to trust such an old record. In the Malay Peninsula it occurs in primary and secondary forest below 2500 ft. (Eliot, 1978).

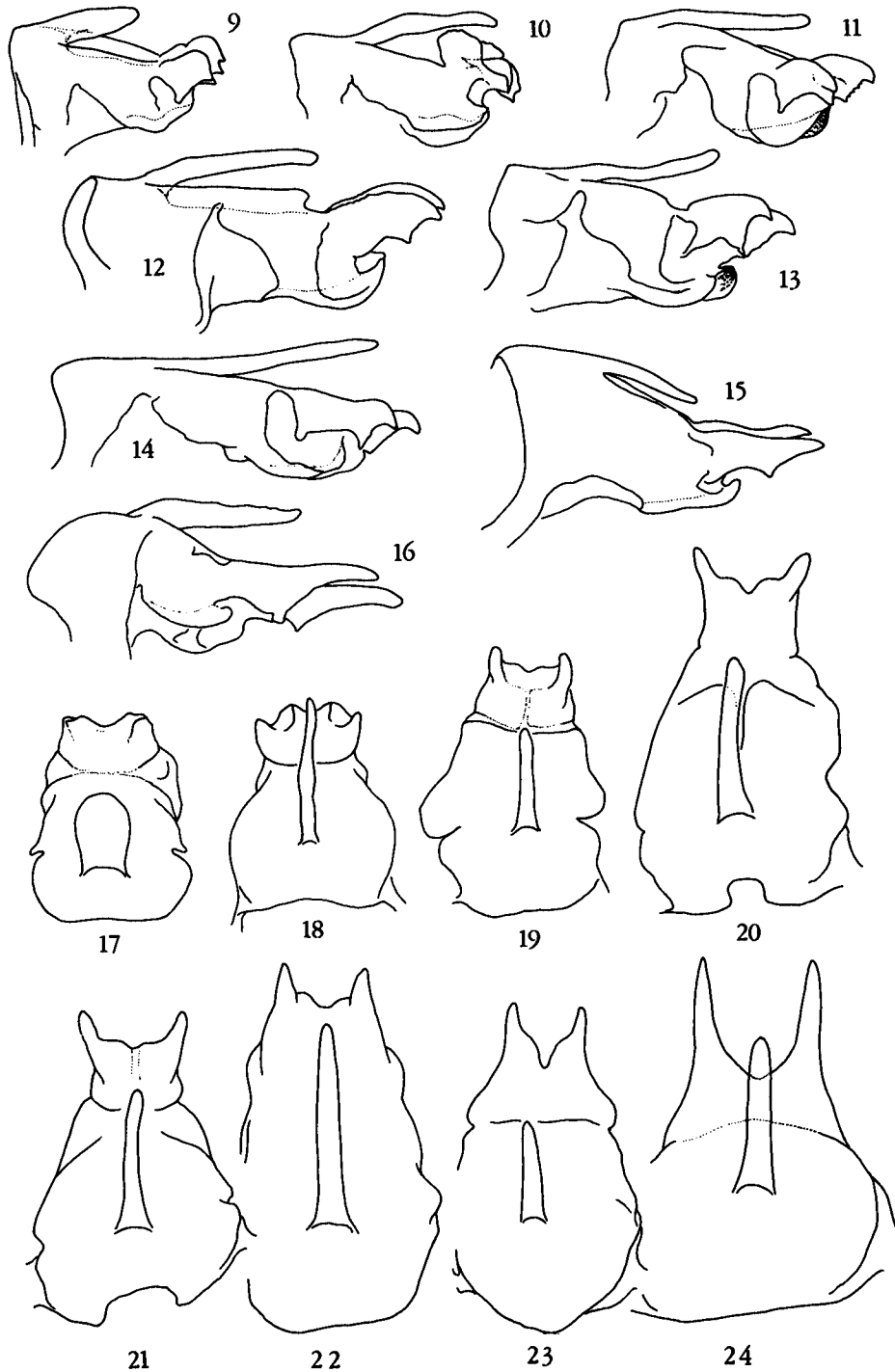
Material examined. — 116 ♂, 58 ♀, from all over the range (BM, RMNH).

Matapa sasivarna (Moore, [1866])

Ismene sasivarna Moore, [1866]: 784. Bengal. Type (♂) in BM.

Description. — Length of forewing, ♂ 17.8–21.3 mm, ♀ 18–22.2 mm. Upper side uniform dark brown, bluish green metallic sheen on palpi, head, thorax and wing bases, especially in female. Underside hindwing fuliginous with black veins. Fringes of hindwing conspicuously yellow, sometimes extending a little onto the wing. End of abdomen deep yellow. Stigma of male (fig. 6) beige-coloured, conspicuous, straight.

Male genitalia (figs. 11, 19, 27, 35). Tegumen with narrow central process, about 7 times as long as broad, just reaching the uncus. Uncus slightly broader than long, central indentation shallow and wide. Sclerotized fold of inner lamella of valva smooth. Costa short, elongate triangular. Cucullus triangular, dorsal part densely set with short spines becoming bigger towards the rounded



Figs. 9–24. Uncus and tegumen of *Matapa* species, in lateral view (9–16) and in dorsal view (17–24). 9, 17, *M. aria*; 10, 18, *M. druna*; 11, 19, *M. sasivarna*; 12, 20, *M. intermedia*; 13, 21, *M. celsina*; 14, 22, *M. purpurascens*; 15, 23, *M. deprivata*; 16, 24, *M. cresta*. All figures drawn at same scale.

proximo-distal corner. Aedeagus smooth, slightly curved a little before the middle, apex slightly more expanded at the right side; weakly defined plate-like cornutus. Juxta platelike with slightly expanded corners.

Female genitalia (fig. 43). Antevaginally broadly sclerotized, folded, densely set with long microtrichia, laterally of the wide ostium with hornlike, unequally developed extensions which are devoid of microtrichia. Postvaginally a broad but short, smooth, bandlike sclerotization with finely serrate distal edge, followed by an irregularly formed area spinulosa, which is densely set with rather long microtrichia. Antrum almost parallel-sided, about as long as wide, sclerotization not sharply defined toward ductus bursae.

Bionomics. — Early stages have not been recorded in literature.

Distribution (fig. 49). — From Sikkim to Hainan, Sumatra and Pulo Laut (a small island at the southeast corner of Borneo; not known from the latter island). In the Malay Peninsula the species is restricted to primary forest below 2500 ft. (Eliot, 1978).

Material examined. — 83 ♂, 60 ♀, from all over the range (BM, RMNH).

Matapa pseudosasivarna Lee, 1962

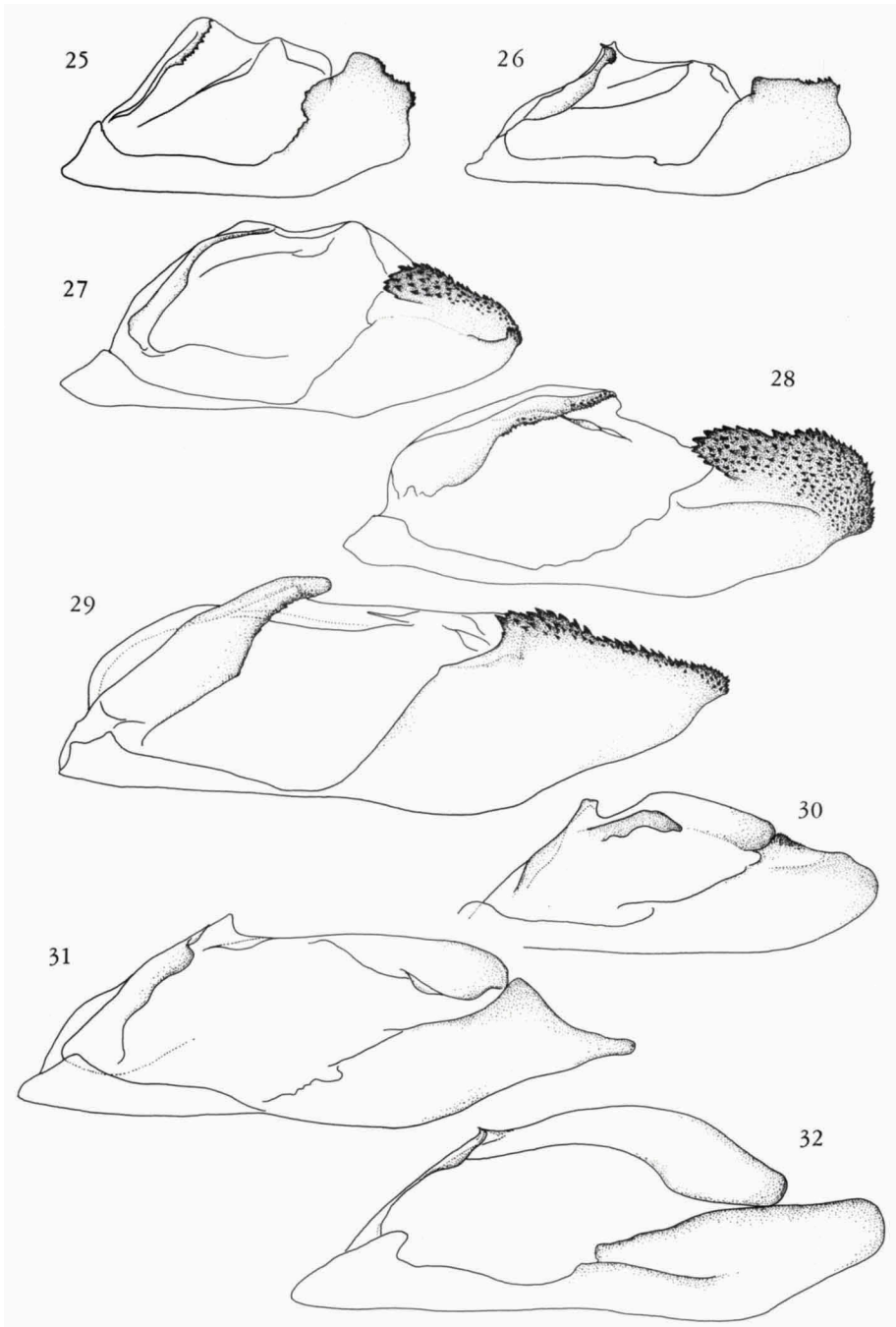
Matapa [sic!] *pseudosasivarna* Lee, 1962: 147, figs. 41–42, 61–62. Yunnan. Depository of type not known.

According to the original description this species differs from *M. sasivarna* in having longer and narrower forewings (length 20 mm), the stigma linear and shorter, about 2 mm, extending obliquely from vein 2 to vein 3 (apparently no parts in space 1b), and different genitalia. The photographs of the genitalia are not clear enough to see details, but the normal-sized, slightly curved aedeagus and the shape of the cucullus, which is probably spined at the proximo-dorsal corner, remind of *M. sasivarna*. The costa seems to have an extension pointing distad, if this is not a torn part of the inner lamella. The proximal fold of the inner lamella seems to have a smooth edge, but it is difficult to make sure from the photograph.

It is apparently only known from the holotype.

Matapa intermedia species nova

Description. — Only males are known. Length of forewing, 22.2–26.6 mm. Upper side uniform dark brown or black, with greenish sheen on palpi, head, thorax, and may extend onto wing bases. Hindwing with the deep yellow of the fringes extending up to about 3 mm on the wing surface between dorsum



Figs. 25–32. Inside of right valve of *Matapa* species. 25, *M. aria*; 26, *M. druna*; 27, *M. sasivarna*; 28, *M. celsina*; 29, *M. intermedia*; 30, *M. deprivata*; 31, *M. purpurascens*; 32, *M. cresta*. All figures drawn at same scale.

and vein 4. Underside as upper side, veins slightly darker than ground colour or concolourous. Tip of abdomen deep yellow. Stigma (fig. 7) consisting of a fusiform part in space 2 with a length of 3.6–3.9 mm, and two small patches in space 1b under the lower end of the large patch in space 2; the upper of the two patches in space 1b slightly broader than high, the lower one about twice as large, as broad as high.

Male genitalia (figs. 12, 20, 29, 36). Tegumen, proximal edge centrally bent inwards; central process long and narrow, about 8 times as long as wide. Uncus square, apically slightly indented, with widely diverging short arms. Valva, inner lamella strongly expanded, sclerotized and folded proximally, with slightly serrate edge; costa almost undeveloped; cucullus rather elongate and bluntly pointed, dorsal edge straight, with strong spines largest at proximo-dorsal corner. Aedeagus straight, in apical half with spined and strongly serrate edges (more strongly spined at right side), apex smooth; elongate, plate-like cornutus, pointed, with finely serrate edge. Juxta platelike, about as long as wide, with distal cornes prolonged into arms.

Bionomics. — Unknown.

Distribution (fig. 51). — Up to now only known from Celebes and Samar. The specimens from the two islands differ so much that a subspecific division appears justified.

Discussion. — Externally as well as in the genitalia the new species reminds of *M. celsina*, and it seems to take an intermediate position between this species and *M. sasivarna*, hence its name. In Celebes it is as large as *M. celsina* and although the male can easily be recognized by its smaller stigma, it is possible that the female looks identical to the female of *M. celsina*. It is, therefore, not impossible that the female of *M. intermedia* is among the short series of females of *M. celsina* studied. See also the discussion on "*Matapa celsina rac-taya* Fruhstorfer" under the latter species.

***Matapa intermedia intermedia* subspecies nova**

Description. — Length of forewing, ♂ 26.6 mm. Upper and underside dark brown, greyish brown stigma conspicuous. Deep yellow area on hindwing up to 3 mm wide.

Material examined. — Holotype, ♂, N. Celebes, Minahasa, 1937–1941, P. Zondervan. In RMNH.

***Matapa intermedia nigrita* subspecies nova**

Description. — Length of forewing, ♂ 22.2 mm. Upper and underside

uniform sooty black. Black stigma inconspicuous. Deep yellow area of hindwing up to 1.6 mm wide.

Material examined. — Holotype, ♂, E. Samar, San Rafael, Camp 5, 1000 ft, 12.iv.1980, C.G. Treadaway. In RMNH.

Matapa celsina (Felder, 1867)

Hesperia celsina Felder, 1867 (March): 512. Celebes. Type (♀) in BM.

Hesperia hyrmina Hewitson, 1867 (April): 24. Tondano. Type (♂) in BM.

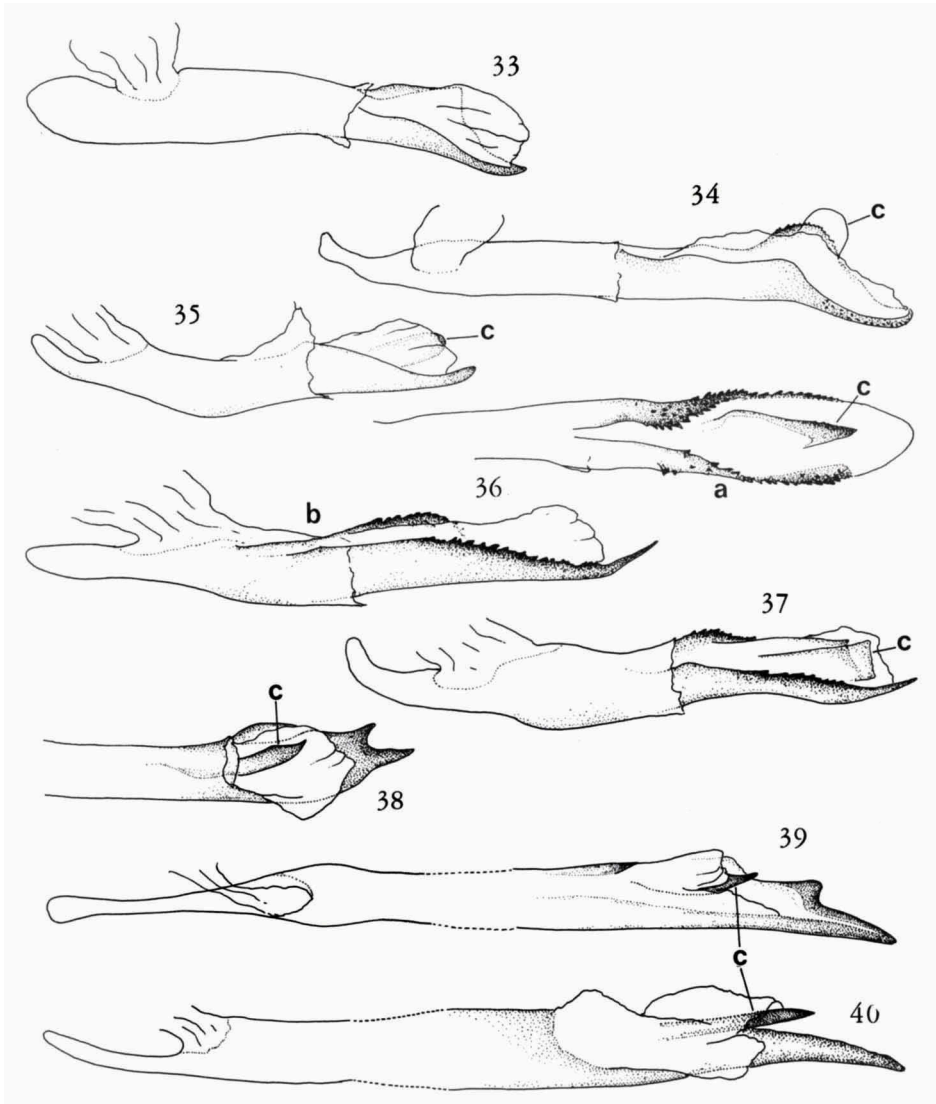
Ismene assur Mabille, 1876: 261. Celebes. Type (♂) in BM.

Matapa celsina ractaya Fruhstorfer, 1910: 101. Mindanao. I have not been able to locate the type.

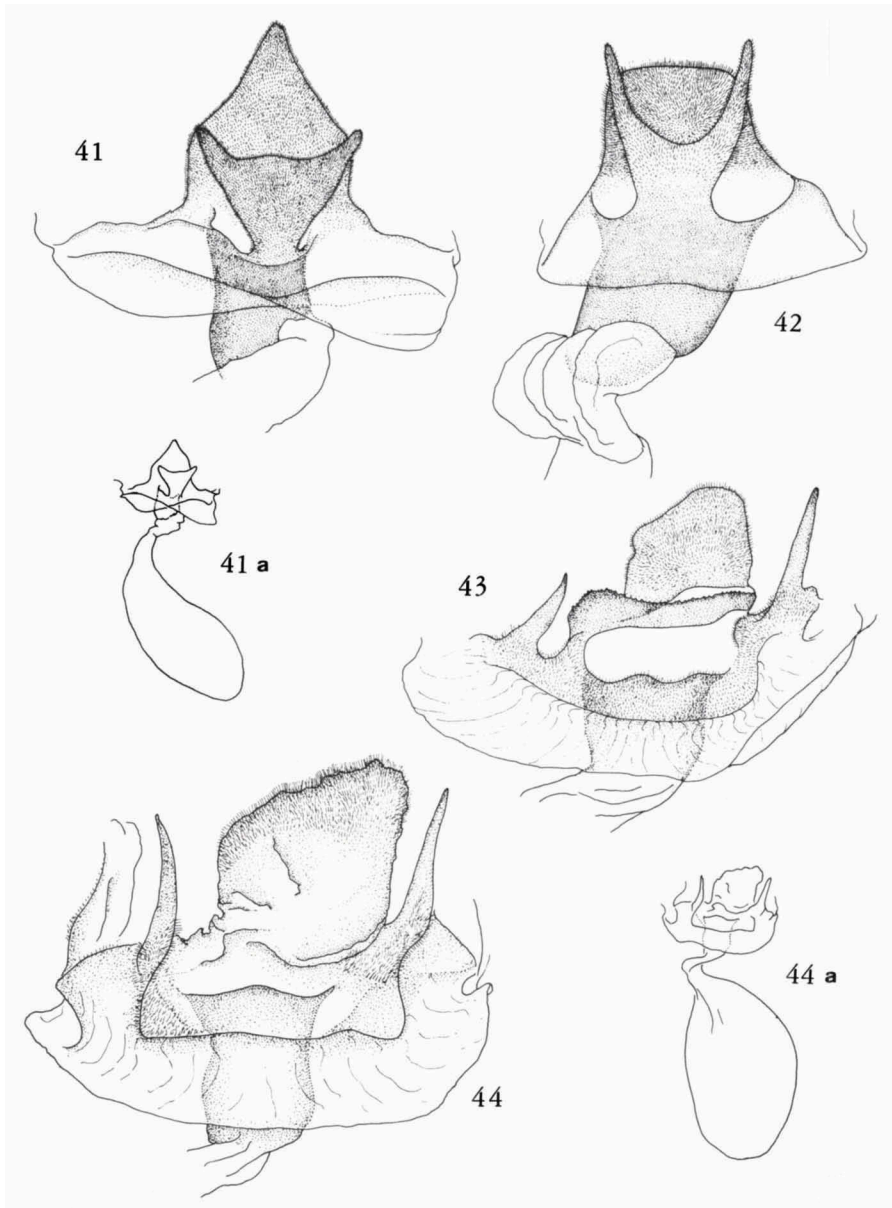
This is unfortunate as the description ("Gelber Terminalsaum der Htflgl. viel schmaler als bei *celsina*") could as well apply to *M. intermedia* and even to *M. sasivarna*. If the description was based on a male, it must refer to *M. celsina*, as Fruhstorfer would certainly have observed the different stigmas of the other species. If it, however, was based on a female, identification is doubtful. According to Evans (1949) the description by Fruhstorfer was actually based on a female and he suggested that it referred to Semper (1892: 294). Fruhstorfer, however, never said so. Semper, who had two females available from E. Mindanao, remarked that the yellow colour on the hindwing was as extensive as in a male from Celebes, while a female from Celebes had a broader yellow area. Actually, the width of the yellow area in Celebes specimens is rather variable. If Semper's specimens belonged to *M. intermedia*, it does not follow that this name must fall for *M. ractaya* as Fruhstorfer did not mention Semper's specimens at all. Therefore, the latter name must be considered a nomen dubium as long as the type is missing. The figure of *ractaya* in Seitz (1927: pl. 169g) made after a specimen from Mindanao does not suggest anything different from *M. celsina*.

Description. — Length of forewing, ♂ (20.6-)22.1–25 mm, ♀ 23.2–25.5 mm. Upper side dark brown with greenish sheen on palpi, head and thorax, and more or less extending to wing bases. Yellow border of hindwing between dorsum and vein 4 variable in ♂, 1–3 mm at widest point (in space 1b), less variable in ♀, 3–4.2 mm at widest point. Underside as upper side. Tip of abdomen yellow. Greyish brown conspicuous stigma (fig. 8) consisting of large fusiform part in basal half of space 2, 5–5.8 mm in length (in one specimen only 4.2 mm), and two smaller patches in space 1b, which are much wider than high, variable and sometimes almost invisible.

Male genitalia (figs. 13, 21, 28, 37). Tegumen, proximal border widely bent inwards centrally; central process long and narrow, about 8 times as long as wide, just reaching uncus. Uncus square, shallowly indented apically, with widely diverging short arms. Valva, inner lamella strongly expanded, sclerotized and folded proximally, with finely serrate edge and short spines; costa practically undeveloped; cucullus elongate, dorsally strongly domed and densely set with numerous spines which are especially strong in the proximo-dorsal area. Aedeagus straight, but caecum curved upwards; in apical half with serrate edges; cornutus a faint bandlike sclerotization. Juxta as broad plate with two distal arms about as long as plate.



Figs. 33–40. Aedeagus of *Matapa* species (c = cornutus). 33, *M. aria*; 34, *M. druna*; 35, *M. sasivarna*; 36, *M. intermedia*; a, lateral view; b, dorsal view of apical half; 37, *M. celsina*; 38, *M. purpurascens*; 39, *M. deprivata*; 40, *M. cresta*. In figs. 39 and 40 the aedeagus has been interrupted (dashed lines); see the text for the length of the aedeagus in these species. All figures drawn at same scale.



Figs. 41–44. Details of female genitalia of *Matapa* species; ventral view of eighth abdominal segment. 41, *M. aria* (41a, overall picture); 42, *M. druna*; 43, *M. sasivarna*; 44, *M. celsina* (44a, overall picture).

Female genitalia (fig. 44). Very much like those of *M. sasivarna*; no postvaginal sclerite with serrate edge; area spinulosa with microtrichia only in upper part; antrum slightly longer than wide, sclerotization not sharply defined.

Bionomics. — Unknown.

Distribution (fig. 50). — Confined to Celebes and Banggai Archipelago. Possibly also Mindanao (see discussion of *M. celsina ractaya*, above).

Material examined. — 35 ♂, 16 ♀, Celebes (all over the island), Banggai (BM, RMNH).

Matapa purpurascens Elwes & Edwards, 1897

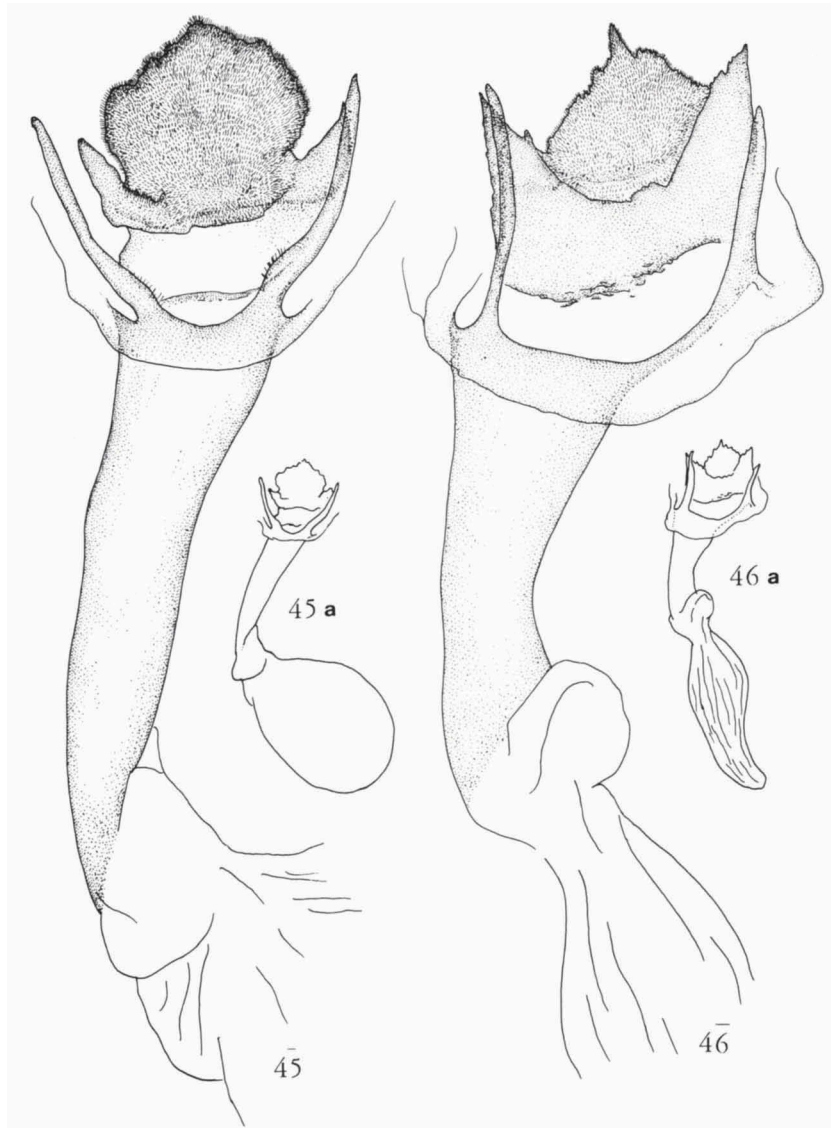
Matapa purpurascens Elwes & Edwards, 1897: 209, pl. 20 fig. 1, 24 fig. 48. Khasi Hills. Type (♂) in BM.

Description. — Length of forewing, ♂ 20.5–23 mm, ♀ 22–24.9 mm. Upper side dark brown, forewing with strong purple gloss especially in male (in female often confined to outer third). Very faint greenish gloss on thorax. Deep yellow of fringes of hindwing not extending onto wing. Underside dark brown in male, may be very slightly paler at apex of forewing; greyish brown in female with paler area between vein 3 and dorsum of forewing. Tip of abdomen yellow. Stigma of male (fig. 4) black, inconspicuous, very gently curved, not reaching vein 1.

Male genitalia (figs. 14, 22, 31, 38). Tegumen elongate, at least 1.5 times as long as wide; central process long, about 9 times as long as wide, reaching to middle of uncus. Uncus slightly broader than long, shallow indentation apically, arms wide apart, short, parallel. Valva, inner lamella with large, smooth, proximal, sclerotized fold; costa well-developed, about 1/3 of total length of valva, smooth; cucullus long and narrow, with dorsal hump where it meets the costa, distally extended narrowly and bluntly ended. Aedeagus very long (in examined male, proximal part broken off), smooth, with double-pointed apex (mainly developed to the right side) and long, pointed cornutus. Juxta a broad band, about 3 times as wide as long, with long, pointed, distal extensions about as long as width of juxta.

Female genitalia (fig. 46). Asymmetrically developed. Ostium very wide, opening into the long funnellike well-sclerotized antrum. Antevaginally a long, almost straight, smooth horn at the left side, pointing distad; a similar horn to the right of the ostium. Postvaginally a large sclerite, laterally triangularly extended, with irregular edges, and with microtrichia in upper part; area spinulosa triangular, with irregular edges and totally, but not densely set with microtrichia.

Bionomics. — Unknown.



Figs. 45–46. Details of female genitalia of *Matapa* species; ventral view of eighth abdominal segment and overall picture (a). 45, *M. cresta*; 46, *M. purpurascens*.

Distribution (fig. 52). — A limited area, from Sikkim and Bengal to South Shan States in Burma. The localities W. Sumatra and Chiem-Hoa (Tonkin) mentioned by Fruhstorfer (1910) relate to *M. cresta* according to the material in the BM.

Material examined. — 8 ♂, 8 ♀, Sikkim, Bengal, Assam, Burma (Ruby Mines, East Pegu, Karens, S. Shan States) (BM).

Matapa deprivata species nova

Description. — A single male known. Length of forewing 20.2 mm. Like *M. purpurascens*, purple gloss slightly less, apex of forewing paler at upper and underside (like *M. cresta*). No stigma.

Male genitalia (figs. 15, 23, 30, 39). Tegumen rounded, a little longer than wide; central process relatively short, about 6.5 times as long as wide, hardly reaching uncus. Uncus at base as broad as tegumen, tapering towards the slightly elongate, parallel arms. Valva, inner lamella with proximal fold weakly sclerotized and developed into an irregularly shaped dorsal tongue; costa well-developed with almost parallel sides; cucullus elongate, distally rounded, dorsally with finely spinulose hump near costa. Aedeagus long, a little less than twice length of valva, straight, smooth, caecum much narrower than main body, apically pointed with a bump to the right; elongate, pointed cornutus. Juxta more or less U-shaped. Saccus relatively long, almost half length of valva.

Material examined. — Holotype, ♂, Burma, Hangathraw Valley, 5.iv.1924. In BM.

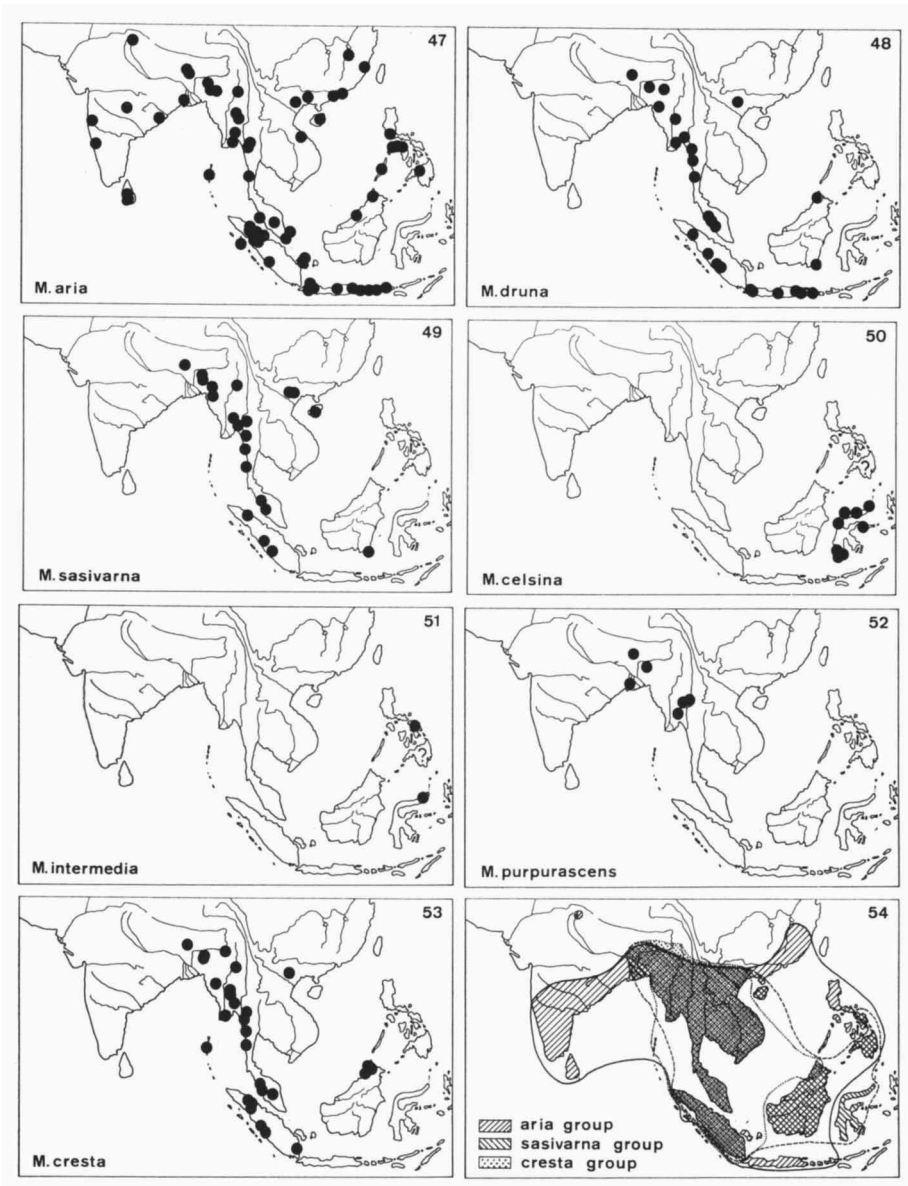
Discussion. — The species corresponds with *M. purpurascens* and *M. cresta* in many details, such as the coloration of the wings, the general shape of the valva and the lengthening of aedeagus and saccus. It can easily be recognized, apart from its smaller size, by the absence of a stigma (hence its name).

Matapa cresta Evans, 1949

Matapa cresta Evans, 1949: 331. Sikkim. Type (♂) in BM.

Description. — Length of forewing, ♂ 21.7–24.9 mm. ♀ 23–26.7 mm. Upper side uniform dark brown, paler at apex of forewing, especially in dry season form of male. Very faint greenish gloss on thorax. Underside dark brown, conspicuously paler at apex of forewing, a broad area along dorsum of forewing, and less conspicuously in basal part of hindwing. In dry season pale areas more conspicuous. End of abdomen yellow. Yellow colour of fringes of hindwing not extending onto wing. Stigma of male (fig. 3) narrow, black, inconspicuous, gently curved from vein 1 to vein 3.

Male genitalia (figs. 16, 24, 32, 40). Tegumen short, 1.5 times as wide as



Figs. 47–54. Distribution of species and species groups of *Matapa*.

long; central process firm, 6 times as long as wide, reaching well beyond edge of indentation of uncus. Indentation of uncus deep, U-shaped, reaching beyond middle, arms parallel. Valva, inner lamella hardly expanded and folded proximally; costa strongly developed, expanding and down-curving towards cucullus. The latter large, simple, elongate, with rounded apex. Aedeagus very long, more than 1.5 times as long as valva, about 14 times as long as wide, smooth; caecum narrow, less than 1/3 width of main body of aedeagus; apex pointed; long, pointed cornutus. Juxta with V-shaped apical indentation to just over middle. Saccus long, more than half length of valva.

Female genitalia (fig. 45). Reminding of those of *M. purpurascens*, but less irregular. Antevaginally two long, diverging horns which are bare, except at the base where they bear some microtrichia. Postvaginally a smooth sclerite with irregular lateral extensions alongside the more or less rounded postvaginal area which has an irregular edge and is densely set with microtrichia. Antrum well-sclerotized, long, funnellike, almost 4 times as long as wide at ostium.

Bionomics. — Unknown.

Distribution (fig. 53). — From Sikkim to North Vietnam, Borneo and Sumatra. In the Malay Peninsula the species flies in primary and secondary forest up to 2500 ft (Eliot, 1978).

Material examined. — 62 ♂, 30 ♀, from all over the range (BM, RMNH).

PHYLOGENETIC CONSIDERATIONS

In this chapter several characters will be examined as to their use for reconstructing the phylogeny of the genus and a cladogram will be drawn up (fig. 55). The numbers in the latter correspond to the numbers in the discussion of the characters. It is common practice to indicate in a cladogram the apomorphous as well as the plesiomorphous character states. It is, however, sufficient to give the apomorphous states, as these are the states used for defining the branching points, and by marking the apomorphous states in the cladogram the presence of the plesiomorphous state of the same character in the sister group is implicit.

The main argument applied here to define the apomorphous and plesiomorphous states is the argument of out-group comparison (see De Jong, 1980). The out-group in this case is formed by the other genera placed by Evans (1949) in the *Plastingia* group. How far this group is monophyletic, has not yet been studied, but as already remarked above in the discussion of the genus, the classification of Evans seems reasonable for the time being. The

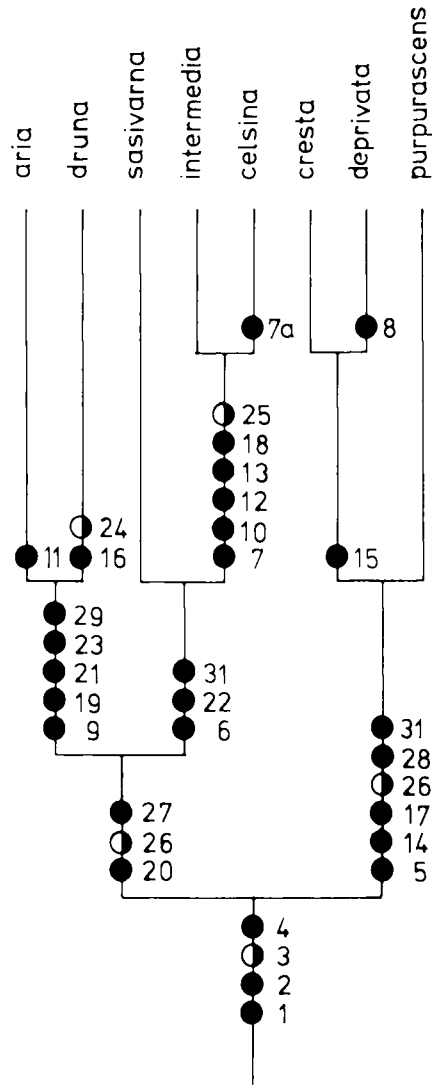


Fig. 55. Cladogram indicating the apomorphous character states in the genus *Matapa*. The numbers refer to the discussion in the text.

sister group of *Matapa* has not yet been identified. Finding of this sister group would be a great help as it would establish the characters of the common ancestor and hence help to find the direction of change in *Matapa*.

Most of the characters discussed below refer to the male genitalia, simply

because there are so many characters in these structures. Characters of the female genitalia must be used with some care as the females of two species are not known at present. Early stages will undoubtedly also yield useful information, but up to now the early stages of only two species are known.

a. Characters defining the genus

1. Venation of hindwing. The peculiar venation with the origin of vein 2 opposite the origin of vein 6 is unique and must be regarded an autapomorphy of the genus.

2. Inner lamella of valva. The sclerotization, expansion and folding of the proximal part of the inner lamella of the valva is unique and must, for that reason, be considered an autapomorphy of the genus.

3. Absence of spots. Loss of spots is so wide-spread in the Hesperidae that it must have evolved many times independently. In the *Plastingia* group it occurs in the genus *Pirdana* and in several species of other genera. On the basis of this character alone there is no need to suppose a close relationship between these species and *Matapa*, nor between the species of *Matapa*, for that matter. Only after accepting the autapomorphy of the two character states discussed above, and after establishment of the sister group of *Matapa* can we be reasonably confident of the apomorphy of this character in *Matapa*. Therefore it has been indicated as of doubtful use in fig. 55.

4. Central process of tegumen. All *Matapa* species possess a conspicuous central process of the tegumen. A similar structure is not found in the other members of the *Plastingia* group, though in *Hidari irava* (Moore) an indication, more like a short transverse ridge, can be found in the same place. The occurrence of similar processes in some American genera like *Saliana* Evans, can hardly be considered to be the result of common ancestry. Because of the uniqueness of this character in the *Plastingia* group, it is considered an autapomorphy of *Matapa* here.

b. External characters

5. Purple gloss on upper side forewing. Mainly developed in the male (in *M. cresta* sometimes absent). Glossy wings are quite common in Hesperidae and also found in several species of the *Plastingia* group. The deep purple gloss of the *Matapa* species referred to here, mainly developed moreover in the outer half of the wing, is not found in the out-group and therefore is considered apomorphous here.

6. Extension of yellow colouring on hindwing. In two species of *Matapa*,

and in some specimens of a third, the yellow colour of the fringes of the hind-wing extends for some distance on the wing surface. A similar character is found in *Pirdana*. There are, however, no reasons to suppose that *Matapa* is more closely related to *Pirdana* than to any other genus; this character can easily have evolved independently in the two genera, as it did in several genera outside the *Plastingia* group.

7. Stigma of male. Stigmas are very common in HesperIIDae and occur in many forms. The narrow, more or less linear shape of the stigma found in most *Matapa* species is found in many other HesperIIDae, in the *Plastingia* group as well as outside. The peculiar form found in *M. intermedia* and *M. celsina*, however, is unique and, for that reason, considered apomorphic. As apparently evolution proceeded by broadening of the linear stigma, the very broad stigma of *M. celsina* must be considered apomorphic (7a) with respect to the less extreme condition found in *M. intermedia*.

8. Loss of stigma. Loss of secondary sexual characters is very common in HesperIIDae and apparently occurred many times independently (see also De Jong, 1975). The common occurrence of stigmas outside *Matapa* of the type found in most *Matapa* species suggests that the common ancestor of the *Matapa* species already had this character and that the loss in one species is apomorphic.

9. Hairs at tip of abdomen of females. The obviously protective function of the densely set but loosely attached hairs at the end of the abdomen of females of *M. aria* and *M. druna* implies that loss of the character is unlikely as it would mean a lower survival rate. On the other hand, a character with such an obvious advantage can be supposed to have arisen more than once. Indeed, it is not only found in some other HesperIIDae outside the *Plastingia* group (e.g. *Tagiades*), but also in other lepidopterous families (e.g. LymantrIIDae). Thus, the occurrence of woolly hairs in females of *Hidari irava* (Moore), a member of the *Plastingia* group, does not a priori mean a close relationship with *Matapa*. As moreover the hairs in *Hidari* are pointed, while in the two *Matapa* species they end with disklike broadening, I consider the occurrence of the hairs in the two *Matapa* species an apomorphic character state.

c. Male genitalia

10. Tegumen, central inwards curving of proximal edge. This character, found in two species only, is unique and therefore considered apomorphic.

11. Central process of tegumen. This process occurs in two forms in *Matapa*, viz., (a) slender, at least 6 times as long as wide, and (b) broad, flaplike, 1.5 times as long as wide. If the long narrow type would represent the derived

state, it would mean that either this character arose twice or the woolly hairs at the tip of the abdomen in females of *M. aria* and *M. druna* originated twice (see fig. 55). It seems more likely (and at least is more parsimonious) that the broad process of *M. aria* is the derived state.

12. Basal part of uncus. In the members of the *Plastingia* group the uncus is either narrow or broad. In *Matapa* it is broad in all species, but varies in length. The basal part is generally wider than long, except in *M. intermedia* and *M. celsina*, in which it is as long as wide. For the sake of parsimony the latter condition is considered to be most likely the apomorphic state.

13 and 14. Development of uncus arms. Generally speaking the broad uncus in members of the *Plastingia* group ends with a shallow central indentation, as in *Matapa* species. The distal corners can be elongated into short arms, which are so differently developed that it can be concluded that the different types evolved independently from a more simply built uncus. Thus, the almost undeveloped arms of *M. aria* and *M. druna* can be considered the plesiomorphic state, while the divergent arms of *M. sasivarna*, *M. intermedia* and *M. celsina* (13), and the slightly differently shaped parallel arms of *M. purpurascens*, *M. deprivata* and *M. cresta* (14) can be considered apomorphic states.

15. Length of uncus arms. As a consequence of the discussion above the lengthening of the arms in *M. cresta* and *M. deprivata* must be considered apomorphic.

16. Lateral expansion of uncus. The uncus comes in many forms in the Hesperidae. Although lateral expansions are not common, they occur scattered throughout the family, apparently unrelated as they show quite different shapes. The expansions found in *M. druna*, unique in *Matapa* and in this form in the *Plastingia* group, can be seen as an independent development and thus as an apomorphy.

17. Lengthening of saccus. The saccus in *Matapa* species is hardly developed at all except in *M. cresta*, *M. deprivata* and *M. purpurascens*, where it is strongly produced towards the base of the abdomen. Such a lengthening does not occur in the out-group, where the saccus is often as undeveloped as in the other *Matapa* species. Lengthening of the saccus is well-known in other genera of the Hesperidae, such as *Carterocephalus* Lederer and *Thymelicus* Hübner, which are only very distantly related judged from the many different characters. It is therefore concluded that the lengthening in the three *Matapa* species is apomorphic, the alternative being that the saccus was shortened many times independently. The lengthening of the saccus is always accompanied by lengthening of the aedeagus and it is obvious to suppose a direct correlation as the saccus may help to support the aedeagus. Also in the

three *Matapa* species with a long saccus the aedeagus is remarkably long. Because of the correlation the length of the aedeagus has not been used here as a separate character to define the branching points in the phylogram.

18 and 19. Inner lamella of valva. As discussed under (2), the expansion and sclerotization of the proximal part of the inner lamella seems to be an autapomorphous character state of the genus. As it undoubtedly started with a simple, smooth fold, getting spined only after it attained a certain degree of sclerotization strong enough to support the spines, the spined condition must be considered apomorphous. This condition is found in *M. aria* and *M. druna* on the one hand, and *M. celsina* and *M. intermedia* on the other. The folds are differently developed in the two pairs of species, in the former comprising a much larger part of the inner lamella, in the latter being more strongly developed in the dorsal part. It is, therefore, concluded that the two pairs represent two different developments of the fold. Therefore, this character has been indicated in the phylogram by the number 18 for *M. intermedia* and *M. celsina*, and by the number 19 for *M. aria* and *M. druna*.

20. Reduction of costa. The costa is generally well-developed in the outgroup. It is possible that the reduction found in *M. aria*, *M. druna*, *M. sasivarna*, *M. intermedia* and *M. cresta* is correlated with the development of a strongly spined cucullus, but it is not clear why this should be so and the simultaneous occurrence could as well be incidental. For the time being it seems safe to consider the reduction of the costa an independent development.

21 and 22. Cucullus. The cucullus occurs in so many different forms in the outgroup that it is impossible to get a good idea of what the cucullus of the most recent common ancestor of the *Matapa* species looked like. In *Matapa* three basic types occur, viz., (a) smooth, or at most finely spinulose, (b) strongly and densely spined, and (c) with irregularly serrate dorsal edge. As the first type occurs with what is considered the primitive type of costa (see under 20), it could be the plesiomorphous type. It is also possible that the ancestor had a slightly spinulose cucullus that became smooth in some species and strongly spined or serrate in others. This seems to be a plausible explanation as it is easier to imagine that a smooth or slightly spinulose cucullus developed into a serrate one on the one hand and a strongly spined one on the other, than to see how the serrate type developed into the spined type or vice versa. Therefore, in the phylogram the serrate and the spined types are considered separate apomorphous character states (21 for the serrate type, 22 for the spined type).

23–25. Apart from variation in size (see under 17), the aedeagus varies in shape and degree of spining. Three types can be distinguished, viz., (a) long and smooth, apical part more or less asymmetrical (*M. cresta*, *M. deprivata*,

M. purpurascens), (b) short, smooth or slightly spined with strong square expansion of apical sclerotization at right side (*M. aria*, *M. druna*), and (c) short, smooth or spined, apical part only slightly asymmetrical (*M. sasivarna*, *M. intermedia*, *M. celsina*). The long aedeagus was already supposed to be derived (see discussion under 17). The development found in *M. aria* and *M. druna* is not found elsewhere and can for that reason also be considered apomorphic (23). That leaves the short, slightly asymmetrical type the plesiomorphic condition. If the spined condition was original, it was lost at least three times (once in each basic type). If the smooth condition was original, the spined condition arose twice (only in the short types). Applying Occam's razor the latter possibility is taken as the most probable one. As, however, this discussion is based on a phylogeny already established with the help of other characters, the apomorphic conditions in *M. druna* (24) and *M. intermedia* + *M. celsina* (25) are indicated in fig. 55 by half-closed circles.

26. Cornutus. The cornutus is either spinelike (*M. cresta*, *M. deprivata*, *M. purpurascens*) or platelike (the other species, may be scarcely developed at all). Cornuti occur in many forms in the Hesperidae. In the members of the *Plastingia* group they are commonly absent, as in many other Hesperidae. For this reason it is impossible to infer which condition existed in the ancestor of the *Matapa* species. There are three possibilities: (a) the platelike condition is apomorphic, (b) the spinelike condition is apomorphic, and (c) both conditions are apomorphic. Because of this uncertainty both conditions have been indicated in fig. 55 by a half-closed circle; at least one of these is correct, at most one of these is incorrect.

27. Juxta. In the out-group as well as in other Hesperidae in which a juxta is well-developed, it is usually V- or U-shaped. For this reason, the broadening found in a number of *Matapa* species (extreme in *M. aria*) is considered apomorphic.

d. Female genitalia

28. Length of antrum. The very long antrum found in *M. cresta* and *M. purpurascens* is unique in the *Plastingia* group and can, for that reason, be considered apomorphic. The female of *M. deprivata* is unknown, but if the classification on the basis of other characters is correct, it can be supposed to have a similarly shaped antrum. It is remarkable that the long antrum occurs in species with a long aedeagus, and it is obvious to suppose a correlation between the two. However, as long as the need for a long antrum because the male has a long aedeagus has not been established, the characters can be considered separately.

29. Antevaginal plate. The large triangular or horned antevaginal plate in

M. aria and *M. druna* covering the ostium as a big lid, is unique and can, for this reason, be considered apomorphous. Apparently it arose from a partial fusion of the lateral horns found in the other species.

30. Postvaginal plate. The distal edge of this plate may be indented, scalloped, wavy, straight, curved, even bipartite, but the edge is usually regular. The very irregular serration of the edge in *M. cresta* and *M. purpurascens* (possibly also in *M. deprivata*) must be considered a derived state.

31. Asymmetry. The strangely asymmetrical genitalia found in *M. sasivarna* and *M. celsina* (possibly also in the unknown female of *M. intermedia* as this species has many characters in common with the other two) is not found in the other *Matapa* species nor in the out-group. Therefore this condition is considered apomorphous here.

CONSIDERATIONS ON THE HISTORICAL GEOGRAPHY OF *MATAPA*

In the preceding chapter it was argued that there are three monophyletic groups of species, viz. (a) *M. aria* and *M. druna*, (b) *M. sasivarna*, *M. intermedia* and *M. celsina* (and, possibly, *M. pseudosasivarna*), and (c) *M. cresta*, *M. deprivata* and *M. purpurascens*. For convenience these groups will be named here the *aria* group, the *sasivarna* group and the *cresta* group, respectively.

From fig. 54 it is clear that the groups are largely sympatric. If the initial splittings of the genus were the results of allopatric speciation, this is entirely obscured by secondary sympatry.

As demonstrated by Holloway (1974) there are no traces of Gondwanaland butterflies in India, the butterfly fauna apparently having originated from invasions from the west and the east after the collision of India with the Asian continent. The present distribution and diversification of *Matapa* species agree with this picture. The only species occurring in the Indian subcontinent is *M. aria*. A Gondwanaland origin of this species with a subsequent splitting off of the other *Matapa* species to the east is contradicted by the supposed phylogeny of the genus, some splittings having occurred before the origin of *M. aria*. Theoretically it would be possible to suppose that the ancestor of *Matapa* inhabited India before its collision with Asia, and thereafter gave rise to the other *Matapa* species by splitting off to the east, meanwhile evolving in India to *M. aria* which as the latest invader from the west colonized Southeast Asia. There are, however, no arguments in favour of this view, while the absence of diversification in India and the large number of assumptions needed strongly militate against such an idea.

The very wide distribution (from W. India to Sumbawa and the Philippines), without geographic variation, suggests that *M. aria* is a good colonist.

There are no indications that in the origin of *M. aria* and its sister species, *M. druna*, the distribution area of which is entirely overlapped by that of *M. aria*, the occurrence of *M. aria* in India played a part. It rather seems that *M. aria* after its origin somewhere in Southeast Asia and helped by its ability to live in secondary growth, invaded India from the east. Part of the range extension of *M. aria* may well be very recent: in Hong Kong the species lives on introduced bamboo (Johnston & Johnston, 1980) and one wonders how far the northward extension is due to such introductions.

The distribution of the three species groups over Sundaland was made possible by lowering of the sea level during the Pleistocene (see, e.g., Holloway & Jardine, 1968: fig. 21; Roesler & Küppers, 1974: fig. 3; Zeuner, 1941: fig. 2). It implies that the origin of the groups, and of the species as far as they are distributed over Sundaland, dates back from before the lowering of the sea level. As there are no vicarious distributions within Sundaland, there are no indications that the fragmentation of Sundaland by rise of the sea level prompted to speciation. On the other hand, the distribution of the species of the *sasivarna* group strongly suggests allopatric speciation subsequent to colonization. *M. sasivarna* is restricted to Sundaland (actually, it is not known from Borneo, but its occurrence in Pulo Laut, a small island off the south-east corner of Borneo, makes it clear that it must exist or have existed in Borneo), while its sister group, *M. intermedia* + *M. celsina*, is restricted to the Philippines and Celebes. In view of the supposed origin of the species groups in mainland Southeast Asia discussed above, and of the high number of derivative character states in *M. intermedia* and *M. celsina*, it is most likely that the ancestor of these species arose by colonization of, and later isolation in the area east of the Line of Huxley (cf. Holloway & Jardine, 1968: fig. 4). The occurrence of *M. celsina* in the Philippines remains to be proved, but *M. intermedia* certainly occurs in Celebes as well as in the Philippines, illustrating the faunal contact that was possible between Mindanao and Celebes. As matters stand a plausible interpretation would be that *M. intermedia* arose by isolation in the Philippines subsequent to an invasion from the west by a *M. sasivarna*-like ancestor. It migrated to Celebes where it evolved in isolation to *M. celsina*. At a later period of low sea-level it invaded Celebes for the second time, where it became isolated again, but too recently to have given rise to a new species. This explanation concurs with Holloway's (1973) demonstration of the occurrence of at least two waves of invasions into Sundaland due to fluctuations in the disposition of land in the Pleistocene. It also agrees with the tentative finding (unpublished) that in the Hesperiidæ the faunal contact between Celebes and Borneo usually runs via the Philippines.

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