Discovery of the previously overlooked female of *Athyma reta* (Lepidoptera: Nymphalidae), and its taxonomic implications

Laurence G. Kirton¹*, Horace Tan², Chooi-Khim Phon¹ & Sin-Khoon Khew³

**Abstract.** The nymphalid butterfly *Athyma reta* Moore is shown from field observations and breeding experiments to have a black-and-orange female that has in the past been confused with *A. neftina* (Frühstorfer) (Frühstorfer). Its life history is described, and the morphology of its early stages compared with *A. neftina* and other species of *Athyma* Westwood. Morphological analysis of specimens in collections confirmed that *A. reta* is sexually dimorphic and has a monomorphic female that can be differentiated from *neftina* by at least two characters. Numerous females of *A. reta* have been misidentified in the literature and in collections as *A. neftina* female-form *neftina*, and many black-and-white males of *A. reta* have been misidentified as its female. Misidentifications in the literature are corrected. Descriptions in literature of the female of *A. reta* being black-and-grey in India are shown to be caused by historical confusion between taxa. This confusion may also have caused it to be wrongly reported from Burma and India. Evidence suggests that unlike *A. neftina*, which ranges from the Southeast Asian islands to the Asian continent, the distribution of *A. reta* does not extend further north than southern Thailand. Implications of the early stage and adult morphology to previously suggested infrageneric groupings of *Athyma* are discussed. Based on shared larval and pupal morphology, sexual dimorphism, and adult venation, *Athyma reta* is closely related to *A. neftina* and *A. cama* Moore, but distant from *A. kanwa* Moore with which it has been grouped in the past. A revised key is given for the species of *Athyma* in the Peninsula that have hairless eyes and a closed forewing cell.

**Key words.** butterflies, taxonomy, morphology, life history, *Athyma reta*, *Athyma neftina*

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**INTRODUCTION**

The butterfly genus *Athyma* Westwood in the Nymphalidae comprises numerous butterflies of varying morphology. Many are black on the upperside of the wings, with spots of varying shape that are usually white, often arranged to form stripes and band-like markings. In some species, however, some or all the spots are a shade of brown, yellow or orange, especially in females. *Athyma neftina* and the larger *A. cama*, are two such species, exhibiting sexual polymorphism and dimorphism, respectively. Their males are typical in having white markings, although some of the male’s distal markings in *A. neftina* are orange in the continental races. The monomorphic female of *A. cama* is marked orange but the markings may be paler and more yellow in dry season forms. The female of *A. neftina* is sometimes dimorphic, having an orange-marked female-form throughout its range, and a grey-brown-marked female-form that occurs in the southern half of its range with occasional intermediates. Here we use the female-form names *neftina* and *subrata* Moore for the orange- and grey-brown-marked females, respectively, across their range, as used in the Peninsular Malaysian subspecies.

*Athyma reta* is thought to be a species from Sundaland, occurring from Sumatra to Borneo through Peninsular Malaysia and Singapore, southwards to Java, with a continental range extension into northeast India and eastern Burma (Frühstorfer, 1913). Sexual dimorphism or polymorphism is said to be absent in *A. reta*, as in some other species of *Athyma*, throughout the insular and peninsular part of its stated range. The keys to the species of Peninsular Malaysian *Athyma* in the second to fourth editions of Corbet & Pendlebury (1956, 1978, 1992) state that the sexes are similar in *A. reta*, as in *A. kanwa*, but dissimilar in *A. selenophora* (Kollar), *A. neftina* and *A. cama*. Both editions of Fleming (1975, 1983) figure a male and state that the sexes of *A. reta* are similar. Tsukada (1985) figured white-marked males of *A. reta* from across Sundaland and similar looking females for a few subspecies. Similarly, Otsuka (1988) figured a white-marked male and female from Borneo, and said that, like *A. asura* Moore, the female has a paler ground colour, with larger wings and wing-markings. Other publications describe or figure the male of *A. reta* (see Corbet & Pendlebury, 1934; Morrell, 1960; D’Abrera, 1985; Pinratana & Eliot, 1996; Ek-Ammuay, 2012; Kimura et al., 2016) but do not mention the female, and hence inherently
imply that the species is sexually monomorphic. However, the female has also been said to have pale brown band-like markings that are rather narrow on the hindwings (Evans, 1932), a view adopted by literature on the butterflies of India (e.g., Wynter-Blyth, 1957; Kehimkar, 2008), which suggests that the female may not resemble the male in the continental part of its stated range, and may vary geographically.

In this study, we show that A. reta is, in fact, sexually dimorphic, with an orange-marked female that has been confused with the orange-marked female of Athyma nefte, female-form neftina. We provide evidence for the female of A. reta being orange-marked from breeding experiments. The life history of A. reta moorei (Frühstorfer) is described, and the morphology of its early stages compared with that of A. nefte subrata. We also analyse morphological differences between the very similar females of these two species and discuss the taxonomic implications of the morphology of the early stages and occurrence of sexual dimorphism.

Field observations and life histories reported in this article are the work of the second author, and the discovery of sexual dimorphism in A. reta was a direct result of this. Specimens for the morphological analysis of adult females were sourced or photographed by all authors. Analysis of character differences between the adult females are the work of the first and third authors, and the taxonomic descriptions and decisions are that of the first author.

**MATERIAL AND METHODS**

**Breeding experiments and analysis of early stages.** Field observations and the collecting of early stages for breeding were conducted from December 2015 to March 2016 at a site in western Singapore. Larvae and eggs were taken from a cluster of host plants during multiple visits and bred indoors at room temperature (24–27°C). Most of the eggs and larvae collected were successfully bred through to the adult stage, with premature mortality in only a few samples. A total of 36 adults were bred from the 20 larvae and 16 eggs, all of which were collected from the field. Three of the eggs collected and bred through to adult were observed to be laid by a single adult female in the field.

Male imagoes, which were easily identified as either A. reta moorei or A. nefte subrata, enabled early stage morphology to be differentiated for the two species. The external morphology of the early stages was studied and photographed. Comparisons were made between the morphology of the early stages of A. reta moorei and that of A. nefte subrata bred during the same period, and with published illustrations of the early stages of the latter (Igarashi & Fukuda, 2000; Tan & Khew, 2012). In addition, mating was also observed in the field in A. reta.

**Analysis of adult female morphology.** Since the female of A. reta moorei and female-form (hereafter abbreviated as f.-f.) neftina of A. nefte subrata were very similar, bred females were first identified based on their larval morphology, and these females that could be identified with certainty were used to investigate differences between the orange-marked females of the two species. Based on observed differences, eleven measured and two categorical wing characters (Table 1, Fig. 1) were taken for a larger sample of females of both species that were examined in public and private collections in Peninsular Malaysia and Singapore. These specimens were from the following collections:

- **Chong-Arshad** – The joint private collection of Chow-Yang Chong and Sabri John Arshad
- **FRIM** – Entomological Reference Collection, Forest Research Institute Malaysia, Kepong
- **Kirton** – The joint private collection of Eric, Colin and Laurence Kirton
- **Liew** – The private collection of Nyok-Lin Liew
- **MNM** – Malaysian National Museum, Kuala Lumpur
- **MZUM** – Museum of Zoology, University of Malaya, Kuala Lumpur
- **Neo** – The private collection of Stephen Neo
- **Tan** – The private collection of Horace Tan
- **ZRC** – Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore

Measurements were made from digital photographs of specimens and a photographed ruler scale using the image analysis software Digimizer® v. 4.6.1 (Medcalc Software). Images were taken such that the wings to be measured were parallel to the camera lens. The scale was either included...
in the photograph and supported level with the wings or separately photographed at identical focus and focal length.

A total of 102 females were measured, that is 34 specimens each of A. reta moorei, A. nefte subrata f.-f. neftina (including five intermediates with varying degrees of brown tinge to the orange markings), and A. nefte subrata f.-f. subrata. Specimen collection localities were from a wide geographic range from north of Peninsular Malaysia to Singapore. Principal components analysis (PCA) was used to determine the major sources of differences between the females. Discriminant function analysis (DFA) with cross-validation was then used for A. reta and A. nefte f.-f. nefina, to determine the most diagnostic differences between these very similar looking taxa. PCA was conducted using Minitab® v. 18.1. DFA and Box’s M test were carried out using SPSS® v. 20.0.0. Multivariate normality was tested using the MVN package (v. 5.5) in R v. 3.5.1.

In addition, the possibility of sexual polymorphism in A. reta was investigated, since the female of A. reta is usually said to have white markings like the male and sometimes said to have light brown markings like A. nefte f.-f. subrata. The sex of numerous white-marked phenotypes in collections was determined by careful examination and comparison of the abdomens, and the possibility of a brown phenotype was also investigated through morphological analysis of wing patterns. Descriptions of both species in older literature were also examined to determine historical accounts of the female that may have influenced present-day opinion.

### RESULTS

**Field observations and adults bred from early stages.**

The hostplant of both A. reta moorei and A. nefte subrata in Singapore was Glochidion zeylanicum var. zeylanicum (Gaertn.) A.Juss. (Phyllanthaceae). In the field, a male A. reta was observed in copulation with a female that had orange markings (Fig. 2A). A female with orange markings was observed laying eggs in the field (Fig. 2B). Three adults were reared from the eggs it laid, of which two were male A. reta and one was an orange-marked female.

<table>
<thead>
<tr>
<th>No.</th>
<th>Abbreviation</th>
<th>Character</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>FwL</td>
<td>Forewing length (cm) measured from the base of the cell to the tip of the apex.</td>
</tr>
<tr>
<td>2</td>
<td>CEAH</td>
<td>Height of the arrowhead-shaped marking at the forewing cell-end measured from the origin of vein 3 to the top of the arrowhead in a line parallel to the termen.</td>
</tr>
<tr>
<td>3</td>
<td>CEAA</td>
<td>Area (mm²) of the arrowhead-shaped marking at the forewing cell-end, including its distal-most extension.</td>
</tr>
<tr>
<td>4</td>
<td>CEAW</td>
<td>Widest width of the arrowhead-shaped marking at the forewing cell-end measured from the origin of vein 3 to the top of the arrowhead in a line following the cell-end (discocellular veins).</td>
</tr>
<tr>
<td>5</td>
<td>CEAL</td>
<td>Length of the arrowhead-shaped marking at the forewing cell-end measured on a straight line from the point at which it joins the lower cell streak on the cubitus to its furthest extent just above vein 4.</td>
</tr>
<tr>
<td>6</td>
<td>FwSp4SmS</td>
<td>Size of the forewing submarginal spot in space 4. (A) Wide: a spot or streak with a maximum width that is at least a third of its height and that stretches across most of the height of space 4; (B) Narrow: as in wide, but narrower, with maximum width less than a third the height; (C) Partial: a narrow and sometimes faint line or streak that does not extend into the lower half of space 4 or is partially obliterated by the postdiscal band; (D) Absent: lacks a submarginal spot in space 4 or is completely obliterated by the postdiscal band.</td>
</tr>
<tr>
<td>7</td>
<td>FwSp5Bw</td>
<td>Width of the forewing orange postdiscal band in space 5.</td>
</tr>
<tr>
<td>8</td>
<td>FwSp3Bw</td>
<td>Width of the forewing submarginal spot in space 3 at its widest point.</td>
</tr>
<tr>
<td>9</td>
<td>FwSp2Bw</td>
<td>Width of the forewing orange postdiscal band in space 2.</td>
</tr>
<tr>
<td>10</td>
<td>HwSp5Dbw</td>
<td>Width of the hindwing subdiscal orange band in space 5.</td>
</tr>
<tr>
<td>11</td>
<td>HwSp5IBw</td>
<td>Width of the hindwing discal inter-band black ground colour in space 5.</td>
</tr>
<tr>
<td>12</td>
<td>HwSp5PdBw</td>
<td>Width of the hindwing postdiscal orange band in space 5.</td>
</tr>
<tr>
<td>13</td>
<td>TBC</td>
<td>Colour of the mid-dorsal transverse thoracic band, or its residual scaling in worn specimens. (A) White: predominantly creamy white; (B) Yellow: orange to pale yellow.</td>
</tr>
</tbody>
</table>

Characters 7 and 9–12 measured midway between the bounding veins. All measurements taken on the upperside, on the right-side wings wherever possible, and in millimetres unless otherwise stated.
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Fig. 2. A, an identifiable male of *A. reta moorei* mating with an orange-marked female in the field; B, a similar female laying an egg at the tip of a leaf of its host plant.

Fig. 3. Upperside (left sides) and underside (right sides) of adults: A, *A. reta moorei* male; B, *A. reta moorei* female; C, *A. nefte subrata* male; D, *A. nefte subrata* f.-f. *neftina*.
Eggs, and larvae up to the third instar, as well as pupae of *A. reta moorei* very closely resembled those of *A. nefte subrata* and could not be differentiated. However, the larvae differed visibly between species from the late fourth instar onwards. Adults that emerged as male *A. reta* had late-instar larval morphology that was identical to that of many of the emerging orange-marked females that would normally be identified as *A. nefte* f.-f. *nelfina* (Fig. 3). All females that had larval morphology associated with *A. reta* had orange markings. Over the four-month period, 16 males and 15 females of *Athyma reta* emerged, and four males and one female of *Athyma nefte* (Fig. 3).

**Description of the early stages and life history of *Athyma reta moorei***. Host plant: Malayan Pin-flower Tree, *Glochidion zeylanicum* var. *zeylanicum* (Gaertn.) A.Juss. (Fig. 4A), sometimes called *Phyllanthus zeylanicum* (Gaertn.) Müll. Arg. or *Glochidion brunnneum* Hook.f. (synonym). Life cycle duration. 23–25 days for females, and 21–24 days for males.

**Egg** (Fig. 4B, C). Typically laid at the tips of mature leaves (Fig. 2B). Dome-shaped, with polygonal ridges tipped with fine, translucent spines at the angles of the polygonal ridges. Colour yellowish when laid. Basal diameter approximately 1.0 mm. Incubation period: invariably three days at room temperature.

**Larva** (Fig. 4D–M). Undergoes five instars described below. Bears setae that are branched in later instars. Ground colour initially brown with dorsal patches, turning green in the final instar. Behaviour: Feeds on mature leaves throughout its development, from the leaf tip towards the petiole, leaving the midrib intact. Builds an extension of the exposed midrib in the early instars, using frass held together by silk. Frass is also sewn together beneath the midrib. Rests on either the frass extension or the exposed midrib of the leaf above the bundle of frass. Abandons this habit in the fifth instar, resting on the upperside of the leaf surface and feeding irregularly from the leaf edge. Similar feeding and resting behaviour have also been observed in *A. nefte* (see Igarashi & Fukuda, 2000; Tan & Khew, 2012), *A. cama* and *A. selenophora* (by Igarashi & Fukuda, 2000), and is probably shared by other species.

**First instar** (Fig. 4D, E). Body with fine setae and dorso-lateral, lateral and subspiracular tubercles. Body ground colour pale, dull brown; head brown. Length 2.2–4.8 mm. Duration of instar: two days.

**Second instar** (Fig. 4F, G). Dorso-lateral, lateral and subspiracular body tubercles with short, branched setae. Head with tubercles and short peripheral spines. Body colour dark brown. An obscure, pale brown diamond-shaped dorsal patch stretches from A5 (the 5th abdominal segment) to A4, and a similar coloured triangular dorsal patch extends from A3 to A4. Head brown, with tubercles pale brown. Length reaches 7.0 mm. Duration of instar: two days.

**Third instar** (Fig. 4H, I). Structurally similar to the second instar, but with the body tubercles and setae and the head spines longer and more prominent. Ground colour of body and head darker. Pale brown dorsal patches more distinct. A further pale brown triangular dorsal patch becomes visible from T3 (3rd thoracic segment) to A1. Subspiracular processes on A7–A9 whitish. Length reaches 10.5 mm. Duration of instar: two days.

**Fourth instar** (Fig. 4J, K). Dorso-lateral branched setae in T2 and T3 distinctly longer than the other setae; peripheral head spines longer than in the previous instar. Dorsal patches in T3–A1 and A2–A4 green in the latter half of instar; that in A5 and the distal-most end of A4 reddish brown. Length reaches 15 mm. Duration of instar: three days.

**Fifth instar** (Fig. 4L, M). Dorso-lateral setae elongated and branched distally; peripheral spines on head pointed. Body ground colour initially brown, turning green in a day. Dorso-lateral and lateral processes reddish. Dorsal patches on T3–A1 and A2–A4 disappear when the body colour turns green. Dorsal patch on A5 rectangular, black initially, but turning purplish to reddish brown as the body turns green. Head dark brown to black, with off-white or pale pinkish frontal stripes flanking the adfrontal suture. Tubercles on head of the same colour as the frontal stripes. Length reaches 32 mm. Duration of instar: 4–5 days.

Pre-pupa. Body decolourised to pale brown. Pre-pupal duration: 1 day. Attaches itself before pupation to the underside of the midrib of a leaf or, rarely, to the underside of a branch.

**Pupa** (Fig. 4N, O). Cephalic protuberances with their apices extended laterally. Dorsal protuberances on T1 and A1 long, keeled and pointed towards each other. Colour orange-brown with golden patches. Length 22–23.5 mm. Pupal period: seven days.

**Differences in the early stages of *A. reta moorei* and *A. nefte subrata***. The early stages of *A. reta moorei* and *A. nefte subrata* bear strong resemblance. They share the same host plant, and their eggs, pupae, and larvae in the first three instars are superficially indistinguishable. When the larvae are in the fourth and fifth instars, the two species can be easily distinguished (Fig. 5).

On the first day of the fourth instar, the three dorsal patches of both species are still a shade of brown, with the patch in A4–A5 paler than the other patches and contrasting with the ground colour in *A. nefte* (Fig. 5A), but slightly darker than the other patches and barely contrasting in *A. reta* (Fig. 5B). As the two anterior dorsal patches turn green, the patch on A4–A5 turns a contrasting pale pink-brown in *A. nefte* (Fig. 5C), while that of *A. reta* turns a dark red-brown of nearly the same shade as the ground colour (Fig. 5D).

During the fifth instar, the ground colour of the body is still a shade of brown on the first day. At this stage, *A. nefte* has three somewhat diffuse black dorsal patches from the
Fig. 4. Hostplant and early stages of *A. reta moorei*: A, the hostplant, *Glochidion zeylanicum* var. *zeylanicum*; B–O, lateral and dorsal views, respectively, of egg (B, C), first instar (D, E), second instar (F, G), third instar (H, I), fourth instar (J, K), fifth instar (L, M), pupa (N, O).
Fig. 5. A–H, differences between the dorsal body markings of fourth and fifth instar larvae of *A. nefte subrata* (left) and *A. reta moorei* (right): A, B, early fourth instar; C, D, late fourth instar; E, F, early fifth instar; G, H, late fifth instar. I–K, differences in the anterior markings of the head of the fifth instar: I, *A. nefte subrata*; J, K, *A. reta moorei*. 
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posterior half of A4 to A5 (Fig. 5E), while *A. reta* has a single well-defined black patch on A5 (Fig. 5F). After the body colour turns green, the central patch in *A. nefte* becomes a paler reddish brown, flanked anteriorly and posteriorly by smaller black patches (Fig. 5G). However, in *A. reta*, the single patch turns dark purplish brown (Fig. 5H). The two species are also readily differentiated by their head markings in the fifth instar — the head capsule of *A. nefte* is uniformly dark brown to black with no pale-coloured stripes (Fig. 5I) and, in contrast, the head capsule of *A. reta* has pale coloured stripes running down the front of the head (Fig. 5J, K).

**Morphological differences between the adult females of *A. reta moorei* and *A. nefte subrata*.** Among all the black and white phenotypes of *A. reta moorei* that were examined closely in collections, none were females. Wing shape of the orange-marked female of *A. reta* is similar to the wing shape of the females of closely related *A. nefte* and *A. cama*. The females have the appearance of a more elongate forewing, and the length of the hindwing costa relative to the hindwing dorsum is greater in females than in males because their hindwing apex is more pronounced and their hindwing tornus more rounded. Wing shape of all white-marked specimens of *A. reta*, though slightly variable, were characteristically male. None had wing shape typical of females.

Based on larval morphology of bred specimens, it was possible to match the sexes of a small number of *A. nefte subrata*, sufficient to enable a comparison and determine differences between the female of *A. reta moorei* and *A. nefte subrata* f.-f. *neftina*. Females of *A. reta* had a yellow or orange thoracic band unlike the whitish thoracic band of *A. nefte* f.-f. *neftina*. They also had wider orange markings, especially on the hindwing. A submarginal spot was present in space 4 in *A. reta* between the orange postdiscal band and marginal line. In addition, the arrowhead-like discal spot in space 4 was convex at its upper margin near the upper discocellular; in *A. nefte* it was concave. On the underside, females of *A. reta* were more orange-looking than *A. nefte* f.-f. *neftina*, which tended to look browner and therefore darker. There was more orange scaling on the edges of the underside bands and spots in *A. reta* than in *A. nefte* f.-f. *neftina*, and the centres of the bands and spots were a shade of pale orange. In *A. nefte* f.-f. *neftina*, the centres were almost white with a slight pink or pale orange tinge, contrasting against the relatively dark and brown ground colour.

However, in the larger series of specimens examined from the Peninsula and Singapore, the thoracic band was sometimes virtually worn off in damaged or old specimens, making it difficult to use for identification, and there was variation in the other characters. The most consistent character was the shape of the forewing cell-end arrowhead marking in space 4.

PCA of forewing length and band-width measurements for all females of *A. reta moorei* and *A. nefte subrata* showed that the primary differences in the sample were in a contrast between the size of individuals and width of the markings against the hindwing inter-band width (Table 2). This was evident from the first principal component, which contributed to 55.2% of the variation, and had positive values for forewing length and all markings, but a negative value for the hindwing inter-band width. This component also provided the greatest separation between taxa (Fig. 6).

<table>
<thead>
<tr>
<th>Character</th>
<th>Component 1</th>
<th>Component 2</th>
<th>Component 3</th>
</tr>
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<tbody>
<tr>
<td>FwL</td>
<td>0.116</td>
<td>-0.860</td>
<td>-0.050</td>
</tr>
<tr>
<td>FwSp5Bw</td>
<td>0.421</td>
<td>0.070</td>
<td>-0.469</td>
</tr>
<tr>
<td>FwSp3Bw</td>
<td>0.353</td>
<td>-0.046</td>
<td>0.607</td>
</tr>
<tr>
<td>FwSp2Bw</td>
<td>0.404</td>
<td>-0.108</td>
<td>-0.409</td>
</tr>
<tr>
<td>HwSp5DBw</td>
<td>0.465</td>
<td>-0.008</td>
<td>-0.125</td>
</tr>
<tr>
<td>HwSp5IBw</td>
<td>-0.396</td>
<td>-0.471</td>
<td>-0.080</td>
</tr>
<tr>
<td>HwSp5PdBw</td>
<td>0.386</td>
<td>-0.139</td>
<td>0.468</td>
</tr>
</tbody>
</table>

| Eigenvalue         | 3.8627      | 1.2084      | 0.7783      |
| Accumulated variance (%) | 55.2       | 72.4         | 83.6        |

Fig. 6. Scatter diagram of the scores for the first and third principal components of PCA for forewing length and band-width measurements of all taxa.
The second principal component was mainly the influence of wing size and did not contribute to separation of taxa. The best secondary separation of taxa was in component 3, a contrast between the widths of the forewing submarginal spot in space 3 and hindwing postdiscal band against the width of the other wing markings. This component provided some degree of separation in *A. nefte subrata* f.-f. *neftina* (Fig. 6). Neither component provided full separation of taxa.

When DFA with cross-validation was used on band-width measurements of *A. reta moorei* females and *A. nefte subrata* f.-f. *neftina*, separation of taxa was incomplete, with 83.8% classified correctly. The eigenvalue and correlation coefficient of the resulting canonical discriminant function were 1.154 and 0.732, respectively. The discriminant function was significant (Wilk’s Lambda = 0.464, $\chi^2 = 48.342$, df = 6, $P < 0.001$), and the classification functions were *neftina* = $-212.047 + 3.334 (FwSp5Bw) + 6.673 (FwSp3Bw) + 10.845 (FwSp2Bw) + 16.720 (HwSp5DBw) + 36.191 (HwSp5IBw) + 21.453 (HwSp5PdBw)$, and *reta* = $-227.052 + 3.582 (FwSp5Bw) + 9.389 (FwSp3Bw) + 9.229 (FwSp2Bw) + 19.508 (HwSp5DBw) + 36.376 (HwSp5IBw) + 22.519 (HwSp5PdBw)$. The data fulfilled the assumptions of homogeneity of covariance (Box’s M = 35.53, $p = 0.058$) and multivariate normality (Royston’s H = 4.25, $p = 0.642$ in *A. reta moorei*; H = 5.07, $p = 0.511$ in *A. nefte subrata* f.-f. *neftina*).

PCA and DFA confirmed that females of *A. reta moorei* generally have wider orange markings on the forewing and hindwing than *A. nefte subrata* f.-f. *neftina*, but that the difference is not diagnostic due to variation between individuals (Fig. 7). A measure of overlap occurs in the widths of the bands relative to the inter-band width. The PCA also showed that *A. nefte subrata* f.-f. *neftina* has narrower markings on average than f.-f. *neftina*.

In females of *A. reta moorei*, the forewing submarginal spot or streak in space 4 was wider than in females of *A. nefte subrata*, being classed as wide in 94% of specimens and narrow in only 6% (Table 3). In the latter, the streak was more variable but generally narrower if present. Specimens of *A. nefte subrata* f.-f. *neftina* had narrow or partial streaks and sometimes no streak at all (21%), while specimens of *A. nefte subrata* f.-f. *subrata* usually had a narrow streak (79%), sometimes a partial streak, and only occasionally a wide spot or streak (Table 3). Therefore, this character was helpful in differentiating the orange females but not reliably diagnostic.

Using PCA for cell-end arrowhead measurements of all females, virtually complete separation of *A. reta moorei* and *A. nefte subrata* f.-f. *neftina* was achieved with components 1 and 3 (Fig. 8), which contributed to 66.7% and 10.3% of the total variation, respectively. However, *A. nefte subrata* f.-f. *subrata* was more variable, overlapping with both *A. reta moorei* and *A. nefte subrata* f.-f. *neftina*. Component 1, with its positive loading values for all measurements, was a size contrast of the cell-end marking (Table 4). Component 2, which did not separate the taxa adequately, was primarily a contrast between the width and height of the cell-end marking with its length and to a lesser extent its area. Component 3 was a contrast between its width and to a lesser extent length compared to its height and to a lesser extent area (Table 4).

---

Table 3. Differences in the size of the forewing submarginal spot in space 4 in females of *A. reta moorei* and *A. nefte subrata* shown as percentages of individuals in each category ($n = 34$ per taxon).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Wide</th>
<th>Narrow</th>
<th>Partial</th>
<th>Absent</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. reta moorei</em></td>
<td>94</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>A. nefte subrata</em> f.-f. <em>neftina</em></td>
<td>0</td>
<td>44</td>
<td>35</td>
<td>21</td>
</tr>
<tr>
<td><em>A. nefte subrata</em> f.-f. <em>subrata</em></td>
<td>3</td>
<td>79</td>
<td>18</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 4. Loading values for the first three components of PCA on cell-end arrowhead measurements of all taxa.

<table>
<thead>
<tr>
<th>Character</th>
<th>Component 1</th>
<th>Component 2</th>
<th>Component 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>CEAA</td>
<td>0.591</td>
<td>-0.081</td>
<td>0.214</td>
</tr>
<tr>
<td>CEAW</td>
<td>0.471</td>
<td>0.459</td>
<td>-0.746</td>
</tr>
<tr>
<td>CEAL</td>
<td>0.370</td>
<td>-0.844</td>
<td>-0.243</td>
</tr>
<tr>
<td>CEAH</td>
<td>0.540</td>
<td>0.266</td>
<td>0.582</td>
</tr>
</tbody>
</table>

Eigenvalue: 2.6684, 0.8485, 0.4115
Accumulated variance (%): 66.7, 87.9, 98.2
When DFA with cross validation was used for the cell-end arrowhead measurements of *A. reta moorei* females and *A. nefte subrata f.-f. neftina*, it led to complete separation of the two taxa. All individuals were classified correctly. The canonical discriminant function had an eigenvalue of 5.496 and correlation coefficient of 0.920, and was significant (Wilk’s Lambda = 0.154, $\chi^2 = 119.754$, df = 4, $P < 0.001$). The classification functions were $\text{neftina} = -351.792 - 25.619 \times \text{CEAA} + 170.631 \times \text{CEAW} + 47.350 \times \text{CEAL} + 40.181 \times \text{CEAH}$, and $\text{reta} = -344.243 - 23.070 \times \text{CEAA} + 145.261 \times \text{CEAW} + 44.790 \times \text{CEAL} + 61.561 \times \text{CEAH}$. As in the analysis of band widths, the data fulfilled the required assumptions of homogeneity of covariance (Box’s $M = 16.38$, $p = 0.121$) and multivariate normality (Royston’s $H = 3.51$, $p = 0.457$ in *A. reta moorei*; $H = 3.49$, $p = 0.488$ in *A. nefte subrata f.-f. neftina*).

The numerical analyses of the shape of the cell-end arrowhead marking therefore confirmed that it is a more reliable diagnostic feature than band widths. In females of *A. reta moorei*, the arrowhead marking is usually larger in area and shorter, and its upper margin is usually convex or straight as it progresses outwards from the cell-end. It then curves downwards and rapidly tapers to a point. In *A. nefte subrata*, the arrowhead marking is smaller in area and, at least in *f.-f. neftina*, more elongate. Its upper margin rapidly becomes concave as it leaves the cell-end and thereafter it forms a long, tapered streak. Therefore, in the PCA of arrowhead measurements for *A. reta moorei* and *A. nefte subrata*, the orange-marked individuals were marginally separated into their respective taxa in an ordination of component 1, which reflected overall arrowhead size, and component 3, which contrasted height and area with width and length. Height, as defined (Table 1), measured the arrowhead parallel to the termen and therefore further from the cell-end than width, which by definition measured it along the discocellular veins. Since *A. nefte subrata* has a more rapid narrowing of the cell-end arrowhead compared to *A. reta moorei*, these two measurements contributed much to the separation of the two taxa in component 3.

The colour of the transverse mid thoracic band is a consistent character but may be difficult to see in old and worn specimens. It is a very useful character in clear photographs of open-winged orange females in the field, in which the scales are less likely to have rubbed off. In all the females of *A. nefte subrata f.-f. neftina* that we examined, the colour of the band, or at least the residual scaling that remained, was white or off-white. In all females of *A. reta moorei*, it was orange or at least pale yellow.

No single character is always easy to use in separating *A. reta moorei* and *A. nefte subrata f.-f. neftina*. The widths of the orange markings vary but are on average narrower in the latter than in the former. Based on figured specimens in Tsukada (1985) and Otsuka (1988), this trend of generally narrower orange markings in *A. nefte* holds true throughout the peninsular and insular distribution of *A. reta* and *A. nefte* in Sundaland. The shape of the arrowhead is the most diagnostic wing character in this region, although it also varies to the point of occasional difficulties in separating the species (Fig. 9). However, in the continental races of *A. nefte*, that is *asita* Moore, *inara* Westwood and *seitzi* (Frühstorfer), the orange females bear an even closer resemblance to the female of *A. reta* as they have much wider orange markings, sometimes exceeding that of any specimen of *A. reta*, and on the underside are even more orange than *A. reta*, sometimes having a reddish tinge. In addition, the forewing cell-end arrowhead marking on the upperside is often straight, or slightly convex at its upper margin as in *A. reta*. It may be long and somewhat evenly tapered like *A. reta* or short and very abruptly tapered unlike *A. reta*, forming an almost triangular mark with a streak-like extension. These races, however, do have a faint white thoracic band typical of *A. nefte* and lack...
the forewing submarginal spot in space 4. Since it appears unlikely that *A. reta* occurs north of Peninsular Thailand, as explained later in the discussion section, confusion of *A. nefte* females on the continent with *A. reta* is unlikely to be an issue. However, clearly, multiple characters should be used when identifying the orange females of these two species. The geographic location, width of the bands, spot pattern, shape of the arrowhead and colour of the thoracic band should be examined, and an identification reached based on these multiple considerations.

**Material used in the analysis**

**Athyma nefte subrata f.-f. subrata**: Peninsular Malaysia — Kedah: Langkawi (7 specimens: 5 ZRC, 2 MNM); Langkawi, Bukit Tembak (Chong-Arshad) — Selangor: Batang Berjuntai (2 specimens: ZRC); Bukit Tairik (2 specimens: Chong-Arshad, ZRC); Gombak (MZUM); Rantau Panjang (2 specimens: ZRC); Templar Park (2 specimens: MZUM, ZRC) — Pahang: Kuantan, Bukit Sekilau (Kirton); Fraser’s Hill (2 specimens: ZRC, FRIM); Genting (MZUM); Lanachel (Liew); Lata Jarum (Liew); Tanum, Sungai Yu Corridor (FRIM) — Negeri Sembilan: Kenaboi (2 specimens: MZUM); Seri Menanti (Chong-Arshad) — Johor: Batu Pahat (MZUM); Panti FR (3 specimens: FRIM); Skudai (Neo). **Singapore** — Nanyang (2 specimens: Tan).

**Athyma reta moorei** female: Peninsular Malaysia — Kedah: Langkawi (7 specimens: 5 ZRC, 2 MNM); Langkawi, Bukit Tembak (Chong-Arshad) — Selangor: Batang Berjuntai (2 specimens: ZRC); Bukit Tairik (2 specimens: Chong-Arshad, ZRC); Gombak (MZUM); Rantau Panjang (2 specimens: ZRC); Templar Park (2 specimens: MZUM, ZRC) — Pahang: Kuantan, Bukit Sekilau (Kirton); Fraser’s Hill (2 specimens: ZRC, FRIM); Genting (MZUM); Lanachel (Liew); Lata Jarum (Liew); Tanum, Sungai Yu Corridor (FRIM) — Negeri Sembilan: Kenaboi (2 specimens: MZUM); Seri Menanti (Chong-Arshad) — Johor: Batu Pahat (MZUM); Panti FR (3 specimens: FRIM); Skudai (Neo). **Singapore** — Nanyang (2 specimens: Tan).

**Description of the female of *A. reta***. The following is a first description of the female of *A. reta*. Upperside ground colour of wings black-brown from above vein 1a of the hindwing and on the whole forewing, with contrasting white cilia on the mid margins of each of spaces 1b–4 on the forewing and spaces 1b–7 of the hindwing, and marked with orange spots, bands and lines as follows. On the forewing: a streak running narrowly from the base of the wing into the lower half of the cell where it expands and is broken on its upper margin then tapers slightly at the end of the cell; an arrowhead-shaped marking in space 4 just beyond the cell, tapering towards mid vein 4 and always at least slightly convex at its upper margin in the first quarter of space 4; an irregular band comprising four spots from mid space 1a to the lower half of mid space 3; a series of submarginal spots starting in space 1a and running parallel to the termen to space 3, thereafter continued as a postdiscal band that arcs to the costa in spaces 4–6, flanked by a costal dash in space 10; a small submarginal spot or streak in space 4 forming an arc with subapical spots in spaces 5 and 6, flanked by a costal dash in space 8; a marginal line from space 1b to space 6, sometimes faintly present in spaces 1a and 7. On the hindwing: a subdisclal band from vein 1b to vein 8;
The female of *A. reta* can be distinguished from the orange female form of *A. nefte* by the orange or yellow thoracic band, which is white in *A. nefte*. In the Sundanian region, to which it may be restricted, it is also reliably distinguishable by the convex upper margin of the basal half of the cell-end arrowhead, which is concave in *A. nefte*. Other less reliable differences in the Sundanian region, which are described in more detail above are (i) wider orange markings in *A. reta*, (ii) a clearer submarginal spot in space 4 of the forewing upperside between the postdiscal and narrow marginal bands, (iii) a generally stronger orange color on the underside, (iv) more orange scaling flanking the underside markings, and (v) pale orange underside bands and spots, instead of almost white markings with a pink or pale orange tinge as in *A. nefte* f.-f. *neftina*.

**Recognised subspecies of *A. reta***

The following subspecies of *Athyma reta* are recognised:  
*syma* (Frühstorfer, [1913]) – Nias  
*riambo* (Corbet, 1942) – Mentawai Islands  
*moorei* (Frühstorfer, 1906) – Southern Thailand, Peninsular Malaysia and Singapore  
*kresna* Moore, 1858 – Borneo  
*retina* (Frühstorfer, 1906) – West Java

The name “eurylena” attributed by Frühstorfer (1906) to Hagen (1898) as a subspecies of *Athyma* (“Pantoporia”) *reta* in Sipora is a misspelling and misdating of *eurylena* Hagen, 1898, rightly considered by Corbet (1942) to be a subspecies of *A. kanwa* from Mentawai. The taxon *adunora* Kheil, described from Nias, was once placed as a subspecies of *A. reta* by Frühstorfer (1906), but is a subspecies of *A. clerica* Butler (see Eliot & Kirton, 2000; see also specimen figured in original description).

**Misidentifications in the literature.** The following specimens figured as females of *A. reta* are in fact males of this species: Frühstorfer (1913), pl. 124, row d, third fig. from left, *reta syma*, Nias — Tsukada (1985), pl. 143: fig. 13–16, *reta syma*, Nias; figs. 18–20, *reta riambo*, Mentawai — Otsuka (1988), pl. 58, row a, second and third figs. from left, both *reta kresna*, Borneo.


**Implications to the relationships of species.** Pinratana & Eliot (1996) attempted to assign species traditionally placed under *Athyma* in subgenera using names originally described as genera by Moore (1898). They placed *A. kanwa*, *A. reta*, *A. nefte* and four other species of *Athyma* in subgenus *Tatisia* Moore based on their closed forewing cell and hairy eyes. Prior to this, *A. reta* and allied species have also been placed in a common group with *A. kanwa* (in Evans, 1932) or placed in a systematic position that suggests it is closely related to this species (e.g., Corbet & Pendlebury, 1992). This is probably because the males of both *A. reta* and *A. kanwa* have the forewing cell-end spot separated from the cell streak and the forewing spot in space 2 separated from the spot in space 1b. In addition, the female of *A. reta* was thought to resemble the male, as in *A. kanwa*.

However, the discovery that the female of *A. reta* has orange markings, and an analysis of the morphology of its early stages, enables some new inferences on the relationships of the species. Firstly, *A. reta* is closely related to *A. nefte* and *A. cama*. The early stages of *A. reta moorei* closely resemble those of *A. nefte subrata*, which is compared alongside *A. reta* in this study, and has also been figured by Igarashi & Fukuda (2000) from Peninsular Malaysia and by Tan & Khew (2012) from Singapore. The two species also share a common hostplant, *Glochidion zeylanicum* var. *zeylanicum*. Both species share very similar larval characteristics with *A. cama zoroastres* Butler (Taiwan) for which the early stages have been illustrated by Igarashi & Fukuda (2000), and in common with this species they also exhibit sexual dimorphism.

*Athyma reta*, *A. nefte* and *A. cama* have a few early stage characters in common with *A. selenophora laelia* (Frühstorfer) (Taiwan), *A. perius perius* (Linnaeus) (Peninsular Malaysia), *A. gutama teldeniya* (Frühstorfer) (Palawan), *A. speciosa Staudinger* (Palawan) and *A. libnites libnites* (Hewitson) (Sulawesi), for which the early stages have been figured by Igarashi & Fukuda (2000). The same characters are seen in...
A. pravara helma (Frühstorfer), A. clerica clerica and Pandita sinope sinope Moore, which have been bred by L.C. Goh (personal communication, photographs seen). The fifth instar larvae of all these species have narrow, elongated thoracic and abdominal setae that branch into three or four at their tips. They also have small peripheral conical head spines and small rounded frontal head tubercles. In the pupae of these species, the cephalic protuberances that encase the palpi are relatively short, flexed sideways and drawn to a fine-tipped point.

The larval and pupal stages of all the above species differ starkly from those of A. kanwa, which has thick and densely branched setae in the final larval instar and greatly elongated cephalic protuberances that encase the palpi in the pupa, resembling A. venata Staudinger from Palawan (Igarashi & Fukuda, 2000). Athyma kanwa and A. venata also differ structurally from these other species in the adults, in having the origin of forewing vein 3 located on vein 4 beyond the lower discocellular vein, instead of located on the cubitus before or beside the lower discocellular vein. These clear structural differences in the early stages and adult indicate that A. reta and other allied species are not closely related to A. kanwa, with which they have in the past been grouped (Pinratana & Eliot, 1996).

In view of the above, the name Tatisia, if applied as a species grouping at any infra-generic level, would likely include only A. kanwa (the type species of Tatisia) and A. venata. The name Zabana Moore is available as an infra-generic name for A. nefte and allied species if required, since its type species, Athyma urvasi C. & R. Felder, is a male of A. nefte with white markings that are broader than usual. Most of the remaining species placed in Tatisia by Pinratana & Eliot (1996), including A. nefte, were originally placed in Pantoporia Hübner by Moore (1898) who considered the type species of this genus to be Athyma nefte, having overlooked that the type species was fixed by Scudder (1875) as Pantoporia hordonia (Papilio hordonia Stoll), as pointed out by Hemming (1967).

Recent molecular studies (Dhungel & Wahlberg, 2018; Wu et al., 2018) have provided new insights into the relationships of species within the Limenitidini. These studies suggest that some of the species traditionally placed in Athyma merit being placed in genera of their own (Tacola Moore) or, in other cases, should be placed under Limenitis Fabricius (e.g., asura). Conversely, they suggest that some species placed in other genera (Samalia Moore) or genera of their own (Pandita Moore) are congeneric with Athyma. These findings broadly agree with the larval and pupal morphology of species for which the life histories are known. For example, all the species mentioned earlier that share the larval and pupal characters of A. reta are grouped within a common clade in the mitochondrial 37 gene analysis of Wu et al. (2018). However, the phylogenetic tree is less in agreement with the very divergent larval and pupal morphology of A. kanwa, a species included in the same clade. Clearly, further studies on adult and early stage morphology, host plants, gene sequences and behaviour will be needed to fully clarify the relationships of species in the Limenitidini. It is also certain that a revision of the subgeneric divisions of Athyma proposed by Pinratana & Eliot (1996) will be required.

Revision of the key to species of Athyma with hairless eyes and closed forewing cell

A revised key to the species of Athyma in Peninsular Malaysia and Singapore that have hairless eyes and a closed forewing cell is given below, modelled after and using a similar format to the key in Corbet & Pendlebury (1992), but using characters that apply also to races outside of the region.

1 (2) Vein 3 originates beyond the lower discocellular vein. Upperside forewing cell-streak entire and separated from the spot beyond. Sexes similar ....................... A. kanwa

2 Vein 3 originates on the cubitus before the lower discocellular vein. Upperside forewing cell-streak close to or touching the spot beyond, and often divided. Sexes dissimilar.

3 (4) Upperside forewing with the postdiscal spot in space 4 located below the larger postdiscal spot in space 5 and not or barely extending beyond the outer edge of the spot in space 5, except sometimes in females. Female black-brown with off-white macular upperside markings, the spots in spaces 1b, 2 and 3 separate and in line ....... A. seleophora

4 Upperside forewing with the postdiscal spot in space 4 extending well beyond the outer edge of the larger postdiscal spot in space 5. Female with orange, brown or grey upperside markings, the spots in spaces 1b, 2 and 3 virtually joined.

5 (6) Male with the white spots in mid spaces 1b and 2 well separated. Female with upper margin of the arrowhead-like spot at the base of space 4 convex just beyond the upper discocellular; markings orange ..................................... A. reta

6 Male with the white spots in mid spaces 1b and 2 joined. Female with upper margin of the arrowhead-like spot at the base of space 4 concave or nearly straight just beyond the upper discocellular.

7 (8) Upperside forewing postdiscal spots in spaces 4 and 5 with their basal edges greatly out of line. Posdiscal spot in space 4 small if present in male, located at the distal edge of the postdiscal spot in space 5, larger in female, with its basal edge often step-like with the spot in space 5. Female with orange markings .............................................. A. cana

8 Upperside forewing postdiscal spot in space 4 always present and usually almost as large as the postdiscal spot in space 5, with its distal and basal edges in line or sinuous with the edges of the spot in space 5. Female with markings brown (E.-f. subrata) or orange (E.-f. nefteina) ...... A. nefte

DISCUSSION

The existence of sexual dimorphism in A. reta was clear from field observations, breeding experiments and subsequent analysis of the morphology of the females. This alone did not preclude the possibility of a female-form of A. reta that is black-and-white or black-and-brown, as suggested by various authors who describe the female of A. reta as being like the male (e.g., Fleming, 1983; Otsuka, 1988; Corbet & Pendlebury, 1992) or as having light brown markings (e.g., Evans, 1932; Wynter-Blyth, 1957; Kehimkar, 2008).
Examination of numerous white-marked specimens of *Athyma reta moorei*, however, showed no evidence of the presence of females. The genitalia of *Athyma* are well hidden in the abdomen in both males and females, and the abdomens of the sexes are superficially similar. To add to the ease of confusion, the males of *A. reta* can be variable in wing shape, having a very angular forewing apex and hindwing tornus or slightly rounded wings. They also vary slightly in ground colour from black to black-brown. It is easy to assume that individuals with lighter colour or less angular wings are females. However, the females of *Athyma* have a recognisably different wing shape from the males, as described in the results section. This makes it highly unlikely that any of the white-marked individuals illustrated in the literature or seen in collections, which have wing shapes resembling males, are females, a possible exception being the specimens of *A. reta riamba* from Mentawai Island figured in Tsukada (1985), which have wing shape approaching that of females. However, it is unprecedented for a species of *Athyma* to have both a banded female-form with coalesced forewing markings as in the orange female of *A. reta* and a spotted female-form with macular forewing markings as in the male of *A. reta*. In the unlikely event that a female of the latter type is found that identifies as *A. reta*, it would suggest the existence of a cryptic species within what we know as *A. reta*.

The existence of a brown-marked form of *A. reta* is also highly unlikely. Firstly, the colour of the thoracic band in all brown-marked individuals examined was whitish as in orange-marked *A. nefte subrata* f.-f. *neftina*. Secondly, the shape of the forewing cell-end arrowhead marking of all brown phenotypes resembles that of orange *neftina* in being concave on its upper margin from just beyond the cell-end. In no individuals that we examined was it convex as in *A. reta*, or even straight. Thirdly, all brown phenotypes tend to have even narrower markings than orange *neftina*, and contrast too greatly with the broad markings of *A. reta*. It is a logical conclusion, therefore, that all brown phenotypes are *A. nefte* f.-f. *subrata*.

The prevailing view in literature on the Indian butterfly fauna that the female of *Athyma reta* has grey-brown markings (Evans, 1932; Wynter-Blyth, 1957; Kehimkar, 2008) appears to be a result of a historical confusion of taxa. Moore (1858) described *A. reta* based on males from Sumatra, and along with it, *A. kresna* from Borneo and Sumatra, which is now considered the Bornean subspecies of *A. reta*. He later said that the female of *A. kresna* usually has reddish markings, without providing a diagnosis that would separate it from *A. nefte* (see Moore, 1886). In addition, he said it was dimorphic, with a brown-marked female-form that he had originally named as a species, *subrata*. Moore (1898) also considered the brown-marked nominal taxon *gandara* C. & R. Felder from Java to be the female of *A. reta*. Distant, who initially thought the female of *kresna* was like the male, at least in Borneo (Distant, 1883), later followed Moore, and believed that the female of *kresna* might even be trimorphic, with an orange-, brown- and presumably white-marked form (Distant, 1886).

De Nicéville & Martin (1896) were responsible for sorting out the taxa as we know them today. De Nicéville argued that *reta* and *kresna* were the same species, and that *subrata* was both a race and female-form of *A. nefte*. The female of *A. nefte*, he pointed out, was monomorphic and orange-marked in subspecies *inara* (India) and subspecies *asita* (Burma and Thailand), and dimorphic with both an orange- and brown-marked form in subspecies *subrata* (Sumatra, the Peninsula and Borneo) and subspecies *nefte* (Java). Frühstorfer (1906) agreed with de Nicéville & Martin but retained *kresna* as the Bornean subspecies of *reta*, as it remains today. He gave the subspecific name *moorei* to the phenotype in Peninsular Malaysia and Singapore, into which he included the continental population of *kresna* as used by Moore (1898) and Bingham (1905). He also pointed out that *gandara* was a female of *A. nefte nefte* and not the female of *A. reta*, which he believed to be like the male, at least in the mainland race. In view of the sexual dimorphism in some races of *nefte*, he named the orange-marked female-form of *nefte*, which he noted had not been named yet, as *neftina*. He also noted that Bingham (1905), in his book Butterflies of India, had not adopted the views of de Nicéville & Martin (1896). Bingham still considered the female of *kresna* (in fact *reta*) to have markings that were “pale brownish white and diffuse.” Frühstorfer (1913) subsequently figured a white-marked specimen of mainland *A. reta* as the first female and described the female of the race *syma* from Nias as resembling the male but having yellowish white markings. The females of the remaining insular races, he said, remained undiscovered. Corbet (1942) later named *A. reta riamba* from the Mentawai Islands, which he described as having a black-and-white female.

A dichotomy appears to have arisen thereafter in the descriptions of the female of *A. reta* in subsequent literature. Literature on the Indian butterfly fauna did eventually adopt the name *reta* in place of *kresna*, initially placing *kresna* as a subspecies (Evans, 1924), but later adopting Frühstorfer’s subspecies *moorei* (see Evans, 1927, 1932). However, the female of *reta* continued to be considered as having brown markings, probably as a result of its prior mistaken association with *subrata* and *gandara*. Evans’ (1924, 1927, 1932) description of the female as well as Wynter-Blyth’s (1957) and Kehimkar’s (2008) appear to have followed that of Bingham (1905). On the other hand, literature on the Southeast Asian butterfly fauna considered the female to be similar to the male (e.g., Corbet & Pendlebury, 1956, 1978, 1992; Fleming, 1975, 1983; Tsukada, 1985; Otsuka, 1988), probably following Frühstorfer (1906, 1913). Moore’s (1886) original view and Distant’s (1886) suggestion of sexual polymorphism in *A. reta* was no longer discussed or considered. It has, however, been shown to be partly correct by this study. While the species is sexually dimorphic with an orange-marked female as suggested by Moore (1886), the female itself is monomorphic; Moore’s brown-marked females are a female-form of *A. nefte* (f.-f. *subrata*) and Frühstorfer’s white-marked females are male *A. reta*.

The confusion surrounding *A. reta* in early literature may also have caused and perpetuated some confusion about its
distribution. Although Moore (1898) stated that *A. reta* (which he called *kresna*) occurs in “Assam; Eastern Bengal; Burma; Tenasserim; Malay Peninsula; etc.,” actual records of the species in India and Burma, all of which have been listed by Moore (1898), appear to be limited to several specimens identified as *A. kresna* or *A. subrata*. Wynter-Blyth (1957) described it as very rare. A female from “Eastern Bengal” (Moore, 1865, not 1856 as wrongly given in Moore, 1898) and three females from “Mergui” (Moore, 1886) cannot be *A. reta* as they were originally identified as *A. subrata*. Since *A. nefte* / *A. subrata* does not occur on the continent, they could be females of *A. selenophora* or *A. zeroca* Moore, which have females with light brown markings that can resemble *subrata* in these parts of their range. The remaining four specimens listed from India and Burma by Moore (1898) comprised a male from “Assam” (Rothschild coll.), a specimen of unspecified sex from “Ponggadaw” (about 30 miles to the west of Thayetmyo) in “Upper Burma” (Watson, 1888), which Moore said was a male, and two males from “Minhantoung” (Tenasserim), collected by John Anderson (Moore, 1886).

There have been no recent records or sightings of *A. reta* in north-east India (Kunte et al., 2020; K. Kunte, personal communication), and it is omitted from more recent literature on the butterflies of Bangladesh (e.g., Larsen, 2004; Shihan, 2018) and the Andaman and Nicobar Islands (Veenakumari et al., 2008). There have been few recent surveys of the butterflies of Burma. But in Thailand where extensive collecting has been done, it has only been recorded in the southern half of the Isthmus of Kra (Kimura et al., 2016; Inayoshi, 2020). It seems likely, therefore, that *A. reta* is restricted to the Sundanian subregion and does not extend beyond southern Thailand. Further investigation of historical specimens would be needed to fully confirm this, but it is a fair inference from the above evidence that the distribution of *A. reta* (Fig. 10) is confined to southern Thailand, Sumatra, including Nias, Mentawai, Belitung, Bangka and Lingga, Peninsular Malaysia, Singapore, Borneo, and Java where it appears to be restricted to the west.

The discovery of sexual dimorphism in *A. reta* and past confusion of its female with *A. nefte* has potential implications to the nomenclature of *A. nefte*. The type of *nefte* is a black-and-orange female from Bali named and figured (Cramer...
female of A. reta but a female of A. nefte figureed by Tsukada (1985: p. 186, pl. 152, no. 22) from western Java. However, a small element of ambiguity arises from the hand-painted illustration of the underside of the right forewing cell-end arrowhead marking (pl. 256, fig. E). Since the type of nefte is an orange-marked female, this female-form would have been better called f.-f. nefte (as used by Corbet, 1942) instead of f.-f. neftina, abiding by prevailing norms for the selection of form names. However, since infraspecific names and their usage are not governed by the International Code of Zoological Nomenclature, the actual choice of nefte or neftina as a female-form name is somewhat arbitrary. Continuing the prevailing more common usage of f.-f. neftina would serve the interests of nomenclatural stability.

Two subspecies of A. nefte have syntypes that could include orange-marked females. The question therefore arises whether any of these are in fact females of A. reta. Athyma nefte matthioli (Frühstorfer) was described from the male and both female-forms (Frühstorfer, 1913). The “type” is from North Borneo, but the sex is unspecified. The orange-marked female figured by Frühstorfer (locality unstated) is A. nefte (pl. 9, row b, third fig. from left). The type series of Athyma nefte tigrina (Corbet) should include at least one orange-marked female because Corbet (1942) in his original description listed one male and two females from Sipora (one of the Mentawai Islands) and said the types are from Sipora (B.M. Types Rhop. Nos. 490 and 491). In the interests of nomenclatural stability, it would be best that a lectotype is eventually designated if it is found that one or more females of A. reta occur among the syntypes of the above-mentioned subspecies. Clearly such a lectotype, if chosen, should be a specimen that is without doubt A. nefte, in accordance with Recommendation 74A of the International Code of Zoological Nomenclature (ICZN, 1999). The same recommendation should apply to A. nivifera Butler (now a synonym of A. nefte), which appears to have been described from a male and female (Butler, 1879).

In the Peninsula is very similar and, to the status of a single species nefte that has a continental, peninsular and insular distribution (Fig. 10). Tsukada (1985) is credited, however, with recognising that glora Kheil from Nias and marguritha Frühstorfer from Lombok should be considered subspecies of A. nefte.

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LITERATURE CITED


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