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Cryptic diversity within the *Anisoneura aluco*-group (Lepidoptera: Erebidae)

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Abstract
The *aluco*-group of the Indo-Australian genus *Anisoneura* is revised with characterisation of its component species and updating of their distribution. Types of all but one nominal taxa of the group are illustrated. The concept of *Anisoneura zeuzeroides* Guenée, 1852 is restricted to sole populations from Western New Guinea, while Moluccan (including Kei Islands') populations previously ascribed to this nominal taxon are distinguished as *Anisoneura sphingoides* C. Felder, 1861 **stat. rev.** (= *Anisoneura depressa* Hulstaert, 1924, **syn. nov.**), and those from Eastern New Guinea are re-evaluated as *Anisoneura papuana* Hampson, 1913 **stat. rev.** The unusual circumstances of the scarce divergence in genitalia characters between species looking externally different (either *sphingoides* or *zeuzeroides* vs *aluco*) and vice versa, that is species almost indistinguishable in habitus albeit strongly differentiated in genitalia (either *sphingoides* or *zeuzeroides* vs *papuana*), is stressed. Lectotypes to *Anisoneura hypocyana* Guenée, 1852 and *Anisoneura sphingoides* C. Felder, 1861 are designated.

Key words: taxonomy, moths, Indo-Australian Region.

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Introduction

Compared to other genera of the family Erebidae, *Anisoneura* Guenée, 1852 has mostly remained taxonomically stable, likely in consequence of the small number of species involved and the conspicuous size of the moths, that has made visual comparisons comparatively easy. As a matter of fact, the only relatively recent major change has been the synonymisation of *Anisoneura papuana* Hampson, 1913 with *Anisoneura zeuzeroides* Guenée, 1852 established by Poole (1989), who thence recognised five species within the genus as a whole, namely *A. salebrosa* Guenée, 1852, *A. inermis* Tams, 1924, *A. aluco* (Fabricius, 1775), *A. zeuzeroides* Guenée, 1852 and *A. depressa* Hulstaert, 1924. It has to be noted though that Holloway (2005) raised doubts on the status of the latter.

During re-curation of holdings of this genus at the Natural History Museum (London), the current delimitation of species revealed to be unsatisfactory, in particular as regards the aforementioned synonymy. The present work will therefore review the taxonomy of the section of this genus which comprises these nominal taxa, which can collectively be referred to as the *A. aluco*-group. Members of a second section, the *A. salebrosa*-group, where a number of taxonomic updates are also due, will be reviewed in a forthcoming article.

Material and methods

Types of five of the seven nominal taxa described within the *Anisoneura aluco* group and other study material were directly examined in the collections of the Natural History Museum (London) and Rijksmuseum van Natuurlijke Historie (Leiden), while of another type high-quality pictures were available online. For genitalia preparations, abdomens were removed and macerated overnight in cold 10% KOH (aqueous). They were then dissected, descaled and the genitalia cleaned. Aedeagi were removed from apparatus and vesicae everted with an insulin syringe; structures with membranous parts were stained in saturated chlorazol black (75% ethanol) for 20 seconds and transferred to absolute ethanol before permanent mounting onto slides in Euparal (formulation by Anglian Lepidopterist Supplies). Pictures of adults were taken with a camera Canon Eos 600D equipped with lenses Sigma DG Macro 70mm, those of genitalia with a Canon 5DSR with lenses Canon 58mm, equipped with a Stackshot system operated by software Helicon Remote (version 3.8.4 W); the latter were eventually stacked with software Helicon Focus (version 6.7.1). Final cropping and editing of pictures were performed with Adobe Photoshop CC 2014. Diverticula of vesicae were noted with Greek letters to highlight relevant homologies and allow detailed comparisons between taxa.

Due to the remarkable external similarity of species, (re) describing in words previously misidentified taxa or sexes not yet formally described seemed as an unnecessary exercise to be better substituted by detailing the actual diagnostic differences, supplemented by adequate illustrations.

Abbreviations are as follows:

BMNH	British Museum (Natural History), London (currently as NHMUK)
fwl	forewing length
MNHN	Muséum National d'Histoire Naturelle, Paris
N	number of specimens measured
NHMUK	Natural History Museum, London
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
x	average
vs	versus

Taxonomic section

Anisoneura Guenée, 1852
Anisoneura Guenée, 1852. *Histoire naturelle des Insectes. Species général des Lépidoptères 7. Noctuélites* ***3***: 160. Type species: *Anisoneura salebrosa* Guenée, 1852, by subsequent designation by Desmarest ([1857]: 130).

Taxonomic remarks. The genus consists of two sections, one of large-sized species detailed herein (*aluco*-group) and the other comprising smaller-sized species (*salebrosa*-group). Characters allowing delimitation of the genus have been reviewed by Holloway (2005), but study of additional taxa with respect to this author revealed many morphological derivations within each group which make far difficult to reconcile the two sections under a single generic concept. However, all species show in the male hindwing weaker scaled interspaces M_2-M_3, M_3-CuA_1 and CuA_1-CuA_2 (adjacent interspaces also partially so) which are bounded by veins in relief, along which thicker scaling develops on both upper- and underside. This structure, on which the generic etymology is based, much resembles a "folding fan" and appears to be a consistent synapomorphy. Accordingly, it seems unwise to split the genus into two monophyletic groups which are sister to each other, and both sections will provisionally be retained here under *Anisoneura*. Function of this structure, commonly referred to as androconial (Gaede, 1938), seems in reality to be sound producing after rubbing against the forewing, as clearly addressed by elder authors (Haase, 1888; Stephan, 1912). In fact, scales of both interspaces and vein-lining brands do not appear to be modified, at least under optical microscopy.

In analogy to several other Erebidae, however, scent structures are instead found on the male mesotibiae (Haase, 1887), where they take shape of a long hair pencil concealed at rest in a longitudinal groove on the outer side of tibia.

Anisoneura aluco-group

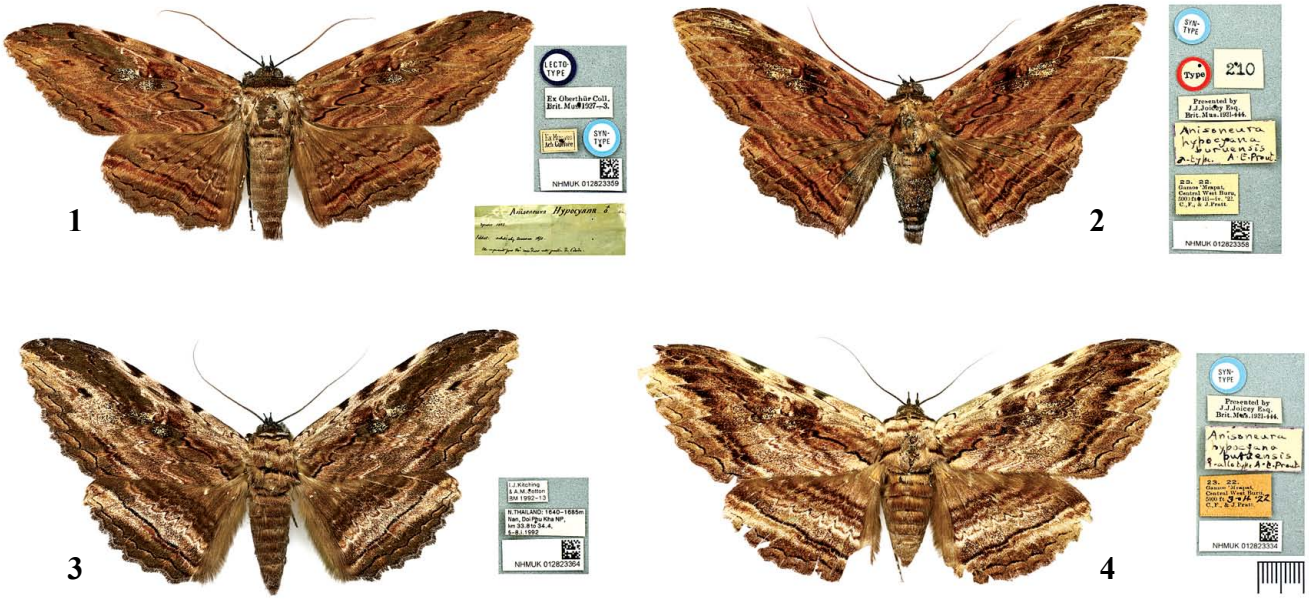
Diagnosis. Large- to very large-sized species of *Anisoneura*, with wingspan from above 8 cm. Hindwing with Rs + M_1 stalked, the stalk being very long in male, shortly so in female. Valvae terminated by long processes, juxta in shape of large plate; ductus bursae a stiff rigid, wholly sclerotised structure.

Anisoneura aluco (Fabricius, 1775)
(Figs 1-4, 20-21, 26-27, 33-34)

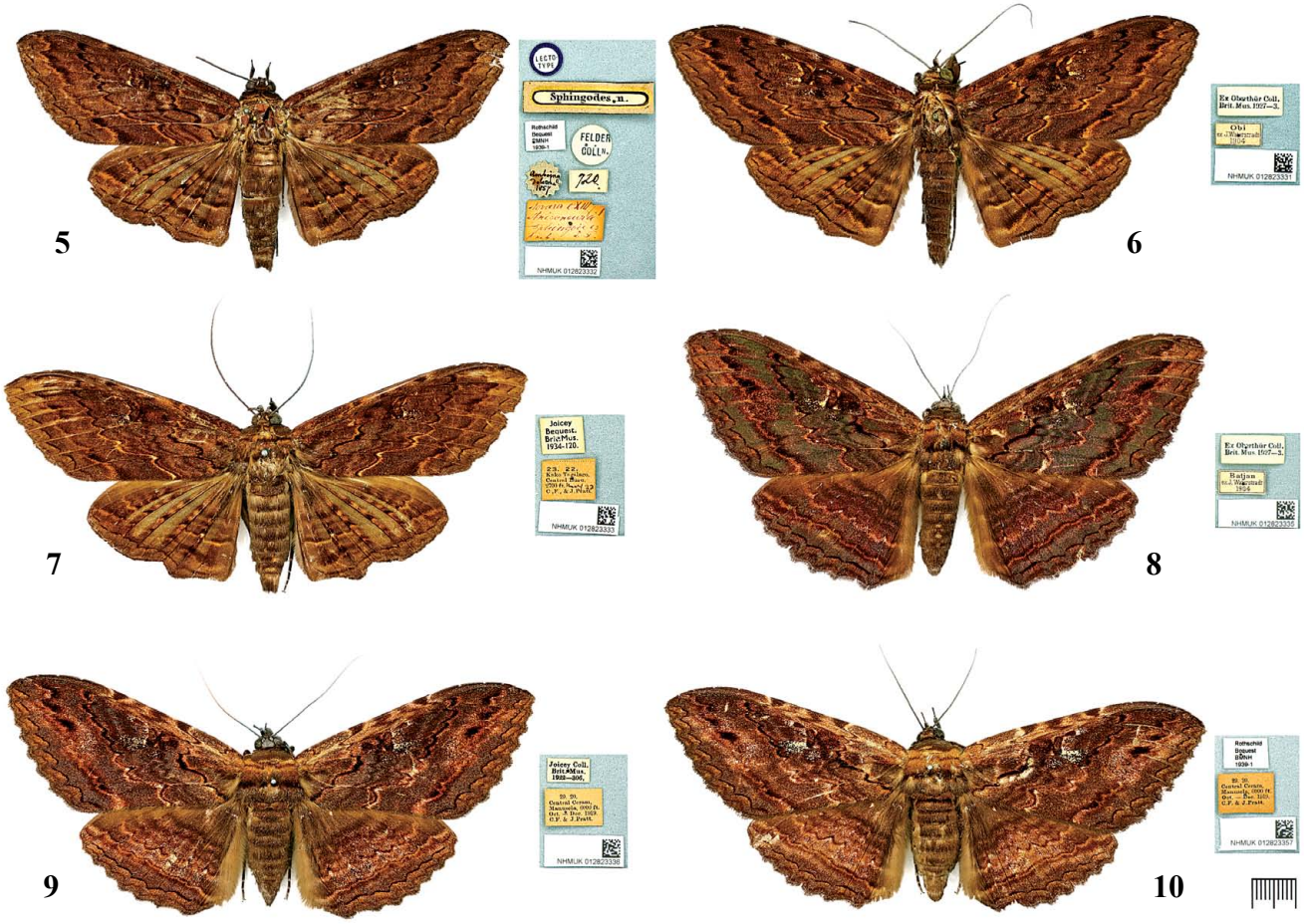
Noctua aluco Fabricius, 1775. *Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*: 591. Locus typicus: China. Typi: not stated, likely in ZMUC; description more compatible with the female sex. Fabricius (1775) stated that the original material was in the collection by Monson, that is Lady Anne Monson, botanist and collector of plants and insects, who passed away in 1776 in Calcutta. Other Fabrician types based on Monson's specimens such as *Papilio europa* Fabricius, 1775, have been retrieved in ZMUC (2018).
= *Anisoneura hypocyana* Guenée, 1852. *Histoire naturelle des Insectes. Species général des Lépidoptères 7. Noctuélites* ***3***: 162, pl. 17, fig. 3 (♂). Locus typicus: Silhet. Typi: ♂♀ syntypi (number not specified); 1♂ syntypus, in NHMUK [examined], here designated as lectotypus and illustrated in fig. 1. Another ♀ from Guenée's collection labelled as syntypus in NHMUK [examined] cannot be regarded as such in that clearly labelled as from "Inde centrale".
= *Anisoneura hypocyana buruensis* A.E. Prout, 1926. *The Entomologist*, **59** (3): 73. Locus typicus: [Buru] Gamoe 'Mrapat, 5000 ft.'; Lek Soela. Typi: 2♂♂, 2♀♀ syntypi, in NHMUK [examined] (1♂, 1♀ syntypi here illustrated in figs 2, 4).

Taxonomic remarks. This species was long known with the name coined by Guenée (1852) until the senior synonym *Anisoneura aluco* (originally sub *Noctua*) came into usage, essentially after Holloway (1976) and, subsequently Sugi (1982). The junior synonym is still occasionally being used as the valid name for this species (e.g., Sambath, 2014) or as of an additional species with respect to *A. aluco* (e.g., Sivasankaran et al., 2012).

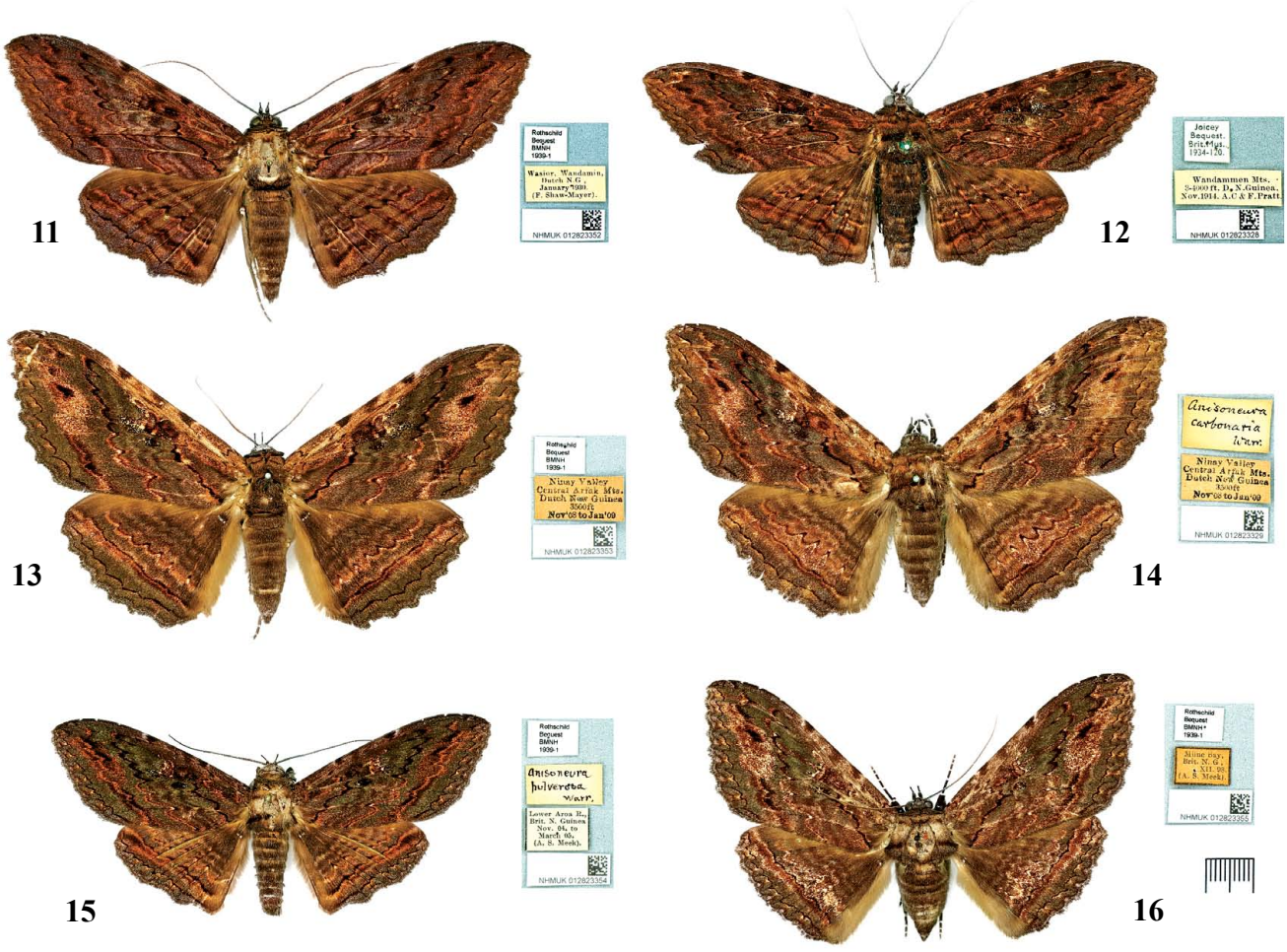
Poole (1989) sank with the nominate subspecies Prout's (1926) ssp. *buruensis* which had been erected for populations from Buru, whose females show particularly variegated patterns mottled with pale and dark blotches. As contrastingly pale and dark blotched specimens are also known from other areas (e.g. Thailand, Luzon) and no meaningful differences could be found in the genitalia, despite Poole's (1989) act was driven by refusing *a priori* validity to any subspecies, it is fully agreed here that no Moluccan subspecies should be distinguished within *A. aluco*.



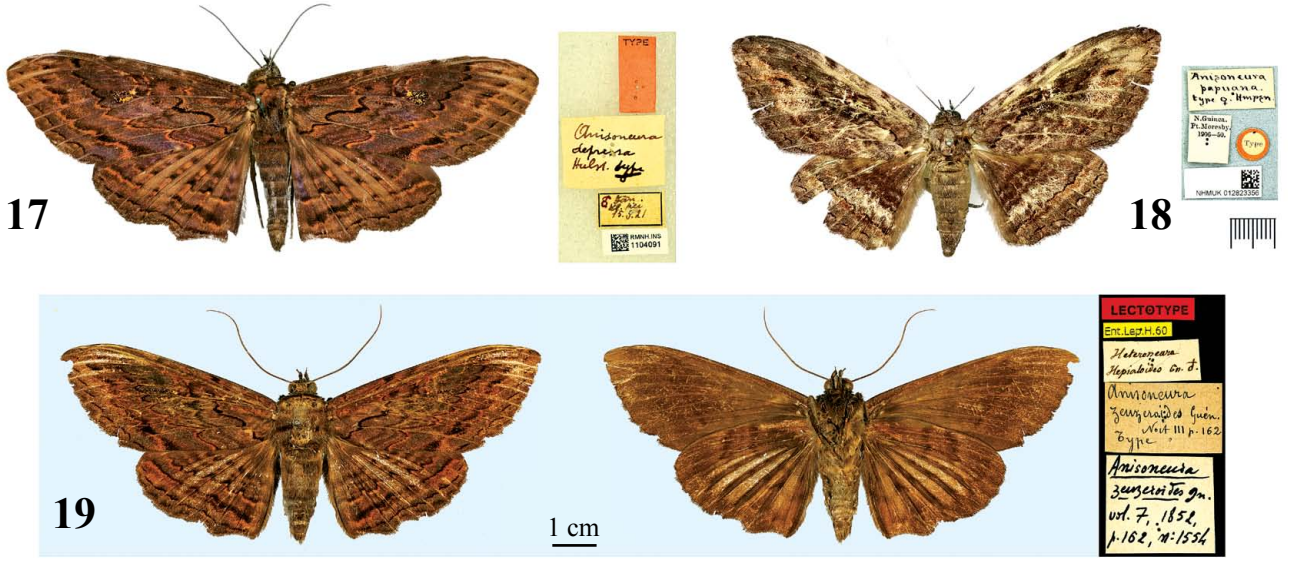
Figs 1-4 – Adults of *Anisoneura aluco* (Fabricius, 1775): **1**, ♂ (lectotypus of *Anisoneura hypocyana* Guenée, 1852, here designated), Silhet; **2**, ♂ (syntypus of *Anisoneura hypocyana buruensis* A.E. Prout, 1926), Moluccas, Buru; **3**, ♀, Thailand, Doi Phu Kha National Park, Nan; **4**, ♀ (syntypus of *A. h. buruensis*), Buru. Scale bar = 10 mm.



Figs 5-10 – Adults of *Anisoneura sphingoides* C. Felder, 1861 **stat. rev.**, Moluccas: **5**, lectotypus ♂ (here designated), Amboina [= Ambon]; **6**, ♂, Obi; **7**, ♂, Buru; **8**, ♀, Batjan [= Bacan]; **9 & 10**, ♀♀, Ceram [= Seram]. Scale bar = 10 mm.



Figs 11-16 – Adults of *Anisoneura* spp., New Guinea: **11 & 12**, *A. zeuzeroides* Guenée, 1852, ♂♂, Western New Guinea, [Indonesia, West Papua Province] Wandammen Peninsula; **13 & 14**, *ibidem*, ♀♀, Doberai Peninsula, Arfak Mts; **15**, *A. papuana* Hampson, 1913 **stat. rev.**, ♂, Eastern New Guinea, [Papua New Guinea] Aroa River; **16**, *ibidem*, ♀, Milne Bay. Scale bar = 10 mm.



Figs 17-19 – Type specimens of *Anisoneura*: **17**, holotypus ♂ of *Anisoneura depressa* Hulstaert, 1924 (**syn. nov.** of *A. sphingoides* C. Felder, 1861 **stat. rev.**), Little Kei I., Fan; **18**, *Anisoneura papuana* Hampson, 1913 **stat. rev.**, holotypus ♀, Port Moresby; **19**, *A. zeuzeroides*, lectotypus ♂, locality unknown [Western New Guinea, by inference] (by courtesy of MNHN, licensed under CC BY-NC-ND 4.0, https://creativecommons.org/licenses/by-nc-nd/4.0/). Scale bars = 10 mm.

Diagnosis. *Anisoneura aluco* is characterised by the slenderest wings amongst members of its group, which reflects into the particularly oblique termen and acute apex of forewing, especially in the male (Figs 1-4). Main and accessory crosslines are very oblique too and more consistently parallel to each other with respect to the more sinuous or bowed ones of other relatives. The three triangular patches on forewing costa which mark the beginning of main crosslines, viz. antemedial, median shade and postmedial, are best expressed in this species. The section of the double submarginal line of forewing below 1A+2A is straight, and obliquely reaches the anal margin. In the hindwing of both sexes a most reliable diagnostic feature of pattern is the innermost of the bundle of submarginal lines, which is always a neat sharp black or blackish brown line. In the male hindwing the "folding fan"-like area is not particularly enhanced and together with *A. papuana* (see below) the vannus is the least developed among members of the group.

The male genitalia of *A. aluco* (Figs 20-21) closely match those of all other species of the group, with the exception of *A. papuana*, but a consistent difference occurs in the vesica (Figs 26-27), which shows a subbasally branched diverticulum β not seen in relatives, in which this is single. The dorsal processes of valvae are also consistently slenderer and longer than in other group members, and longer than the ventral processes. In the female genitalia (Figs 33-34) the ductus bursae is the least sinuous with respect to its relatives.

Distribution. From the Himalayas, India, Ceylon [Sri Lanka], and South-eastern China eastwards to Japan, the whole Philippines, Celebes [Sulawesi], part of the Moluccas (Ternate, Buru) and across Sundaland and the Outer Banda arc to Tanimbar I. and Northwest Territory of Australia (iBOL, 2018). Records from New Guinea (e.g. Pagenstecher, 1895; Swinhoe, 1900; Gaede, 1938) are likely based on misidentification for true *A. zeuzeroides*. Sympatric occurrence with *A. sphingoides* in Buru should be noted.

Anisoneura sphingoides C. Felder, 1861 **stat. rev.**
(Figs 5-10, 17, 22, 28-29, 35)

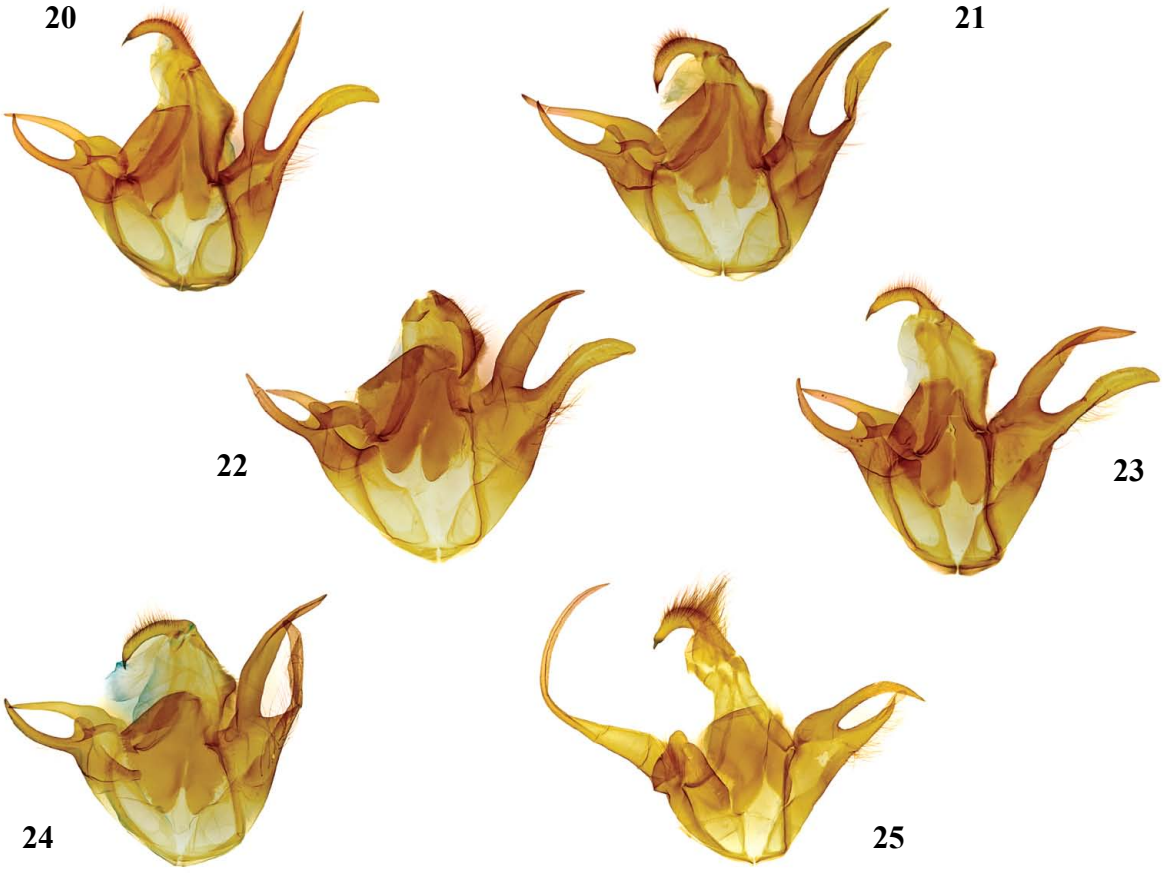
Anisoneura sphingoides C. Felder, 1861. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften*, (1) **43** (3): 42. Locus typicus: Amboina. Typi: ♂♀ syntypi (number not specified); 1♂, 1♀ syntypi in NHMUK [examined], the male here designated as lectotypus and illustrated in fig. 5.
= *Anisoneura depressa* Hulstaert, 1924. *The Annals and Magazine of natural History*, (9) **13**: 120. Locus typicus: Fān, Kl. Kei. Typi: ♂ holotypus, in RMNH [examined] (here illustrated in fig. 17). **Syn. nov.**

Taxonomic remarks. The issue of whether the Moluccan and West Papuan populations referable to *Anisoneura zeuzeroides* are conspecific or not is the most difficult taxonomic problem involving the *aluco*-species group. On the one hand the females appear to be indistinguishable, on the other, while examining large series of males these can be separated into two visually distinct clusters. As it will be shown below, in the *aluco*-group species markedly different in pattern may show extremely similar genitalia, whereas externally indistinguishable species may sharply differ in these organs. Pattern features do not thence necessarily provide the best diagnostic clues for separating the eastern members of this group. Differences have however been found in the degree of development and shape of the male hindwing, and these are consistent with differences in vesical diverticula. Accordingly, the Moluccan populations hitherto attributed to *A. zeuzeroides* are here considered to represent a distinct species, whose valid name thence becomes *Anisoneura sphingoides*. This name had been maintained as of a valid species after its description (e.g. Haase, 1887, 1888; Pagenstecher, 1888; Stephan, 1912), though the similarity with *A. zeuzeroides* had early been noted by Pagenstecher (1884), until the merging of the two concepts under *A. zeuzeroides* done by Hampson (1913).

During this work two previously unrecognised syntypes of *Anisoneura sphingoides*, a male and a female (likely the whole original series), have been discovered in the NHMUK collections. Due to the complex situation shown by the *aluco*-group in the Wallacean-Papuan area, the male, better showing than the female external differences, is hereby selected as lectotype (Fig. 5). This is in all evidence the same specimen illustrated by Felder et al. ([1874], in [1865]-1875: pl. 113, fig. 1).

As specimens from Kei Islands present in RMNH, including the holotype of *Anisoneura depressa* from Little Kei I. (= Kai Kecil) (Fig. 17), show features fully characteristic of this species, the two names are herewith brought into synonymy.

Diagnosis. Both sexes of *Anisoneura sphingoides* (Figs 5-10) and all the species treated here below can easily be distinguished with respect to *A. aluco* (Figs 1-4) by the less straight, more blurred and weaker expressed inner dark line out of the bundle of hindwing submarginals. All transverse lines are also less consistently parallel to each other, which gives the moths a somewhat less regularly geometric pattern. Below forewing vein 1A+2A, the section of the double submarginal is not straight but curved. The ground colour is less variegated, with little contrast between different areas, nor with the conspicuous paler and darker oblique bands which often alternate in *A. aluco* (females, particularly); accordingly, the costal area of forewing is concolorous or just slightly paler than wing disc, never contrastingly paler as often seen in *A. aluco*, and the dark markings along costa in correspondence of the three main crosslines are less evident. Males also show a broader, less narrowly elongated forewing, the apex of which is therefore less acute and termen less oblique. Crosslines and stigmata can be lined with golden yellow against a fairly uniform dark ground colour. Females also



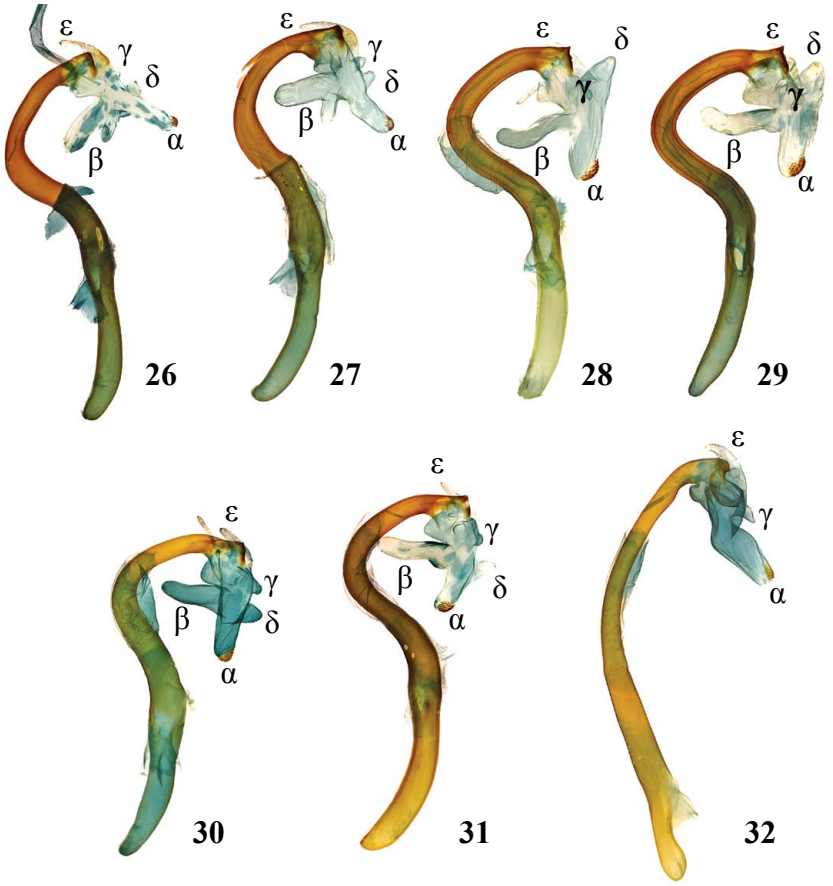
Figs 20-25 – Male genital capsulae of *Anisoneura* spp. (all same scale-sized): **20**, *A. aluco*, topotypus, Silhet (slide NHMUK 010375334); **21**, *ibidem*, topotypus of *buruensis*, Moluccas, Buru, Gamoe 'Mrapat (slide BMNHNoct.22118); **22**, *A. sphingoides*, Moluccas, Buru, Kayeli (slide NHMUK 010375332); **23**, *A. zeuzeroides*, New Guinea, [Indonesia, West Papua Province] Dorey [= Manokwari] (slide NHMUK 010375333); **24**, *ibidem*, Wandammen Mts (slide BMNH Noct. 22113); **25**, *A. papuana*, Papua New Guinea, Mambare River, Biagi (slide BMNH Noct. 22112).

have broader, less elongated wings than *A. aluco*, though the difference is less striking.

With respect to *A. zeuzeroides* (Figs 11-12, 19) and *A. papuana* (Fig. 15), the males of *A. sphingoides* (Figs 5-7, 17) show the most emphasised secondary sexual characters, with depressed interspaces of the fan-like structure varying from being paler coloured than rest of wing albeit with no pattern of crosslines visible on them, so that the lines appear to be interrupted in correspondence with interspaces, to turning particularly semi-hyaline. These interspaces are also slightly wider than in its close relatives and with more bowed veins. The vannus is more extended and terminates into broader terminal lobes, the hindwing margin though is evenly smooth, without evident crenulations in correspondence of veins, even in biggest-sized individuals. In the females (Figs 8-10), no reliable external hint for separation from *A. zeuzeroides* has been found (Figs 13-14), while for diagnosis with respect to *A. papuana* (Figs 16, 18) see under this species.

The genitalia of both *A. sphingoides* (Fig. 22) and *A. zeuzeroides* (Figs 23-24) are outstandingly similar to those of *A. aluco* despite the conspicuous differences existing in habitus. Both species show however thicker and shorter dorsal processes of valvae than *A. aluco*, equating in length or being slightly shorter than the ventral processes. Their best diagnostic feature consists though of the single, unbranched diverticulum β of vesica (Figs 28-31). Between *A. sphingoides* (Figs 28-29) and *A. zeuzeroides* (Figs 30-31), the main difference consists of the main corpus of vesica in the former which is essentially taken by directly opposite diverticula α and δ, with the second of these greatly enlarged with respect to allied species, and γ (the closest diverticulum in continuation of the carinal plate of the aedeagus) which lies laterally on the vesica without projecting beyond the outline. In the female genitalia, the ductus bursae of *A. sphingoides* (Fig. 35) is larger and more tightly sinuous than in *A. zeuzeroides* (Fig. 36), and the ovipositor longer, as seen by the longer intersegmental membrane A8-A9 and longer posterior apophyses.

Distribution. So far known from the Moluccas (Morotai, Halmahera, Bacan, Obi, Buru, Ambon, Seram) and Kei Islands. There are a number of old specimens both in NHMUK and RMNH labelled as from Java, but this indication of locality seems to be spurious.



Figs 26-32 – Aedeagi of *Anisoneura* spp. (all same scale-sized, slide numbers as in figs 20-25 except when otherwise stated): **26**, *A. aluco*, topotypus, Silhet; **27**, *ibidem*, topotypus of *buruensis*, Moluccas, Buru, Gamoe 'Mrapat; **28**, *A. sphingoides*, Moluccas, Obi (slide BMNH Noct. 22115); **29**, *ibidem*, Buru, Kayeli; **30**, *A. zeuzeroides*, New Guinea, [Indonesia, West Papua Province] Dorey [= Manokwari]; **31**, *ibidem*, Wandammen Mts; **32**, *A. papuana*, Papua New Guinea, Mambare River, Biagi. Greek lettering refers to main vesical diverticula.

Anisoneura zeuzeroides Guenée, 1852
(Figs 11-14, 19, 23-24, 30-31, 36)

Anisoneura zeuzeroides Guenée, 1852. *Histoire naturelle des Insectes. Species général des Lépidoptères 7. Noctuélites **3***: 162. Locus typicus: originally unknown. Typi: 2♂♂ syntypi; lectotypus ♂, implicitly designated by Hampson (1913) and explicitly by Viette (1951), in MNHN [picture examined] (here illustrated in fig. 19).

Taxonomic remarks. In addition to the difficulties in separating *A. sphingoides* and *A. zeuzeroides* noted above, another issue regards the true identity of the latter, due to the fact that Guenée (1852) described this taxon relying on two males in MNHN without indication of origin. Hampson (1913) stated the type to be in the Paris Museum and by adding a single dagger to his statement he meant to have examined the specimen (Hampson, 1898: 15). Indications like Hampson's often fulfil with lectotype designations albeit they are implicit ones, though in this case he must evidently have failed to unambiguously made such a "type" recognisable. His statement was therefore challenged by Viette (1951), who formally designated a lectotype for *A. zeuzeroides*. This specimen is now visible online (MNHN, 2018) and has been reproduced here in fig. 19 by courtesy of MNHN. It shows features in agreement with the western populations of New Guinea, from where it likely originated (cf. Viette, 1951), and obviously drives the concept of *A. zeuzeroides* which is being followed here.

Diagnosis. For the distinction of *A. zeuzeroides* from both *A. aluco* and *A. sphingoides* see under these two species. Interestingly, the males of *A. zeuzeroides* (Figs 11-12, 19) look like less extreme *A. sphingoides* (Figs 5-7, 17), with a sort of revival of *aluco* characters, in particular the hindwing is appreciably smaller because of the less conspicuous fan-structure, the interspaces of which still showing most traces of the crosslines, and the less expanded vannus. Consequently, the terminal vannal lobes are slightly less produced outwardly, but interestingly the wing margin is more irregularly crenulated in that slightly produced at veins. No real external diagnostic features between females could be found though (Figs 8-10, 13-14). The samples studied indicate also a slightly smaller size for the Pap-

Figs 33-37 – Female genitalia of *Anisoneura* spp.: **27**, *A. aluco*, India, Darjeeling (slide NHMUK 010375335); **28**, *ibidem*, topotypus of *buruensis*, Moluccas, Buru, Gamoe 'Mrapat (slide BMNH Noct. 22119); **29**, *A. sphingoides*, Moluccas, Batjan [= Bacan] (slide BMNH Noct. 22116); **30**, *A. zeuzeroides*, New Guinea, [Indonesia, West Papua Province] Kapaur [= Fakfak] (slide BMNH Noct. 22114); **31**, *A. papuana*, Papua New Guinea, Upper Aroa River (slide BMNH Noct. 22117).

uan taxon, precisely in *zeuzeroides* vs *sphingoides* $fwl_{♂}$ = 49-54 vs 48-57 mm (x = 51.20 vs 53.16; N = 5 vs 44) and $fwl_{♀}$ = 49-56 vs 52-59 mm (x = 53.44 vs 55.83; N = 9 vs 29). Diagnostic features in the genitalia with respect to both *A. aluco* and *A. sphingoides* have been discussed under these species. Despite the close external resemblance of *A. zeuzeroides* with *A. papuana*, the latter is sharply differentiated in structural characters of the genitalia.

Distribution. So far confirmed from the western sector of New Guinea, notably from several localities of the Doberai, Bomberai and Wandammen peninsulas (Fig. 38). The fact that this species is less extreme in habitus than *A. sphingoides* and somewhat leaning in pattern towards *A. aluco* is probably the reason why the latter was occasionally recorded from New Guinea (see above under *A. aluco*).

Anisoneura papuana Hampson, 1913 **stat. rev.**
(Figs 15-16, 18, 25, 32, 37)

Anisoneura papuana Hampson, 1913. *Catalogue of the Lepidoptera Phalaenae in the British Museum*, **13**: 262, pl. 226, fig. 11. Locus typicus: Br. N. Guinea, Port Moresby. Typus: holotypus ♀, in NHMUK [examined] (here illustrated in fig. 18).

Taxonomic remarks. The finding that *Anisoneura papuana* is a distinct species from *A. zeuzeroides* is actually one of the most surprising outcomes of this study, in consideration of both their striking external resemblance, which evidently was at the base of their synonymisation by Poole (1989), though it sharply contrasts with outstanding differences in the genitalia of both sexes.

Diagnosis. *Anisoneura papuana* looks like a small-sized *A. zeuzeroides*, e.g. $fwl_{♂}$ = 43-46 mm (x = 44.17, N = 6) and $fwl_{♀}$ = 47-49 mm (x = 48.40, N = 5) (values of *zeuzeroides* are given under this). The only appreciable differences seen in males are the straighter termen of forewing of *A. papuana* (Fig. 15) with respect to the slightly convex one of *A. zeuzeroides* (Figs 11-12, 19), the posterior lobes of the outermost line out of the bundle of hindwing postmedials which are evenly arched and weakly dark-lined internally, not flattened and with the strong dark lining seen in *A. zeuzeroides*, and some stronger jags on the anterior section of the black adterminal line of the hindwing. In the females the pale oval spot present in the distal field of forewing of *A. papuana* is more distinct, with sharper bounds and hence more contrast with respect to the surrounding wing surface (Figs 16, 18). This clearing is variably expressed in the other species and sometimes also indistinct, but when it is well evident it is in any case

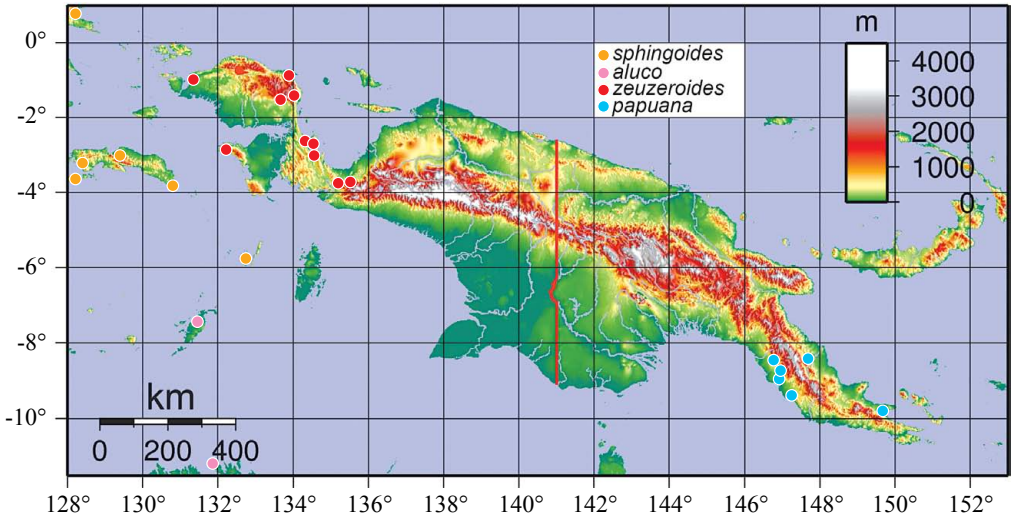


Fig. 38 – Distribution of species of the *Anisoneura aluco*-group in the Papuan Region (base map after https://upload.wikimedia.org/wikipedia/commons/b/b6/New_Guinea_Topography.png)

less sharply defined than in *A. papuana*. The innermost of the submarginal lines of the hindwing is thinner and sharper black in female *A. papuana*, so is the adterminal line, which is also somewhat stronger jagged than in female *A. zeuzeroides*.

Both the male and genitalia are strongly differentiated with respect to the apparatus of other species. Most noteworthy features are the left valva prolonged into only one markedly elongated process instead of two shorter ones (Fig. 25), the distal half of the aedeagus not sharply bent into "C" shape, the greatly different vesical configuration with no β and δ diverticula and γ long and tapered (Fig. 32), the extremely long, flat and evenly arched ductus bursae which is greatly dilated posteriorly and regularly tapered anteriorly, and the appreciably smaller, globular corpus bursae (Fig. 37).

Distribution. Known only from the eastern part of New Guinea (Fig. 38), specimens examined being from Upper Aroa River, Milne Bay, Ekeikei, Mambare River, Biagi and Port Moresby.

Discussion

The taxonomic arrangement of the *Anisoneura aluco*-group presented here leads to recognising at least four species in the Indo-Australian region, namely *A. aluco*, *A. sphingoides*, *A. zeuzeroides* and *A. papuana*. Interestingly, the two species at the middle of the overall geographic distribution of the group, i.e. *A. sphingoides* and *A. zeuzeroides*, are very similar in genitalia characters to the most different in habitus and westernmost species (*A. aluco*), while they closely match in habitus *A. papuana*, viz. the genitalically most different and easternmost species. In particular, the right valva of *A. papuana* substantially corresponds to the configuration seen in the other species, but the left one is profoundly divergent and makes its male genital apparatus strongly asymmetric. Criteria of parsimony would make the origin of asymmetry from a symmetric groundplan more likely than regaining symmetry from an originally asymmetric condition. For purely speculative reasons thus, the derivation of *A. papuana* from an *A. zeuzeroides*-like ancestor can be inferred. Available information currently indicates a substantial allopatry in New Guinea between *A. zeuzeroides* and *A. papuana*, western and eastern, respectively (Fig. 38).

However, it is difficult to envisage the evolution of sharply modified characters of the clasping apparatus such as that seen in *A. papuana* without the intervention of strong selective pressures. Notable is that sympatry in a Moluccan islands (Buru) between *A. sphingoides* and *A. aluco* did not lead to divergence in their external genitalia any stronger than in allopatry. Even in lock-and-key structures such as the distal half of the aedeagus and ductus bursae (less hooked and less sinuous, respectively, in *A. aluco*), allopatric samples of either of the two species do not show substantial differences with respect to conspecific individuals originating from overlap zones with the other species (Figs 26-29, 33-34). The ideal context for the strong derivation seen in *A. papuana*, which also affects parts tightly juxtaposing during copula of the aedeagus and ductus bursae, would therefore be a selective regime pushing for the evolution of mechanical isolation between closely related species which face the risk of mating mistakes. Such conditions would only develop in areas of sympatry, but the current distribution of the two species in New Guinea suggests instead divergence in allopatry. The issue will not be resolved until materials of these species from the core of that island will be made available.

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