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A new species of the genus *Ambulyx* Westwood, 1847 (Lepidoptera, Sphingidae) from Northern Borneo and adjacent territories

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Abstract: A new hawkmoth species, *Ambulyx* ***zacharovi*** **sp. n.**, is described from the Malaysian state of Sabah in northern Borneo. The new species is closest to *A. substrigilis* and differs in two main diagnostic characters: a strongly darkened first abdominal tergite and a conical and less sclerotized cornutus on the medial lobe of the vesica in the male genitalia. These differences are further supported by analysis of mtDNA barcodes and the sympatric distributions of the two taxa. The male holotype of the new species is deposited in the Natural History Museum, London, UK (BMNH).

Eine neue Art der Gattung *Ambulyx* Westwood, 1847 (Lepidoptera, Sphingidae) aus Nordborneo

Zusammenfassung: Die neue Schwärmerart *Ambulyx* ***zacharovi*** **sp. n.** wird aus dem malaysischen Bundesstaat Sabah im nördlichen Borneo beschrieben. Die neue Art ist ähnlich zu *A. substrigilis* und unterscheidet sich in erster Linie durch zwei Hauptmerkmale: ein stark verdunkeltes erstes Abdominaltergit und einen konischen, weniger sklerotisierten Cornutus des medialen Lappens der Vesica in den männlichen Genitalien. Diese Unterschiede werden durch die Analyse des mtDNA-Barcodes und das sympatrische Vorkommen der beiden Taxa unterstützt. Der männliche Holotypus der neuen Art befindet sich im Natural History Museum, London, Vereinigtes Königreich (BMNH).

Introduction

The hawkmoth genus *Ambulyx* Westwood, 1847 currently contains 58 species (Kitching 2014), making it one of the larger genera in the family Sphingidae. However, the number of newly discovered *Ambulyx* species continues to increase due to both the refinement of traditional morphological techniques and the application of new technologies (e.g. Simonsen & Kitching 2014), including powerful molecular biological tools (Hebert et al. 2003a, b, Regier et al. 2008, Kawahara et al. 2009), which allow us to delineate new characters and markers for distinguishing species. The last direction of research still has significant potential. The application of DNA barcoding (Hebert et al. 2003a, b) in particular, in concert with careful study of morphology and a refined appreciation of biogeography, is now showing that many species that were once considered "widespread and variable" actually comprise complexes of species (e.g. Vaglia et al. 2008, 2010). Within the genus *Ambulyx,* the species *Ambulyx substrigilis* (Westwood, 1847) is one such variable species in terms of wing and body pattern. There have been several previous attempts to tease apart the sources of this variability, but this work is far from finished. The current study adds one more piece to this big puzzle.

Our current understanding of *A. substrigilis* and its relatives can be considered to begin with the famous Sphingidae revision of Rothschild & Jordan (1903), who treated it as a member of their genus *Oxyambulyx* Rothschild & Jordan 1903. They consolidated a number of taxa that had been described as separate species into a single polytypic species consisting of five, geographically distinct subspecies:

- *Oxyambulyx substrigilis auripennis* (Moore, 1879) — Sri Lanka ("Ceylon").
- *O. substrigilis substrigilis* — North India: Sikkim ("Sikhim"), Assam; Andamans.
- *O. substrigilis pryeri* (Distant, 1887) — Peninsular Malaysia ("Malacca"), Sumatra, Borneo.
- *O. substrigilis eteocles* Rothschild & Jordan, 1903 — Java.
- *O. substrigilis staudingeri* (Rothschild, 1895) — Philippine Islands (Luzon, Mindanao).

At that time, only one of these subspecies was known to these authors from each locality or series of localities. The diagnostic morphological character common to the members of the group was "the large black or tawny basal patch of the hindwing". Moreover, Rothschild & Jordan noted that these five subspecies were collectively most similar in wing pattern to *O. liturata* (Butler, 1875), and both these species differed from *O. maculifera* (Walker, 1866), *O. ochracea* (Butler, 1885) and *O. sericeipennis* (Butler, 1875) in "being devoid of the round subbasal costal spot on the forewing". It should be noted, however, that even at this stage, Rothschild & Jordan (1903: 202) had reservations about the conspecificity of these five subspecies. Having decided upon five subspecies in a single species, they went on to say: "The differences in the genital armature between the Indian and Malayan *males* are so very marked, that one cannot fail noticing them when dissecting a specimen. Judging from these organs alone one might be induced to treat the specimens as belonging to at least two species. On examining, however, a series from Borneo and Java we find that the differences are less obvious in some specimens than in others, and we believe that the material from Malacca, Tenasserim and Burma will show intergradations between the armature of the Indian and Ceylonese and the Malayan males. For the present, the Indian and Ceylonese races stand quite apart from the others. Their characters are partly very strange; for both subspecies share the broadly spoon-shaped ventro-distal process of the harpe and the more proximal position of the (middle part of the) submarginal line of the forewing with another species of North India (*liturata*), a similarity in these compatriots which is surely not mimetic resemblance."

The break-up was not long in coming when the description of further species and subspecies demolished the original idea of five allopatric subspecies in *substrigilis*. First, Rothschild & Jordan (1916) described *O. substrigilis wilemani* from the Philippines, then Jordan (1919) described *O. substrigilis tattina* from southeastern Sumatra, and then Rothschild (1920) reinstated *pryeri* to species status and described a new subspecies from Sumatra, *O. p. sumatranus*. This was followed by the description by Clark (1923) of *O. brooksi* from the southwest of the same island, which he also placed in the *substrigilis* group. That same year, Jordan (1923a, b) reinstated *staudingeri* as a species and described two more taxa in the *substrigilis* group from SW India: *O. matti* and *O. substrigilis aglaia*. Next, Jordan (1929) raised *tattina* to species status and synonymized both *eteocles* and *sumatranus* with *pryeri*. Subsequently, numerous other species and subspecies were also added to the *substrigilis* group in the broad sense: *wildei* Miskin 1891, *meeki* Rothschild & Jordan 1903 (and subspecies, *pyrrhina* Jordan 1923 and *makirae* Tennent & Kitching 1998), *bima* (Rothschild & Jordan 1903 (with subspecies *schmickae* Brechlin 1998 and *timoriana* Brechlin 2009), *phalaris* Jordan 1916, *carycina* Jordan 1919, *ceramensis* Joicey & Talbot 1921, *charlesi* Clark 1924, *immaculata* Clark 1924, *clavata* Jordan 1929, *tenimberi* Clark 1929, *tondanoi* Clark 1930, *tattina* subsp. *uichancoi* Clark 1938, *tattina borneensis* Gehlen 1940 (currently a synonym of *tattina tattina*), *siamensis* Inoue 1991, *pseudoclavata* Inoue [1996], *andangi* Brechlin 1998, *naessigi* Brechlin 1998, *sinjaevi* Brechlin 1998, *lestradei* Cadiou 1998, *rudloffi* Brechlin 2005, *marissa* Eitschberger & Melichar 2009, *pryeri tenggarensis* Brechlin 2009 and *viteki* Melichar & Řezáč [2014]. Of the other subspecies of *substrigilis*, *wilemani* was raised to species status by Cadiou & Holloway (1989) and *auripennis* was reinstated as a species by Kitching & Cadiou (2000). These changes, insofar as they directly affect *substrigilis*, are summarized in Tab. 1.

Thus, the current concept of *Ambulyx substrigilis* is much narrower than that proposed by Rothschild & Jordan (1903) and their contemporaries. The species is presently represented by two subspecies: the nominotypical subspecies from continental South-East Asia and Sundaland, and *A. s. aglaia* from the Western Ghats of SW India. All of the other taxa previously considered to be subspecies of *A. substrigilis* are now treated either as valid species (e.g. *A. auripennis*, *A. pryeri*, *A. staudingeri* and *A. tattina*) or as synonyms of one or another species.

One of these synonyms is *O. substrigilis cana*, described by Gehlen (1940) mainly on the basis of its rather remarkable wing pattern as follows: "Im Gegensatz zu den bisher bekannten Unterarten von *substrigilis* ist die Grundfarbe der Vorderflügel und des Körpers oberseits hell olivgrau ohne bräunlichen Ton. Die Zeichnung der Vorderflügel etwas weniger markant als *brooksi*, nur die Diskalbinden treten scharf hervor und die Apikallinien vor SC5, ebenso die Adern R1 und R3. Außenrandfeld an der breitesten Stelle bei R2 über 3 mm breit. Die Submarginallinie des Außenrandes erreicht den Hinterrand ohne mit dem Außenrand zusammenzufließen. Hinterflügel orange bis auf das Analfeld, welches fast bis zur Flügelmitte hellolivgrau übergossen ist. 3 schwarze Querbinden. Die erste gerade und stark, die 2. distal geschwungen und auf den Adern gezähnt, die 3. schwächer, nur vorn durch den Subapikalflek betont. Unterseite ockergelb bis orange. Zeichnungen nur verschwommen. Das gelbraue Submarginalfeld des Vorderflügelaußenrandes proximal durch eine schwarzbraune starke Linie abgegrenzt, welche vom Apex bis M2 geht, also den Hinterrand nicht erreicht." Gehlen probably had only a single ♂ specimen (Fig. 1a), although he did not specifically state this. It came from "Samarinda, southeast Borneo" (now in Kalimantan Timur province, Indonesia) and is currently deposited in the Zoologische Staatssammlung München, Germany.

Oxyambulyx substrigilis cana was synonymized with *O. substrigilis brooksi* by Kernbach (1967). Diehl ([1982]: 18), in his book on Sumatran Sphingidae, wrote that: „In meinem umfangreichen Material lässt sich von der zeichnungsärmsten *brooksi* bis zur intensivst gezeichneten eine lückenlose Reihe aufstellen (s. Tafel II), wobei die Krümmung der Antemarginalen zunimmt" ("In my extensive material a complete series can be established from the most poorly patterned *brooksi* to the most intensely patterned (see Plate II), wherein the curvature of the antemarginal [band] increases"). Thus, Diehl accepted Kernbach's synonymy and further wrote that „*cana* könnte daher allenfalls als Form aufgefaßt werden" ["*cana* could therefore be regarded at best as a form"]. However, it is interesting to note that the type specimen of *cana* in the photograph in Gehlen's article looks different in comparison with the ♂ specimen illustrated by Diehl ([1982]: plate II, fig. 19d). In the original diagnosis of *cana*, Gehlen (1940) characterized the three transverse black bands on the hindwing upperside as "blurred" („Zeichnungen nur verschwommen"), whereas Diehl's "*cana*" has sharply defined transverse bands. Furthermore, close examination shows a more remarkable difference between them. Diehl's "*cana*" ♂ has a strongly darkened first abdominal tergite, which is otherwise seen only in *A. immaculata* (Fig. 2); the type of *cana* lacks this darkening, as does nominotypical *substrigilis*. Of course, Diehl provided the illustration of "*cana*" only as an extreme example of the range of pattern intensity that he considered to occur in the *substrigilis* population on Sumatra. There was no intention to provide a photograph of typical *cana* for the purposes of reliable identification. Unfortunately, the opposite effect occurred and there are now many photographs and identifications on the Internet based on this image in Diehl's book.

Tab. 1: Summary of changes in taxon concepts over time of *Ambulyx substrigilis* and its subspecies. Empty cells imply either the taxon was not referred to in the work concerned or, if it was, then the combination was the same as that to the left.

Rothschild & Jordan (1903)	Rothschild & Jordan (1916)	Jordan (1919)	Rothschild (1920)	Clark (1923)	Jordan (1923a)	Jordan (1929)	Clark (1938)	Gehlen (1940)	Diehl ([1982])	Kitching & Cadiou (2000)
Oxyambulyx substrigilis substrigilis (Westwood, 1847)										*Ambulyx substrigilis substrigilis* Westwood, 1847
				O. brooksi sp. n.		*O. substrigilis brooksi* Clark, 1923		*O. substrigilis brooksi* Clark, 1923	*O. substrigilis brooksi* Clark, 1923	*A. substrigilis substrigilis* Westwood, 1847
								O. substrigilis cana ssp. n.	*O. substrigilis brooksi* Clark, *1923* (*cana* just a well-marked form)	*A. substrigilis substrigilis* Westwood, 1847
					O. substrigilis aglaia ssp. n.					*A. substrigilis aglaia* (Jordan, 1923)
	O. substrigilis wilemani ssp.n.									*A. wilemani* (Rothschild & Jordan, 1916)
O. substrigilis auripennis (Moore, 1879)										*A. auripennis* Moore, 1879
		O. substrigilis tattina ssp. n.				*O. tattina* Jordan, 1919	*O. tattina tattina* Jordan, 1919			*A. tattina tattina* (Jordan, 1919)
								O. tattina borneensis ssp. n.		*A. tattina tattina* (Jordan, 1919)
							O. tattina uichancoi ssp. n.			*A. tattina uichancoi* (Clark, 1938)
O. substrigilis pryeri (Distant, 1887)			*O. pryeri pryeri* (Distant, 1887)							*A. pryeri* (Distant, 1887)
O. substrigilis eteocles Rothschild & Jordan, 1903						*O. pryeri* (Distant, 1887)				*A. pryeri* (Distant, 1887)
			O. pryeri sumatranus ssp. n.	*O. pryeri* (Distant, 1887)						*A. pryeri* (Distant, 1887)
O. substrigilis staudingeri (Rothschild, 1895)						*O. staudingeri* Rothschild, 1895 (not discussed)				*A. staudingeri* Rothschild, 1895

It was this variability in *substrigilis* populations that attracted our attention and led to the present investigation: how many *cana*-like forms exist; is there a “cryptic” species hidden by this variability; and how helpful might molecular markers be for answering these questions?

Materials and methods

During 12 expeditions to the Malaysian state of Sabah in northern Borneo between 2005 and 2014, specimens of hawkmoths were collected in the foothills of Trusmadi Mountains (960–1200 m), near Pensiangan town (530 m) and in Crocker Range National Park (1700 m). Collection dates ranged from January to October. The insects were attracted using either a 125 W or a 250 W mercury-vapour lamp between 19:00 h and 2:00 h local time. Overall, more than 50 specimens of what were initially identified as *A. substrigilis* were caught. In addition to comparisons of the external morphology and dissection of both the ♂ and ♀ genitalia, the specimens collected in 2006 and 2007 were screened for DNA variability using the mitochondrial cytochrome oxidase gene subunit I (COI-5P “barcode region”). Tissue samples (dry legs or pieces of muscle extracted from the thorax of dried adults) were taken from 17 specimens of *A. substrigilis,* including morphological variants considered possibly to represent new species. For comparison and calculations of pairwise distances, sequences for *A. substrigilis* and its putative closest relatives (*A. andangi, A. bima, A. immaculata* and *A. jordani;* see Figure 3 for sample identification numbers) were taken the Published Projects section of the Barcode of Life Data system (BoLD; Ratnasingham & Hebert 2007; www.barcodinglife.org), where detailed data are available.

DNA was extracted using a DIAtomTM DNA Prep kit (Izogen, Moscow). Amplification reactions were carried out in a final volume of 25 µl with 20 pmol of the primer LCO1490 (5’-GGTCAACAAATCATAAAGATAT-TGG-3’), 0.1 g of the isolated DNA and the universal amplification kit GenePak@PCR Core (Izogen, Moscow). PCR was performed in GeneAmpR PCR System 2700 thermal cycler (Applied Biosystems, USA). The PCR thermal regime consisted of an initial denaturisation of 1 min at 94°C; five cycles of 1 min at 94°C, 1.5 min at 45°C and 1.5 min at 72°C; 35 cycles of 1 min at 94°C, 1.5 min at 50°C and 1 min at 72°C, and a final extension of 5 min at 72°C (Folmer et al. 1994). Amplification success was checked by electrophoresis in 1% agarose gel with subsequent control of PCR fragments under UV light after staining with ethidium bromide. The section of mtDNA close to and including the “barcode” region of Cytochrome Oxidase subunit I gene was sequenced using the above primer LCO1490 at the EvroGen laboratory (Moscow). DNA sequences were verified using Technelysium ChromasPro 1.33 (www. chromaspro. com-about. com), and aligned and analysed using MEGA version 6.0 (Tamura et al. 2013).

Specimen data, sequences and images have been deposited in a BoLD project database (www.boldsystems.org) under sample IDs: BC-Ivsh00514, BC-Ivsh00523, BC-Ivsh00524, BC-Ivsh00525, BC-Ivsh00560, BC-Ivsh00752, BC-Ivsh00754, BC-Ivsh00757, BC-Ivsh00766, BC-Ivsh00767, BC-Ivsh00768, BC-Ivsh00785, BC-Ivsh00786, BC-Ivsh00787, BC-Ivsh00788, BC-Ivsh00791, and BC-Ivsh02079.

Results

The 50+ specimens initially identified as *substrigilis* could be divided into two groups on the basis of wing and body pattern. First were those without a darkened first abdominal tergite and a relatively uncontrasting wing pattern, which we assign to nominotypical *substrigilis*. Among these, it was remarkable that there was only one specimen identical to the type of *cana* (Fig. 1b). The second group comprised those moths that matched the appearance of the “*cana*” ♂ illustrated by Diehl ([1982]: plate II, fig. 19d). All of these ♂ *cana*-like speci-

Tab. 2: Pairwise Kimura 2-parameter distances (%) between the taxa shown in Fig. 3. Different haplotypes of the same species are indicated by numbers in [square brackets].

	A. substrigilis [1]	*A. substrigilis* [2]	*A. zacharovi*	*A. andangi*	*A. bima* [1]	*A. bima* [2]	*A. immaculata*
A. substrigilis [1]							
A. substrigilis [2]	0.7						
A. zacharovi	1.3	1.6					
A. andangi	0.5	1.3	1.4				
A. bima [1]	0.9	1.6	1.4	1.4			
A. bima [2]	1.1	1.8	1.3	1.3	0.5		
A. immaculata	1.3	2.0	2.6	1.8	1.8	2.4	
A. jordani	3.3	3.9	3.5	3.5	3.9	3.3	3.9

mens were consistent in having a darkened first abdominal tergite, and so we suspected they might represent a previously unrecognized and unnamed species. Furthermore, the same diagnostic feature separated the ♀♀ into two groups, whence it became clear that there was also a difference in the forewing ground colour in this sex. Those without the darkened tergite (nominotypical *substrigilis*) were olive-green or yellowish-brown, whereas the specimens with the darkened tergite were brown. It is remarkable that Diehl ([1982]) treated the ♂ specimen with this abdominal character as *substrigilis brooksi* f. *cana* but the ♀ with the same darkened tergite as *substrigilis brooksi*. As will be shown below, both these specimens must belong to the new species.

Within the 17 specimens from north Borneo that were sequenced, 3 COI haplotypes were found. All 10 moths with a darkened abdominal tergite (7 ♂♂ and 3 ♀♀) belonged to just one of these three haplotypes. The other two haplotypes characterised the specimens that we consider to be nominotypical *substrigilis*. Statistically, it is a very reliable separation by both morphological characters and the molecular marker, even allowing for the small sample size. A neighbor-joining tree comparing the DNA barcode sequences of the new species with those of its putative closest relatives in the genus is shown in Fig. 3. The tree was rooted on *Amplypterus panopus* chosen as outgroup. The sequences ranged up to 676 bp, with sequences shorter than 500 bp excluded from the comparison. The corresponding pairwise comparisons as percentage divergences between these taxa are shown in Tab. 2.

The genitalia of 5 ♂♂ from each morphological group were then selected for dissection. Differences were found in the shape of the cornutus of the medial lobe of the vesica and to a lesser extent in the shape of the harpe (clasper), all of which confirms the hypothesis about existence of cryptic species hidden within the variability of the *substrigilis* populations.

Due to lack of material, only 2 ♀♀ were compared. The characters of bursa copulatrix showed evident differences but these characters need to be confirmed from a larger sample of females.

Once it became clear that the two taxa could be reliably separated using the difference in abdominal tergite colour, a search was made in other collections for additional specimens. Several more from Borneo were found in the Natural History Museum, London, UK (BMNH) and in the research collection of Jean Haxaire, Laplume, France (CJHL). In addition, specimens that match the phenotype of the new species were found in the BMNH from Sumatra, Peninsular Malaysia and Thailand. However, these, together with the two specimens illustrated by Diehl ([1982]), are excluded from the paratype series and listed below only as "additional material" pending confirmation by study of the genitalia and DNA barcodes.

Description

Ambulyx zacharovi Ivshin sp. n.

Holotype ♂ (Figs. 1c, d): Malaysia, N. Borneo, Sabah, Trusmadi Mountains foothills, 1200 m; 12.–24. i. 2007, leg. A. Sochivko (Bold record BC-Ivsh00560); to be deposited in the Natural History Museum, London, UK (BMNH).

Paratypes (in total 50 ♂♂, 7 ♀♀), all **Malaysia, Borneo, Sabah:** 1 ♂, Tambunan Mountains, 14.–19. iv. 2005, leg. S. Kashevnik (BC-Ivsh00514). 2 ♀♀, Trusmadi Mountains, 960 m, 28. iii.–5. iv. 2006, leg. S. Kashevnik (BC-Ivsh00525, BC-Ivsh02079). 9 ♂♂, Trusmadi Mountains, 1200 m, 12.–24. i. 2007, leg. A. Sochivko, genitalia slide/preparation No. (= GP) 752 (BC-Ivsh00752, BC-Ivsh00753, BC-Ivsh00755, BC-Ivsh00756, BC-Ivsh00757, BC-Ivsh00758, BC-Ivsh00759, BC-Ivsh03987, BC-Ivsh03988). 1 ♀, Trusmadi Mountains, 1200 m, 12.–24. i. 2007, leg. A. Sochivko, GP 754 (BC-Ivsh00754). 6 ♂♂, Trusmadi Mountains, 960 m, 24. iv.–8. v. 2006, leg. P. Udovichenko, GP 787, 791 (BC-Ivsh00787, BC-Ivsh00788, BC-Ivsh00789, BC-Ivsh00790, BC-Ivsh00791, BC-Ivsh03992). 2 ♂♂, Trusmadi Mountains, 1185 m, 5°26′ 35″ N, 116°27′5″ E, 23.–25. ii. 2011, leg. V. Gromenko (BC-Ivsh02100, BC-Ivsh02101). 1 ♂, Trusmadi Mountains, 1185 m, 5°26′35″ N, 116°27′5″ E, 25. iii.–15. iv. 2011, leg. P. Udovichenko (BC-Ivsh02420). 3 ♂♂, Trusmadi Mountains, 1185 m, 5°26′35″ N, 116°27′5″ E, 1.–14. vii. 2011, leg. A. Klimenko (BC-Ivsh02480, BC-Ivsh02509, BC-Ivsh02728). 3 ♂♂, Trusmadi Mountains, 1185 m, 5°26′35″ N, 116°27′ 5″ E, 22.–26. v. 2014, leg. A. Klimenko (BC-Ivsh04031, BC-Ivsh04033, BC-Ivsh04034). 3 ♂♂, Trusmadi Mountains, 1185 m, 5°26′35″ N, 116°27′5″ E, 18.–25. viii. 2012, leg. A. Klimenko, GP 3521, 3523 (BC-Ivsh03521, BC-Ivsh03522, BC-Ivsh03523). 1 ♂, Trusmadi Mountains, 1185 m, 5°26′ 35″ N, 116°27′5″ E, 1.–14. vii. 2011, leg. V. Gromenko (BC-Ivsh02510). 1 ♀, Trusmadi Mountains, 1185 m, 5°26′ 35″ N, 116°27′5″ E, 1.–14. vii. 2011, leg. V. Gromenko (BC-Ivsh02727). 1 ♂, Pensiangan, 530 m, 4°35′16″ N, 116°19′ 27″ E, 1.–6. iii. 2014, leg. A. Klimenko, GP 3929 (BC-Ivsh03929). 1 ♂, Pensiangan, 530 m, 4°35′16″ N, 116°19′27″ E, 27. v.–1. vi. 2014, leg. A. Klimenko (BC-Ivsh04035). 1 ♀, Crocker Range National Park, 1700 m, 20. v.–4. vi. 2014, leg. A. Klimenko (BC-Ivsh04036). 1 ♂, Kinabalu Mountains, iv. 2007 (BC-Ivsh03982). 1 ♂, Trusmadi Mountains, 29. ix.–4. x. 2005, leg. S. Kashevnik (BC-Ivsh03990). These specimens in the research collections of Nikolay Ivshin (CNIM), Andrew Sochivko (CASM), Pavel Udovichenko (CPUM), Viktor Gromenko (CVGM), and Valentin Kalinin, all Moscow, Russia (CVKM). One paratype from CNIM will be deposited in the Zoological Institute of the Russian Academy of Sciences, Saint-Petersburg, Russia (ZIRAS). — 1 ♂, Kundasan [Kundasang], iv. 1981, Cadiou coll. BMNH(E) 2008-107. 1 ♂, Crocker R., iii. 1992, Cadiou coll. BMNH(E) 2008-107. 1 ♂, Keningau, iv.–v. 1981, ex H. Kezuka [H. Inoue collection], Slide 12396 (♂), *Oxyambulyx substrigilis brooksi* Clark, det. H. Inoue 1981, Inoue coll. BM 1992-71. 1 ♂, Keningau, iv.–v. 1981, ex H. Kezuka [H. Inoue collection], Slide 9437 (♂), Inoue coll. BM 1992-71. 1 ♂, Keningau, 8. iv. 1985. Inoue coll. BM 1992-71. 1 ♂, Keningau, 19. iv. 1985, Inoue coll. BM 1992-71. 1 ♂, Mt. Kinabalu, iii. 1982, ex H. Kezuka, Cadiou coll. BMNH(E) 2008-107. 1 ♀, Kinabaru [= Kinabalu], iv.–v. 1981, Cadiou coll. BMNH(E) 2008-107 (all BMNH). – All in CJHL: 3 ♂♂, piste de Keningau à Kimanis, pk 26, 1300 m, 7.–9. viii. 1991 (UV light), leg. Jean Haxaire & Pierre Wident (1 ♂ Bold barcode no. BC-Hax 4817). 3 ♂♂, piste de Keningau à Kimanis, pk 28,5 1300 m, 10.–11. viii. 1991 (UV light), leg. Jean Haxaire & Pierre Wident (BC-Hax4816, BC-Hax0149, BC-Hax0150).

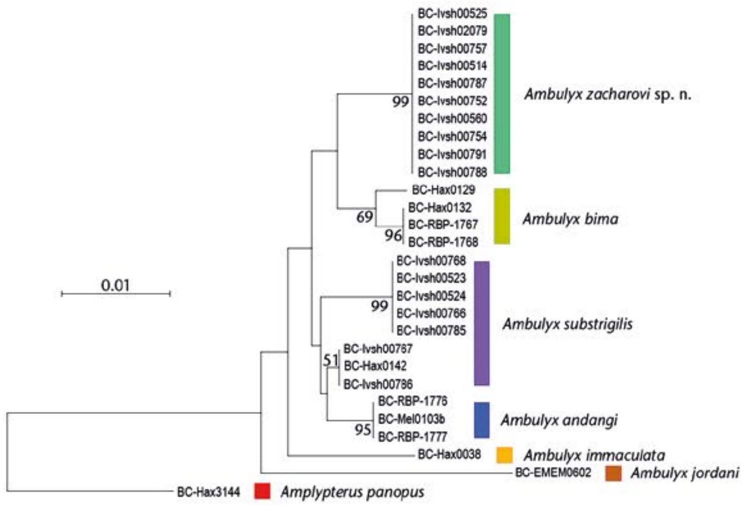
1a

1b

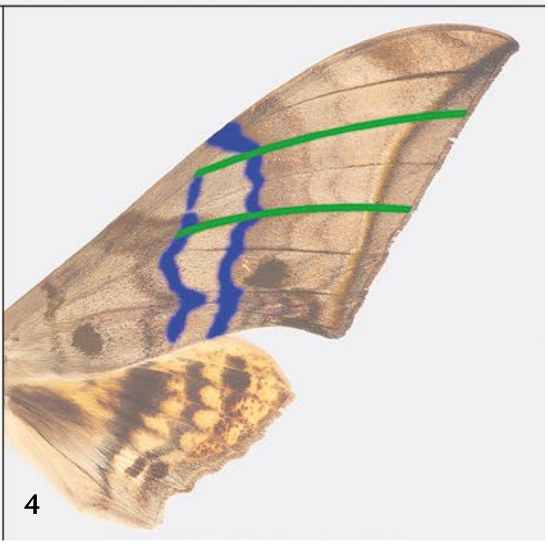
1c

1d

2



3



4

Figs. 1a, b: *Oxyambulyx substrigilis cana* Gehlen, 1940. **Fig. 1a:** Type (in Zoologische Staatssammlung München, Germany). **Fig. 1b:** The only specimen found in the Trusmadi Mts. that matches the habitus of *O. substrigilis cana* (collected I. 2007). — **Figs. 1c, d:** *Ambulyx zacharovi* sp. n., holotype. **Fig. 1c:** dorsal view. **Fig. 1d:** ventral view. — **Fig. 2:** Comparison of three *Ambulyx* species (males above, females below), from left to right: *A. substrigilis*, *A. zacharovi*, *A. immaculata*. — **Fig. 3:** Neighbor-joining tree for species considered to be closest to *A. zacharovi*. Bootstrap support values of >50% are indicated near the branches (tree length/sum of branch lengths [SBL] = 0.141, 500 bootstrap replicates). — **Fig. 4:** Illustration of the character concerning the intensity of the distal margin of the medial band and the basal margin of the postmedial band of forewing upperside (blue marking) compared to the dark scaling along veins M1 and M3 (green marking) of the fw. upperside (see text for explanation and also moths illustrated in Figs. 1 and 2). **Fig. 5:** ♂ genitalia. **Fig. 5a:** *A. zacharovi* (BC-Ivsh03929). **Fig. 5b:** *A. substrigilis* (BC-Ivsh03927). Both specimens were collected in Malaysia, N. Borneo, Sabah, Pensiangan, 4°35′16″ N, 116°19′27″ E, altitude 530 m. — **Figs. 6–8:** ♀ genitalia. **Fig. 6a:** *A. zacharovi* (BC-Ivsh00754). **Fig. 6b:** *A. substrigilis* (BC-Ivsh03525). Both specimens were collected in Malaysia, N. Borneo, Sabah, Trusmadi Mountains foothills, 5°26′35″ N, 116°27′5″ E, altitude 1185 m. **Fig. 7:** Details of the ♀ genitalia of *A. zacharovi*. **Fig. 7a:** 8th abdominal segment. **Fig. 7b:** corpus bursae. **Fig. 8:** Details of the ♀ genitalia of *A. substrigilis*. **Fig. 8a:** 8th abdominal segment. **Fig. 8b:** corpus bursae.

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A.zacharovi                     GGA GAT GAT CAA ATT TAT AAT ACT ATT GTA ACA GCT CAT GCA TTT ATT ATA ATT TTT TTT ATA GTT ATA CCT ATT ATA
A.substrigilis (mt haplotype 1) ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
A.substrigilis (mt haplotype 2) ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...

A.zacharovi                     ATT GGA GGA TTT GGA AAT TGA TTA GTA CCT TTA ATA TTA GGA GCC CCA GAT ATA GCA TTC CCA CGA ATA AAT AAT ATA
A.substrigilis (mt haplotype 1) ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
A.substrigilis (mt haplotype 2) ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...

A.zacharovi                     AGA TTT TGA CTT TTA CCC CCT TCT TTA AGA TTA CTT ATT TCT AGA AGT ATT GTA GAA AAT GGT GCA GGT ACT GGA TGA
A.substrigilis (mt haplotype 1) ... ... ... ... ... ... ... ... ... ... ... ..C ... ... ... ... ... ... ... ... ... ... ... ... ... ...
A.substrigilis (mt haplotype 2) ... ... ... ... ... ..A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...

A.zacharovi                     ACT GTT TAC CCA CCT TTA TCA TCT AAT ATT GCT CAT AGA GGA AGA TCT GTA GAT TTA GCT ATT TTT TCA TTA CAT TTA
A.substrigilis (mt haplotype 1) ... ... ..T ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
A.substrigilis (mt haplotype 2) ... ... ..T ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...

A.zacharovi                     GCA GGT ATT TCC TCT ATT TTA GGA GCA ATT AAT TTT ATT ACT ACA ATT ATT AAT ATA CGA ATT AAT AAT ATA TCA TTT
A.substrigilis (mt haplotype 1) ... ... ... ..T ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
A.substrigilis (mt haplotype 2) ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...

A.zacharovi                     GAT CAA ATA CCA TTA TTT GTG TGA GCT GTA GGA ATT ACA GCA TTC TTA TTA CTT CTA TCT TTA CCA GTT TTA GCT GGA
A.substrigilis (mt haplotype 1) ... ... ... ... ... ..C ..A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
A.substrigilis (mt haplotype 2) ... ... ... ... ... ..C ..A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...

A.zacharovi                     GCA ATT ACT ATA TTA TTA ACA GAT CGA AAT TTA AAT ACA TCA TTT TTT GAT CCA GCT GGA GGG GGG GAT CCA ATC TTA
A.substrigilis (mt haplotype 1) ... ... ... ..G ... ... ... ... ... ... ... ... ... ... ... ... ..C ... ... ... ..A ..A ... ... ... ...
A.substrigilis (mt haplotype 2) ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ..C ... ... ... ..A ..A ... ... ... ...

A.zacharovi                     TAT CAA CAC TTA TTT TGA TTT TTT GGT CAC
A.substrigilis (mt haplotype 1) ... ... ... ... ... ... ... ... ... ...
A.substrigilis (mt haplotype 2) ... ... ... ... ... ... ... ... ... ...
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Fig. 9: COI-5P ("barcode region") mtDNA haplotypes.

3 ♂♂, 1 ♀, piste de Keningau à Kimanis, 1300 m, 9.–19. iv. 1994 (UV light), leg. Denis Bouchard. — **Borneo, Brunei:** 1 ♂, Bukit Retak, Montane forest, 1618 m, 1. v. 1989, [leg.] Col. M. G. Allen, Cadiou coll. BMNH(E) 2008-107.

Etymology. The species is named after the ex-Vice Director of the Vavilov Institute of General Genetics of the Russian Academy of Sciences (Moscow), zoologist and geneticist Prof. Dr Ilya Zakharov-Gezekhus, the populariser of the Barcode of Life Initiative in Russia, and a responsive and decent man.

Additional (non-paratype) material:

Indonesia, Sumatra: 1 ♂, Aek Tarum, south of Dolok Merangir, 250 m, 8. x. [19]77, [leg.] E. W. Diehl, BMNH(E) 2011-163 acq. 1 ♂, Aek Tarum, South of Dolok Merangir, 250 m, 14. xi. [19]77, [leg.] E. W. Diehl, "This is the extremest [*sic*] form of *O. substrigilis* f. *cana*", BMNH(E) 2011-163 acq. 1 ♂, Dolok Merangir, 99°3′ E, 3°7′ N, 180 m, 30. vii. [19]76, [leg.] E. W. Diehl. Nr. 2. Sphingidae GP 295 ♂, BMNH(E) 2011-163 acq. 2 ♂♂, Ketambe, 26. i. [19]74, [leg.] E. W. Diehl, BMNH(E) 2011-163 acq. 1 ♂, W. Sumatra, Lebong Tandai, iii. 1922, [leg.] C. J. Brooks coll., No. 6189, F3, *O. substrigilis brooksi* B.P. Clark, C. J. Brooks Bequest. B.M. 1953-173., Sphing. GP 691 (all BMNH). — 1 ♂, Idi, 2. xii. 1978, leg. Dr. Diehl (Diehl [1982]: pl. II, fig. 19d, as *O. substrigilis brooksi* f. *cana*). 1 ♀, Sindar Raya, 9. i. 1978, leg. Dr. Diehl (Diehl [1982]: pl. II, fig. 19c, as *O. substrigilis brooksi*).

Peninsular Malaysia: 1 ♂, Malaysia, Cameron Highlands, Région de Tanah Rata, i.–ii. [19]79, coll J. M. Cadiou, 20346 *brooksi* ♂, Cadiou coll. BMNH(E) 2008-107 (BMNH).

Thailand: 1 ♀, S. Thailand, Narathiwat, km 17 on Ban Tabing Tinggi to Sri Sakhon rd., 250 m, 1.–3. xii. 1991, [leg.] I. J. Kitching & A. M. Cotton, BM 1992-14. 1 ♂, Peninsula, Trang, xii. 1987, ex A. Pinratana, Inoue coll. BM 1992-71. 1 ♂, Trang, Khao Chong, 18. xi. 1987, pres. by Br. A. Pinratana. 1 ♂, Krerng Kra Wia, 11. xi. 1988, [leg.] Pisuth EA [Ek-Amnuay], Brit. Mus. 1989-64. 1 ♂, Chanthaburi, Khao Soi Dao, ca. 400 m, 24.–25. viii. 1987, leg. S. Moriuti, T. Saito, Y. Arita & Y. Yoshiyasu, Lepidopt. exped. to Thai. 1987, Coll. Ent. Lab. Univ. Osaka Pref., *Ambulyx substrigilis substrigilis* Westw., det. H. Inoue 1990, Inoue coll. BM 1992-71. 1 ♂, Khao Yai N.P., 850 m, 2. iii. [19]89, [leg.] A. M. Cotton, Sphing. GP 591, Brit. Mus. 1989-64. 1 ♂, Chiang Mai, Doi Inthanon Mt., Checkpoint, 1700 m, viii. 1986, (leg. A. Pinratana), coll. J. M. Cadiou, 85.54.8 ♂, Doi Inthanon viii. 1986, Cadiou coll. BMNH(E) 2008-107 (all BMNH).

Description and diagnosis

Morphologically, *A. zacharovi* is closest to *A. substrigilis,* but slightly smaller in size, which can be clearly seen in a series of specimens. The first abdominal tergite is always darkened, which is the most reliable character for identification purposes. The only other *Ambulyx* species with a similar feature is *A. immaculata,* but this belongs to the Philippine fauna. There are no records for *A. immaculata* from Sundaland. A more variable character concerns the intensity of the distal margin of the medial band and the basal margin of the postmedial band of forewing upperside compared to the dark scaling along veins M1 and M3 (Fig. 4). In most *A. substrigilis* (e.g., Fig. 2, left), the intensity of the veins is much stronger than that of the edges of the bands, whereas in *A. zacharovi* (Fig. 2, centre) the intensity of the edges of the bands and the veins are similar. This gives *A. zacharovi* a more "striped" appearance overall. However, some specimens of *A. substrigilis,* such as the type of *cana* (Fig. 1a) and the "*cana*"-like moth from the Trusmadi Mountains (Fig. 1b), can approach the condition seen in *A. zacharovi.*

The ♀♀ of *A. zacharovi* have a brown forewing upperside ground colour, whereas the ♀♀ of *A. substrigilis* are olive-green or dull yellowish-brown.

♂ genitalia (Fig. 5a): In general appearance similar to *A. substrigilis* (Fig. 5b). The overall shape of the harpe, particularly the curvature and direction of the dorsal process, is rather variable. Nevertheless, the Bornean ♂♂ of *A. substrigilis* have a prominent constriction on the distal part of the harpe, whereas *A. zacharovi* have not. In Vietnamese *A. substrigilis* this character is not so clear cut, but here the distal half of the harpe is almost triangular with a rounded apex, which makes it completely different from *A. zacharovi*. However, the shape of the apical cornutus on the medial lobe of the vesica is diagnostic. In *A. zacharovi*, the sclerotized base is hemispherical and the cornutus itself conical, whereas in *A. substrigilis*, the base is much more elongate and both it and the cornutus thorn are laterally compressed and so blade-like.

♀ genitalia (Fig. 6a, 7): The anterior margin of the postvaginal plate in *A. zacharovi* has a broad, rounded excavation (Fig. 7a) rather than the small, narrow notch of *A. substrigilis* (Fig. 8a). Furthermore, the posterior margin of the postvaginal plate in *A. substrigilis* has a broadly rounded median triangular lobe (Fig. 8a), whereas in *A. zacharovi* it is truncate with a slight concavity (Fig. 7a).

The only known mtDNA haplotype of *A. zacharovi* is shown on Figure 9. It was common to all ten examined specimens. It differs from the two haplotypes found in *A. substrigilis* only in 7 or 9 synonymic nucleotide substitutions, so that the resulting polypeptide sequence is the same in all three cases. It is remarkable that with the exception of five species with only a single amino acid substitution (*A. maculifera* and *A. tenimberi*, *A. cyclasticta* and *A. kuangtungensis*, *A. dohertyi*), the polypeptide sequence of the COI “barcode” region is identical among more than 50 barcoded *Ambulyx* taxa. Indeed, the amino acid sequence of the putative sister genus, *Amplypterus*, also differs from that of *Ambulyx* in only a single substitution.

Distribution

In Borneo, the geographical distribution of *A. zacharovi* is rather limited, with specimens captured only in the north of the island, in Brunei and the Malaysian state of Sabah. Discussing Sumatran hawkmoths and, particularly, the variability of *A. substrigilis*, Diehl ([1982]) illustrated specimens of *A. zacharovi* from Sindar Raya and Idi, both of which are in the northwest of the island. The additional specimens found in the BMNH from Sumatra are also mostly from the northwest of the island, the only exception being a single specimen from “Lebong Tandai”, which is in the vicinity of Bengkulu in southwest Sumatra (Diehl [1982]). An unsuccessful attempt to find *A. zacharovi* in central part of island (Pesisir Selatan and Limapuluh Koto regencies) was made in April 2012, at altitudes ranging from about 30 to 800 m, but only a few *A. substrigilis* specimens, and no *A. zacharovi*, were caught. In Thailand, *A. zacharovi* has been captured in the southern provinces of Narathiwat and Trang, the southeastern province of Chantaburi, in the west in Kanchanaburi, in the centre in Nakhon Nayok, and in the north in Chiang Mai. It would thus appear to be quite widespread throughout the country. Overall, the current known range of *A. zacharovi* encompasses Thailand, Peninsular Malaysia, Sumatra and Borneo. It might also reasonably be expected to occur in southern Burma (Myanmar), Laos, Vietnam and Cambodia.

There appears to be a clear difference in the seasonal occurrence of the two species in the Trusmadi Mountains, Borneo (Fig. 10). The figure does not show an actual seasonal distribution because sampling was not undertaken continuously throughout the year but is based on the material provided by various collectors. Likewise, specimen numbers do not reflect actual population sizes. However, the figures do show that *A. substrigilis* and *A. zacharovi* are sympatric and that *A. zacharovi*, at least, occurs almost all year round, with no obvious separate generations, at least between January and August. In Sumatra, *A. zacharovi* has been captured in July, October, November, December and January, suggesting that there might be two generations a year. A similar pattern is seen in southern Thailand, with records from the months of August, November, December and March. However, these are likely to reflect collecting effort rather than flight times and more study is needed to determine the actual number of generations per year in this species.

With regard to the altitudinal range of *A. zacharovi*, less can be said as many specimens lack these data. On Borneo, specimens have been caught between 960 and 1700 m. In contrast, on Sumatra all specimens come from low elevations, between 50 and 800 m. Where known, the southern and central Thailand moths were also captured at low elevations, between 250 and 850 m. It is only the ♂ from Doi Inthanon in Chiang Mai province that was captured at a relatively higher elevation, 1700 m. This is a particularly dark specimen and would merit further study.

It might be expected that the distribution of *A. zacharovi* is host-plant dependent. The host-plants of *A. zacharovi* are currently unknown but are probably the same or very similar to those of *A. substrigilis*, which were listed by Holloway (1987) as *Dipterocarpus* (Dipterocarpaceae), *Lagerstroemia* (Lythraceae) and *Aglaia* (Meliaceae). The representatives of all these genera are common and often dominant components of the lowland equatorial rain forests of Southeast Asia, and for dipterocarp species, north Borneo (Brunei, Sabah, Sarawak) is the richest area in the world (Ashton 2004). Likewise, the various *Aglaia* have their greatest abundances in the Peninsular Malaysia, Sumatra and Borneo (Pannell 1992), where it is rather common to find ten or more species in a single plant society. *Lagerstroemia speciosa* (L.) occurs on Borneo (Jarvie & Ermayanti 1996 onwards) in open vegetation types, often in coastal areas, in regrowth or in swamps, also is also much planted as an ornamental tree up to 100 m altitude. A vegetation survey of Mount Trusmadi (Kitayama et al. 1993) showed that at altitudes above 1500 m none of these three plays a dominant role in the flora. If related species are considered, only Meliaceae are listed among the dominant tree species at this altitude. Thus, if the host-plants of *A. zacharovi*

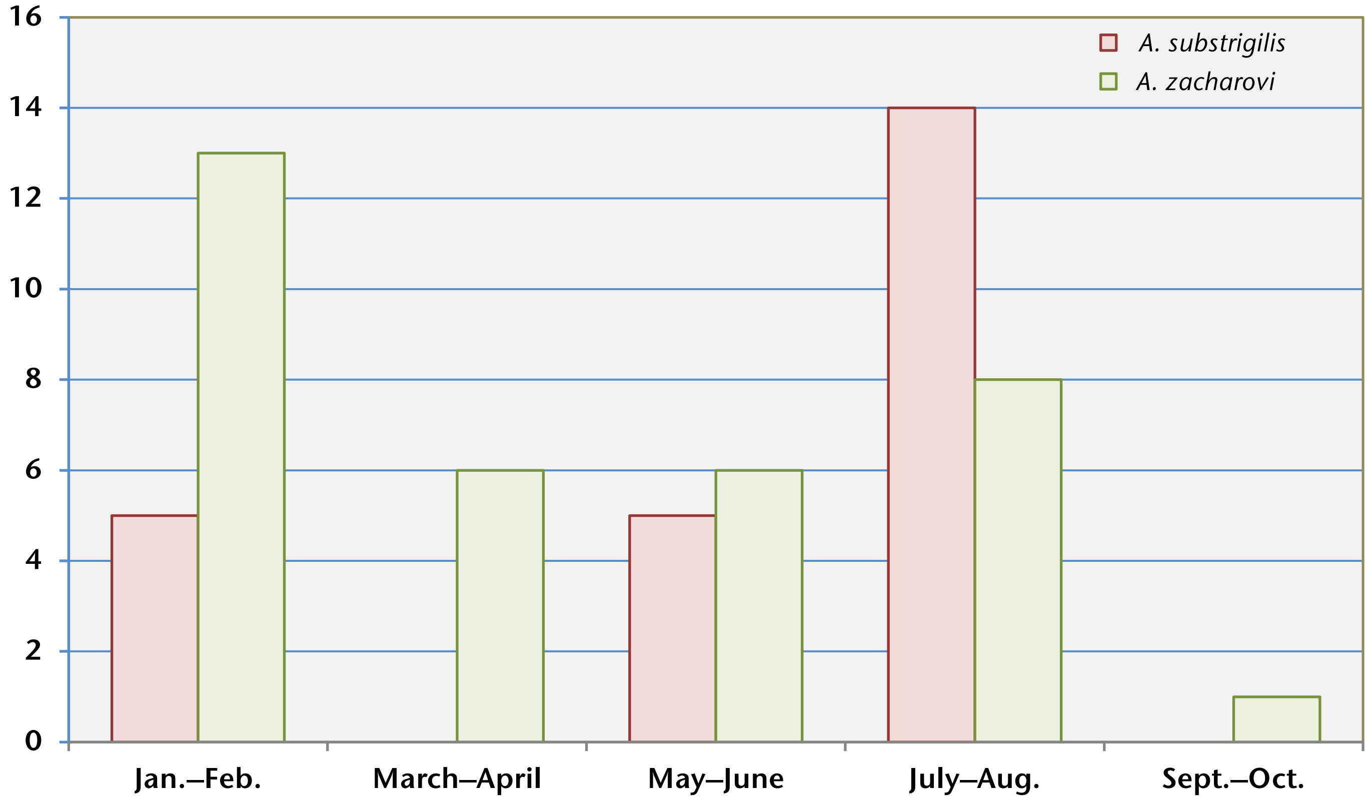

Fig. 10: Capture dates of *A. zacharovi* and *A. substrigilis* in the foothills of the Trusmadi Mountains in northern Borneo (horizontal axis: collecting month, vertical axis: specimen numbers); 2005–2014 collecting period.

are similar to those of *A. substrigilis*, then most records of *A. zacharovi* would be expected to be from localities with altitudes in the range of 0–1500 m above sea level, where the remaining lowland equatorial rain forests are found. Thus, ecologically *A. zacharovi* likely belongs to the fauna of lowland and foothill equatorial rain forests.

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