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Diverzita a endemismus čeledi Lycidae v horských lesích Peninsulární Malajsie

Rigorózní práce

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Vedoucí práce: Prof. Ing. Ladislav Bocák, Ph.D.

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PROHLÁŠENÍ

Prohlašuji, že jsem rigorózní práci vypracovala samostatně pod vedením Prof. Ing. Ladislava Bocáka, Ph.D. a použila jsem pouze uvedené bibliografické zdroje.

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ABSTRAKT

Tribus Metriorrhynchini (Coleoptera: Lycidae) je jeden z druhově nejbohatších tribů síťokřídlých brouků, kteří jsou nejvíce rozšíření v jihovýchodní Asii. Představují typické cantaroidní brouky s nízkou schopností letu, krátkým životem dospělců a jejich nízkou aktivitou pod příkrovem deštných pralesů. Díky nízké schopnosti k šíření mohou být použiti jako modelová skupina pro studování ancestrální distribuce a datování disperzních událostí. Tito brouci představují málo známou skupinu s chaotickou klasifikací a nekompletními znalostmi diverzity a bionomie. Já jsem se zaměřila na podtribus Cautirina, konkrétně na rod *Cautires*, v Orientální oblasti. Zde prezentuji tři nezávislé studie, které porovnávají morfologickou a molekulární delimitaci druhů, diskutují taxonomii rodu *Cautires*, odhadují schopnost těchto brouků osídlit oblasti oddělené mělkým mořem nebo pleistocenními savanami, jejich původ a taxonomii. Tyto studie odhalily velmi vysokou diverzitu v oblasti Velkých Sund, malé areály většiny druhů a ukazují důležitost simultánního hodnocení molekulárních a morfologických dat. Dřívější studie byly založeny na vnější morfologii a zbarvení, avšak obojí je silně ovlivněno evolucí mimikry.

Klíčová slova: mtDNA, morfologie, delimitace, taxonomie
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ABSTRACT

Metriorrhynchini (Coleoptera: Lycidae) is the most species-rich tribe of net-winged beetles and they are most diversified in South East Asia. They represent a typical cantharoid-type beetles with a low flight ability, short adult life span and low-activity life under the rainforest canopy. Due to low dispersal propensity, they can be used as a model group for studying ancestral distribution and the dating of dispersal events. Metriorrhynchini beetles represent poorly known group with chaotic classification and incomplete knowledge of diversity and life history. I focus on the subtribe Cautirina, namely genus *Cautires*, in the Oriental region. Here, I present three independent studies which compare morphological and molecular species delimitation, discuss taxonomy of *Cautires*, and estimate their ability to colonize landmasses separated by shallow sea or Pleistocene savannahs, their origin and taxonomy. These studies revealed very high diversity in the Sundaland, small ranges of most species and show importance of simultaneous evaluation of molecular and morphological data. Earlier studies had been based on external morphology and colouration which both are strongly affected by mimicry.

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CONTENT

INTRODUCTION

To characterize diversity, we need to investigate the numbers of species in local ecosystems or geographically defined regions and the complete geographical distribution of individual species, i.e., to evaluate the alpha-diversity. Then, the phylogenetic structure of local assemblages, i.e. beta-diversity, and the processes leading to the observed patterns must be considered to identify the areas with high phylogenetic diversity. After more than 200 hundred years since the earliest taxonomic studies (e.g., Linnaeus 1758, Fabricius 1801, Lacordaire 1857), the diversity of insects remains partly unknown, especially in the tropical regions (Tvardik and Bocak 2001, Dvorak and Bocak 2007). The first problem is an incomplete sampling, due to which a high number of species have never been discovered and additionally, there are extensive regions which have never been systematically studied, e.g. some areas in the New Guinea interior, the Sahel region in the Central African Republic, Southern Sudan and Somalia or most of the Congo Basin (Myers *et al.* 2000). If an earlier collected material is available in museums, only a part has been formally identified and the results published. The second problem is the reliability of earlier published information which very often cannot be used for any comprehensive study due to poor quality of some records. A good part of dubitable records given in the literature needs revision, but voucher specimens are either improperly cited, destroyed or unavailable, e.g. due to the policy of the type depositing institutions which do not allow to provide critical specimens for loans. The removal of false data from current catalogues seems to be much more difficult than an introduction of a false information for the first time. Therefore, the catalogues, including the newest ones, often include incorrect information, e.g. the repeated unconfirmed records of Caucasian *Platycis schneideri* Kiesenwetter in the catalogues of Czech and Slovak beetles (Jelinek 1993). For taxonomists and students of biodiversity, the ultimate goal is to recognize all species on this planet and build the complete tree of life. Such project would need an intensive and long-time effort, including continuous curation of data and it remains under current situation unattainable. Therefore, limited goals, such as critical studies on local faunas and taxonomically defined groups are the only way how to accumulate biodiversity data (Monaghan *et al.* 2005, Novacek 2008, Riedel *et al.* 2009, Costello *et al.* 2013). Here, I present a study which focus on net-winged beetles (Coleoptera: Lycidae) and the biodiversity hotspot in the Sundaland (Myers *et al.* 2000).

The beetle family Lycidae (Coleoptera: Elateroidea) is an almost world-wide distributed group which is missing only in polar and desert regions (Bocak and Bocakova 2008).

The highest diversity has been recorded in tropical and humid subtropical ecosystems, especially in the rainforests of Southeast Asia, the Wallacea, New Guinea and Southern America (Bocak 2000, Bocak and Bocakova 2008). The number of newly discovered species often surpasses by an order the number of known species from the region in the collected tropical material (e.g. Dvorak and Bocak 2009). The tribe Metriorrhynchini (subfamily Lycinae) is the most diversified group of net-winged beetles and it contains approximately 1400 formally named species (Bocak 2002). The tribe was described by Kleine (Kleine 1926) for the group of net-winged beetle genera with seven areoles on the pronotum, developed transverse costae on elytra, and male genitalia with a round phallobase. The tribe Metriorrhynchini, as currently delimited, contains also earlier described tribes Cladophorini Kleine, 1928, Dilolycini Kleine, 1926 and Trichalini Kleine, 1928 (Bocak and Bocakova 1990). Kleine (1926, 1933) treated the current Metriorrhynchini earlier as the subfamily Metriorrhynchinae and he lowered in to the rank of a tribe in his later world catalogue. This group was reclassified as the tribe Metriorrhynchini after it was merged with many other lineages, e.g. Calochromini or Erotini, in the redefined subfamily Lycinae (Bocak and Bocakova 2008).

Further studies were based on molecular data and the evaluation of the molecular phylogenetic signal along with the morphology of larvae lead to the delimitation of three major lineages in the tribe: Metriorrhynchina Kleine, 1926, Metanoeina Sklenarova *et al.*, 2014 and Cautirina Sklenarova *et al.*, 2014 (Sklenarova *et al.* 2014). The previously recognized subtribes Trichalina Kleine, 1928 and Hemiconderina Bocak and Bocakova, 1990 were included in the subtribe Metriorrhynchina Kleine, 1926. The earlier classification was based only on morphological characteristics of adults and in contrast with previous hypotheses, the molecular studies identified some relationships, which are not robustly supported by adult morphology. The current classification obtained further strong support from the larval morphology. Nevertheless, as larvae are rarely collected and almost all studies are dealing with adults, the adult characters are used for practical identification: the elytra have four or nine strong longitudinal costae, the ridges on pronotum form areoles, seven in the ground-plan and five or three if they are reduced and male genitalia do not have parameres and they often have internal sac with thorns. The Metriorrhynchina net-winged beetle larvae are characterized by movable sclerotized stick-shaped appendages on pleural abdominal membranes and by longitudinally divided tergal sclerites (Sklenarova *et al.* 2014). The subtribe Cautirina has undivided larvae tergites, Metanoeina has longitudinal divided tergites (Sklenarova *et al.* 2014).

The dispersal capacity of Metriorrhynchine beetles is affected by their low-power and slow flight, dependence on humid conditions under rainforest canopy and short life-span of adults (Bocak and Matsuda 2003, Barraclough and Vogler 2000). Metriorrhynchini have a Gondwanan origin, similar to Calopterini Green, 1949, Slipinskiini Bocak and Bocakova, 1992 and Dexorini Bocak and Bocakova, 1989. The biota of the Indian Ocean margin was strongly affected by fragmentation of Gondwana, drift of India, its subsequent collision with continental Asia, and the quite recent dispersal of the Australian fauna northwards due to the recent formation of numerous islands in the Indo-Australian Archipelago which served as stepping stone for many groups (Toussaint *et al.* 2014, 2015, Tänzler 2016, Hall 2002). The origin of the tribe Metriorrhynchini is supposed to be in the Upper Cretaceous (Sklenarova *et al.* 2013). The tribe consists of two lineages with Afro-Oriental distribution (Cautirina and Metanoeina) and a single lineage with ancestral Australian distribution and a limited dispersal westward and northward (Metriorrhynchina). Only a few genera of Australian Metriorrhynchina crossed the Weber's and Wallace's line on their way to the Oriental region and reached to the north up to southernmost China (Bocak and Yagi 2010; Bocak *et al.* 2006, Bocek and Bocak 2017).

The origin of the ancestral lineages of the subtribe Cautirina lies in the East Gondwana and after a separation of India from Australia, these lineages expanded to the north and west. Afrotropical and Madagascar Metriorrhynchini split from their relatives on drifting India 65-62 million years ago (Sklenarova *et al.* 2013). Many already split groups dispersed to continental Asia 35–53 million years ago. Only the genus *Xylobanus* Waterhouse, 1879 dispersed across the Makassar Strait to Sulawesi across Wallace's line and this is its easternmost record (Kubecek *et al.* 2011). The Afrotropical and Madagascar lineages were evolving independently without any reverse dispersal to India or continental Asia. Additionally, due to their low dispersal capacity the Cautirina lineages remained isolated by the Mozambican channel since the Lower Paleocene, i.e. for the last 60 million year. The extant Oriental fauna consists of Indian and Australian lineages with the total dominance of the first named (Kleine 1933, Bocak 2002). The fauna of the islands north of Australia, i.e. the Sula Spur as a north Australian promontory, diversified on Sulawesi and expanded their ranges to the Philippines and in some uncommon cases also to the Moluccas (Sklenarova *et al.* 2013).

The biodiversity of tropical regions is poorly explored though many scientists worked on taxonomy of various beetle groups in these regions. Similarly, fauna of the family Lycidae was not comprehensively studied and contemporary knowledge of this family is based on fragmented, old and unverified information. Many species were described in the Indo-Australian Archipelago, Australia, Africa and continental Asia, but probably they represent only a small part of real numbers (Dvorak and Bocak 2007, 2009). The problem is taxonomical system based only on morphological data and historical descriptions providing short uninformative diagnoses (e.g. Pic 1925). Currently, the methods using molecular data for delimitation of species are available. Their application shows much more complicated taxonomic situation then earlier expected, including the paraphyletic character of some species and high cryptic diversity. Often, different phenotypes were considered as two biological species but their genotypes are so similar that the gene flow makes them a single species. The advantage of molecular data is the ability to identify cryptic diversity or polymorphism of species involved mimetic complexes (Bocek and Bocak 2017). Such examples show that the reliability of morphologically based taxonomic operational units should be tested with additional data whenever possible. Conversely, molecular data are not an all-case solution and in opposite, they must be tested by morphology, ecology and any further information. In some cases, the genetic divergence is limited and yet two reproductively isolated species can be hypothesized if other processes such as selection are so intensive that they keep putative species reproductively isolated (Bray and Bocak 2016, Jiruskova *et al.* 2016, Kalousova and Bocak 2017). Male genitalia are used for morphological delimitation of species because of its fast diversification due to intensive sexual selection when they are used as a reproductive isolation mechanism. Then genitalia with clearly defined differences can be found in otherwise genetically poorly diversified sympatric species (Bocak and Yagi 2010). The consensus between morphological and molecular signal is the best way how to delimit species (Johnson 2012). Metriorrhynchini are taxonomically complicated groups as they are extremely diverse and commonly polymorphic. Using every available data for delimitation in this group is necessary to avoid a typological approach (Kusy *et al.* 2018). The evolution of mimicry patterns is characteristic for the family Lycidae. It has already been documented that selection for similarity in Müllerian mimicry leads first to the advergence to an autochthonous aposematic patterns and then to the evolution of further reproductive isolation mechanism and separation of genetic pools (Bocak and Yagi 2010, Bray and Bocak 2016, Bocek and Bocak 2017).

Currently, the species-level classification of subtribe Cautirina is based on historical descriptions and on the recently published revision of generic classification (Sklenarova *et al.* 2014). There are 4 genera classified in the Cautirina: *Cautires*, *Xylobanus*, *Caenioxylobanus* and *Tricautires*. The two last named genera occur only in Afrotropical region and they have not yet been available for a DNA analysis. *Xylobanus* is known from Oriental and Palearctic regions and the Afrotropical species earlier classified as *Xylobanus* are in fact only members of a terminal clade in the genus *Cautires* (Sklenarova *et al.* 2014).

The aim of this study is to present further studies dealing with taxonomy (part 1), dispersal propensity (part 2) and application of molecular data in the zoogeography and taxonomy (part 3). All three separate studies focus on the subtribe Cautirina, its diversity, ancestral areas and delimitation of species, using both molecular and morphological data. First study deals with species delimitation and taxonomy of *Cautires* (Coleoptera: Lycidae) from Peninsular Malaysia using morphology. The second study deals with dispersal propensity of *Cautires* in the Malay Peninsula and Sumatra and discusses various factors affecting the observed patterns. The third study poses a question if a world-wide diversity sequencing campaign can identify the real ranges of natural taxa and what are the taxonomic consequences. As an example of a taxonomic all-in-one basket were chosen the genera of the Cautirina and Metriorrhynchina and the congruence between DNA-based distribution ranges and catalogue-based ranges was evaluated.

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Part 1

HIGH DIVERSITY AND ENDEMISM IN THE GENUS *CAUTIRES* WATERHOUSE, 1879 (COLEOPTERA: LYCIDAE) FROM THE MALAY MOUNTAIN FORESTS, WITH DESCRIPTIONS OF FOURTEEN NEW SPECIES

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High diversity and endemism in the genus *Cautires* Waterhouse, 1879 (Coleoptera: Lycidae) from the Malay mountain forests, with the descriptions of fourteen new species

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Abstract. We identified a high diversity in the net-winged beetles of the genus *Cautires* in Peninsular Malaysia. Fourteen new species are described: *Cautires alexae* sp. nov., *C. andujari* sp. nov., *C. arribasae* sp. nov., *C. berembanensis* sp. nov., *C. campestris* sp. nov., *C. communis* sp. nov., *C. jasarensis* sp. nov., *C. katarinae* sp. nov., *C. kirstenae* sp. nov., *C. kotatinggensis* sp. nov., *C. linardi* sp. nov., *C. maseki* sp. nov., *C. pahangensis* sp. nov. and *C. renatae* sp. nov. Seven previously described species are discussed, illustrated and differential diagnoses provided; all species are keyed. The *Cautires* species differ in a limited number of diagnostic characters, namely in the shape of male antennae, the relative size of eyes and in the shape of the male genitalia. The females are difficult to assign to a conspecific male due to high intraspecific variability. The characteristically low dispersal propensity of net-winged beetles lead to the evolution of the unique fauna in the Malay mountains and despite an extensive study of the type material we recorded only a single species of *Cautires* occurring simultaneously in Sumatra. We suggest that the Malay mountain fauna is highly endemic and evolved *in situ*.

Keywords. Taxonomy, morphology, Sundaland, Oriental Region, new species.

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Introduction

The high diversity of beetles in tropical regions remains poorly studied and the number of undescribed taxa in the randomly collected samples is often substantially higher than the number of known species. Such lack of knowledge is to be expected in relation to under-investigated and long-inaccessible regions such as New Guinea (Riedel *et al.* 2013; Bocek & Bocak 2016), but, at least in the case of net-winged beetles (Lycidae), we can find a high proportion of undescribed taxa in the whole tropics. This is also true for areas where entomological research has a long tradition, such as Sulawesi (Bocak 2000), the Philippines (Weiszenstein & Bocak 2011) and the Great Sundas (Masek *et al.* 2015). The recent DNA-based study dealing with the *Cautires obsoletus* species group, i.e., the former genus *Bulenides* Waterhouse, 1879 (Jiruskova & Bocak 2015), revealed quite a high number of unknown species, as was also the case in recently collected material from the Malay Peninsula. This region was intensively studied from the late 19th century until WWII (Waterhouse 1879; Pic 1925, Kleine 1930a, b, 1933), but has since been omitted from studies.

The *Cautires* is placed in the tribe Metriorrhynchini, which is the largest lineage of Lycidae as regards the number of species (1200 spp. in 41 genera in the Old World tropics, Kleine 1933; Sklenarova *et al.* 2013) and which, along with Platerodini, is the most common group of net-winged beetles in the Orient. Almost 100 species of *Cautires* have been reported from Sundaland (Kleine 1933; Bocak 2002), whereas the recent molecular study dealing with the delimitation of genera in Metriorrhynchini has shown that the fauna of Sumatra, Borneo and the Malay Peninsula seldom share any common species and that even the mountain ranges within a single island have a highly endemic fauna (Sklenarova *et al.* 2014). The species' high turnover is supposedly a result of biological characteristics of net-winged beetles. Lycidae live under the canopy and, although winged and capable of flight, they have a tendency to remain in the low strata of the forest and do not disperse easily. The low dispersal propensity of net-winged beetles leads to diversification *in situ* and limited dispersal between islands or mountain ranges (Li *et al.* 2015; Masek *et al.* 2015). *Cautires* larvae mainly evolve on the ground in wood at various stages of decomposition. They suck liquids with rich microbial life from small-size organic detritus such as rotten twigs. They can be collected from under the bark of dead tree trunks (Bocak & Matsuda 2003).

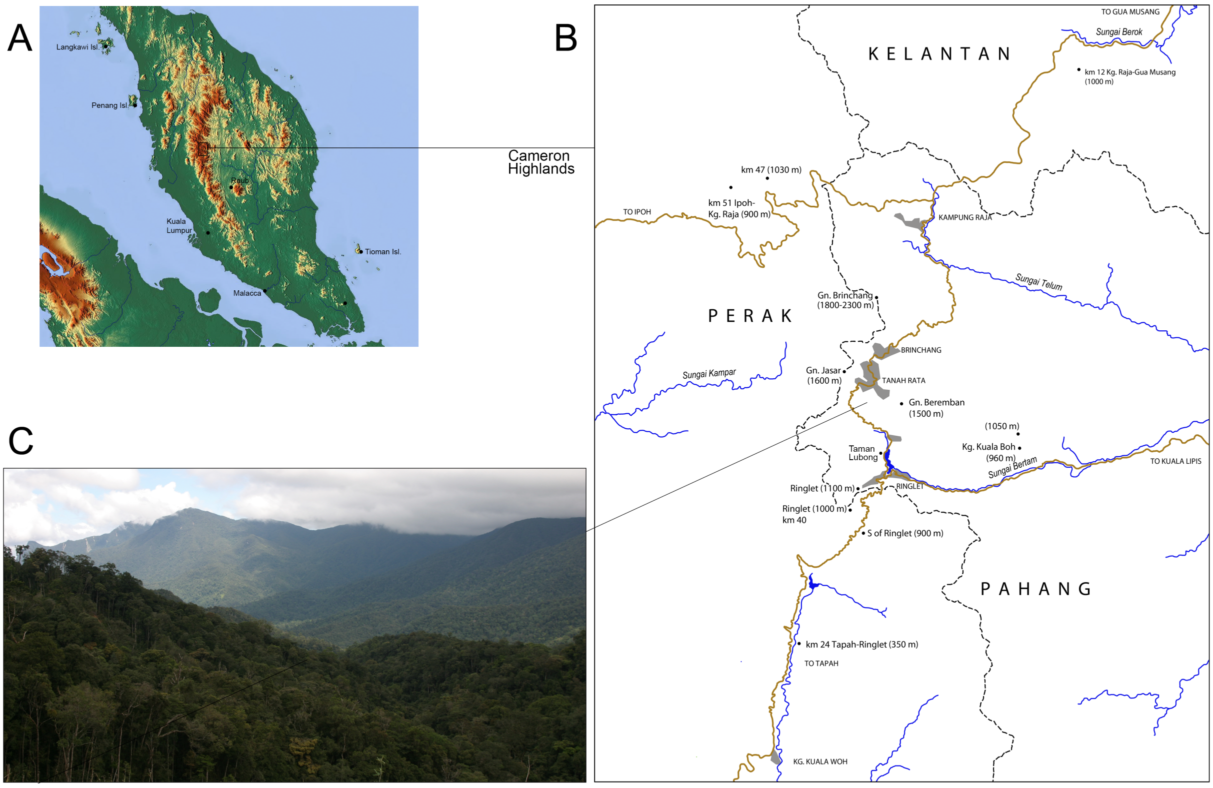


Fig. 1. The sampled localities in the Malay Peninsula. **A**. The localities in the Malay Peninsula. **B**. Detailed map of sampled localities in the Cameron Highlands region. **C**. Habitats in the Cameron Highlands mountain.

Here, we present an alpha-taxonomic review of *Cautires* from the Malay Peninsula. The first species from Malaya were described by the end of the 19th century (Waterhouse 1879; Kirsch 1875), but the fauna was only explored further in the 1920s and 30s when Pic (1925) and Kleine (1930a, b) reported several *Cautires* species in this region. Only a few of them were collected in the mountain forests at that time; most of the field work took place along the coast in the easily accessible lowlands and frequently visited places which were close to Malacca and Kuala Lumpur. Additionally, some species were described from the Penang and Langkawi islands. Due to the inaccessibility of the Malay inland until the late 1960s, the fauna of the mountain ranges remained poorly studied. Recently, an extensive collection of the Malay *Cautires* was assembled from the Cameron Highlands. The study deals with all species bearing more than three areolae in the pronotum, and this group of species corresponds with the original narrow delimitation of *Cautires* (Kleine 1933; Bocak 2002; but not Dudkova & Bocak 2010 and Sklenarova *et al.* 2014). The *Cautires obsoletus* species group, which was earlier given the rank of a genus, i.e., *Bulenides* Waterhouse, 1879, was studied earlier (Jiruskova & Bocak 2015) and all species of this species group are incorporated in the identification key. We delimit species using morphological diagnostic characters and we demonstrate the high species-level diversity of *Cautires* in the Malay mountain rainforests.

Material and methods

We had 159 specimens at our disposition from different localities in the Main Range of Peninsular Malaysia, mainly from the Cameron Highlands in the Titiwangsa Mountains (Fig. 1). Although the area is quite small, about 1000 km^2, it covers various ecosystems from the lowland tropical forests close to Tapah (350 m a.s.l.), mid elevation forests in the area of Kampong Kuala Boh, Ringlet and along the roads from Cameron Highlands to Gua Musang, Kuala Lipis, and Ipoh (600–1000 m a.s.l.), and high mountain and cloud forests in the highest elevations of the Mt. Brinchang, Beremban and Jasar (1500–2000 m a.s.l.). The specimens were collected mostly by sweeping of the low forest stratum and beating of vegetation. The material was preserved in 96% alcohol and each specimen was given a voucher number consisting of two letters and four-digit number. All specimens designated by these voucher numbers are deposited in the collection of the Laboratory of Molecular Systematics, Palacký University, Olomouc, Czech Republic (LMBC). A piece of a metathoracic tissue of each specimen was deposited for future isolation of genomic DNA in the tissue collection of the same institution.

The study is based on adult males (Fig. 2) and, due to the absence of external morphological diagnostic characters and uniformity of female genitalia, we do not delimit any species when only females are available. Some females are included in the type series when they were collected simultaneously with the males and are phenotypically similar. As the identification of females is based on similarity to conspecific males, we do not provide detailed descriptions of females for each species. The differences in the structure of costae and ridges, the shape of the pronotum and colouration are variable in most species and do not provide reliable diagnostic characters. The density of transverse elytral costae depends on the body size of a specimen and colour patterns usually follow the most common co-mimetics in the locality and additionally the colouration partly depends on the altitude where the given population occurs. Generally, the mountain species are darker coloured or uniformly black (Fig. 79).

The tips of abdomen were placed in water to relax soft body parts for at least several hours and then transferred into hot 10% aqueous solution of potassium hydroxide for a short time depending on the level of sclerotization and the persistence of fat bodies and muscles. The phallus was removed from the abdominal sclerites, cleaned and photographed by a Canon EOS 700D camera mounted on an Olympus SZX-16 binocular microscope. A scale in the eyepiece was used to take the measurements of the individual body parts described below.

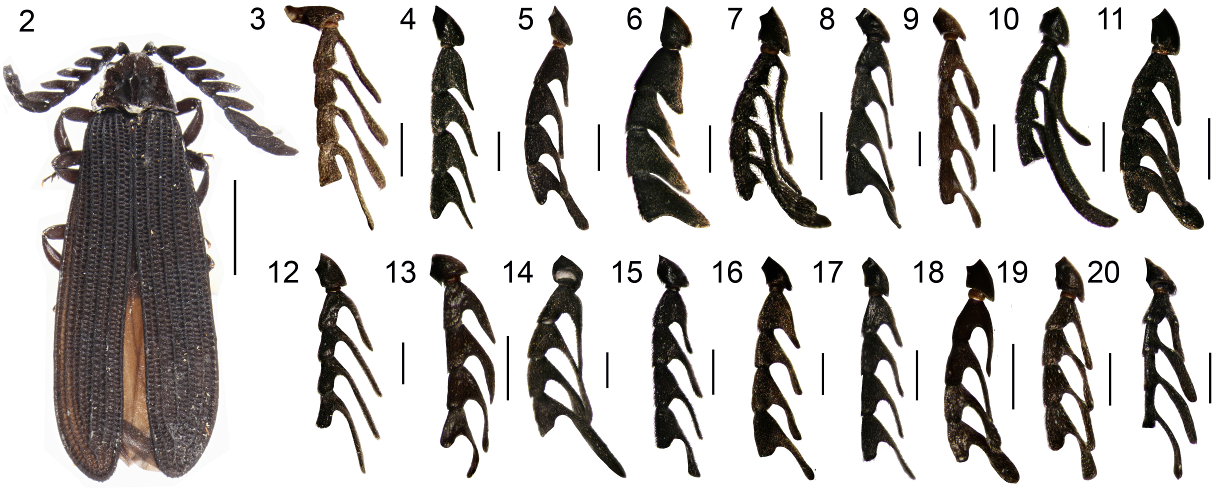
Abbreviations

BL = body length measured from the tip of the clypeus to the tip of elytra
PW = pronotum width at the widest point, usually at the posterior angles
PL = pronotum length along the midline of the pronotum
HW = width at humeri at the point where elytra become parallel-sided
Ediam = maximum eye diameter measured in the lateral view
Edist = maximum eye distance measured in the frons
LP = length of the phallus

Deposition of material

The examined material mentioned in the study is deposited in the following institutions:

BMNH = Natural History Museum, London, UK
LMBC = Laboratory of Molecular Systematics, Palacký University Olomouc, Olomouc, Czech Republic (all specimens designated by the voucher numbers in this study)
MHNP = Museum national d'Histoire naturelle, Paris, France



Figs 2–20. *Cautires* sp. **2**. Habitus in dorsal view. **3–20**. Male antennae. **3**. *C. alexae* sp. nov. **4**. *C. andujari* sp. nov. **5**. *C. arribasae* sp. nov. **6**. *C. berembanensis* sp. nov. **7**. *C. campestris* sp. nov. **8**. *C. communis* sp. nov. **9**. *C. griseus* Kleine, 1930. **10**. *C. jasarensis* sp. nov. **11**. *C. katarinae* sp. nov. **12**. *C. kirstenae* sp. nov. **13**. *C. kotatinggensis* sp. nov. **14**. *C. linardi* sp. nov. **15**. *C. maseki* sp. nov. **16**. *C. pahangensis* sp. nov. **17**. *C. nervosus* Kleine, 1926. **18**. *C. renatae* sp. nov. **19**. *C. reverandi* Pic, 1925. **20**. *C. simillimus* Kleine, 1926. Scale bars: Fig. 2 = 2.0 mm; Figs 3–20 = 0.5 mm.

Results

Order Coleoptera Linnaeus, 1758
Superfamily Elateroidea Leach, 1815
Family Lycidae Laporte, 1836
Subfamily Lycinae Laporte, 1836
Tribe Metriorrhynchini Kleine, 1926
Subtribe Cautirina Sklenarova, Kubecek & Bocak, 2014

Cautires Waterhouse, 1879
Figs 6–20, 41–78

Cautires Waterhouse, 1879: 36. Type species: *Lycus* (gen. 22) *excellens* Waterhouse, 1878 by subsequent designation: Bourgeois 1891: 345.
Bulenides Waterhouse, 1879: 34. Type species: *Lycus* (gen. 21) *obsoletus* Waterhouse, 1878 by subsequent designation: Bourgeois 1891: 345.

Bulenides – Dudkova & Bocak 2010: 34.

Diagnosis

Cautires belongs to the subtribe Cautirina in close relationships to *Xylobanus* (Lycidae: Metriorrhynchini), from which it can be distinguished by continuous larval terga and a simple, usually slender phallus with a pair of sickle-shaped thorns in the internal sac (Sklenarova *et al.* 2014). Almost all Oriental *Cautires* have the male antennae flabellate (Figs 7–20), some species have very short lamellae and the antenna is acutely serrate (Fig. 6). The female antennae are always serrate. Each elytron bears four primary and five secondary longitudinal costae (Figs 41–58) and numerous transverse costae connecting them. *Cautires* species have the lanceolate phallus with membranous internal sac bearing two sickle-shaped thorns at its base (Figs 59–78).

Remark

The revised concept of *Cautires* merged the genera *Bulenides* Waterhouse, 1879 and *Cautires* Waterhouse, 1879 (Dudkova & Bocak 2010). Later, the terminal position of *Bulenides* within the *Cautires* clade was confirmed by subsequent molecular phylogenetic study by Sklenarova *et al*. (2014). The latter study also redefined the limits of *Xylobanus* Waterhouse, 1879, which was originally defined by the absence of secondary costae. Some *Xylobanus* have elytral costae similar to those of *Cautires* and adults of these species can be identified using the shape of male genitalia. The species group of *C. obsoletus* corresponds with the limits of *Bulenides* and these species differ in absence of lateral ridges in the pronotum.

Key to males of *Cautires* from the Malay Peninsula

1. Pronotum with three areolae, i.e., only median longitudinal keel present in pronotum with narrow areola embedded in posterior part (species group *C. obsoletus*) ……………………2
– Pronotum with more than three areolae, i.e. postero- and antero-lateral ridges developed in pronotum, either of them can be vestigial, but always at least some part remains apparent (*Cautires* sensu Kleine, 1933) ……………………11

2. Pronotum wide, flat, with very slender median areola in basal half of median keel ……………………3
– Pronotum narrow frontally, without wide lateral areolae, median areola slightly wider, usually longer than frontal keel ……………………4

3. Only basal part of elytral costae brightly red coloured, phallus slender …………………………… ***C. pauperulus*** (Bourgeois, 1883)
– Basal two thirds of elytra light brown, phallus widened apically …***C. malayensis*** (Kleine, 1930)

4. Whole elytra uniformly black ……………………………………………………………5
– At least humeral part of elytral costae with bright red or orange pubescence or variable humeral part of elytra brightly coloured ……………………………………………………………6

5. Phallus parallel-sided, without any extended part ………***C. parallelus*** Jiruskova & Bocak, 2015
– Phallus widest in apical fourth ……………………………………………***C. imitator*** (Kleine, 1930)

6. The maximum eye diameter 1.2–1.3 larger than interocular distance …………………………7
– The maximum eye diameter small, 0.6–0.9 times their interocular distance ……………………9

7. Phallus very slender, widest in middle part, apical two-fifths parallel-sided, lamella of antennomere 5 about twice longer than its stem ……………………………………***C. coccineus*** (Kleine, 1930)
– Phallus widest in apical third, apical part gradually narrower to apex …………………………8

8. Lamella of antennomere 5 about twice longer than its stem, apex of phallus rounded …………………………… ***C. paraimitator*** Jiruskova & Bocak, 2015
– Lamella of antennomere 5 about 1.5 times longer than its stem, apex of phallus pointed …………………………… ***C. tanahratensis*** Jiruskova & Bocak, 2015

9. Antennomere 5 with lamella about twice longer than its stem, elytral costae with bright pubescence in whole length ……………………………………***C. nebulosus*** (Kleine, 1930b)
– Antennomere 5 with lamella at most 1.5 times longer than its stem, elytral costae with bright pubescence at most in humeral half ……………………………………………………10

10. Phallus widest in middle part ……………………………***C. tapahensis*** Jiruskova & Bocak, 2015
– Phallus widest in apical third ……………………………………………***C. indus*** (Kirsch, 1875)

11. Whole elytra uniformly black ……………………………………………………………12
– At least humeral part of elytral costae with bright red or orange pubescence or variable humeral part of elytra brightly coloured ……………………………………………………………21

12. The maximum eye diameter 1.1 times larger than interocular distance ……***C. linardi*** sp. nov.
– The maximum eye diameter 0.4–0.95 times interocular distance ……………………………13

13. Male antennomeres 3 and 4 with slender basal part of their lamellae, lamella attached to basal part of antennomere (Figs 10, 12) ……………………………………………………14
– Male antennomere 3 and 4 with basally robust lamella, lamella attached to middle or apical part of antennomere (Figs 4, 6, 8, 15, 17, 20) ……………………………………………………16

14. Antennomere 3 with lamella about 1.5 times longer than stem of antennomere, phallus relatively robust, pointed at apex, 6.7 times longer than wide at widest point (Fig. 78) ……***C. tenebricus*** (Kleine, 1930)
– Antennomere 3 with lamella twice or more longer than stem of antennomere (Figs 10, 12), if phallus pointed at apex then very slender, nine times longer than wide at widest point (Fig. 68) ………15

15. The apex of phallus widely rounded, antennomere 3 with its lamella three times longer than stem of antennomere (Fig. 10) ……………………………………………***C. jasarensis*** sp. nov.
– The apex of phallus acutely pointed, antennomere 3 with its lamella about twice longer than stem of antennomere (Fig. 12) ……………………………………………***C. kirstenae*** sp. nov.

16\. Phallus parallel-sided and very slender, at least nine times longer than width in widest part (Figs 62, 64) 17
– Phallus relatively robust, often widened in some part (Figs 60, 71, 73, 76) 18

17\. Phallus extremely slender, almost parallel-sided in apical part, antennomere 3 triangular, without slender lamella (Fig. 6) .... ***C. berembanensis*** sp. nov.
– Phallus slender, gradually narrowed in apical part (Fig. 64), antennomere 3 withlamella about twice longer than stem of antennomere (Fig. 8) .... ***C. communis*** sp. nov.

18\. Maximum eye diameter about 0.9 times interocular distance 19
– Maximum eye diameter 0.5–0.8 times interocular distance 20

19\. Basal part of phallus considerably slenderer than apical half (Fig. 60) .... ***C. andujari*** sp. nov.
– Basal part of phallus only slightly slenderer than apical half (Fig. 76) ... ***C. simillimus*** Kleine, 1926

20\. Maximum diameter of eyes about 0.7–0.8 times larger than interocular distance, the phallus very wide in apical half (Fig. 71) .... ***C. maseki*** sp. nov.
– Maximum diameter of eyes about 0.5–0.6 times larger than interocular distance, the phallus moderately wide in apical half (Fig. 73) .... ***C. nervosus*** Kleine, 1926

21\. Maximum eye diameter equal or larger than interocular distance 22
– Maximum eye diameter 0.7 times interocular distance .... ***C. alexae*** sp. nov.

22\. Maximum diameter of eyes equal or up to 1.4 times interocular distance 23
– Maximum diameter of eyes extremely large, more than 1.6 times interocular distance, phallus moderately robust, parallel-sided (Fig. 65) .... ***C. griseus*** Kleine, 1930

23\. Pronotum as wide as long at midline, phallus slender, gradually narrower from widest part at two fifths of its length to base and apex (Fig. 77) .... ***C. selangorensis*** Kleine, 1930
– Pronotum at least 1.1 times wider than long at midline, in most species 1.3–1.4 times wider, phallus robust, parallel-sided or wide part spoon-shaped 24

24\. Maximum eye diameter smaller than 1.2 times interocular distance 25
– Maximum eye diameter larger than 1.25 times interocular distance 27

25\. Male antennomeres 3 and 4 with slender basal part of lamella, lamella attached to basal part of antennomere (Fig. 7) .... ***C. campestris*** sp. nov.
– Male antennomeres 3 and 4 with basally robust lamella, lamella short, about 1.5 times length of antennomere stem (Figs 13, 17) 26

26\. Parallel-sided part of phallus occupies lightly more than basal half of its length .... ***C. kotatinggensis*** sp. nov.
– Parallel-sided part of phallus occupies about one basal third of its length, phallus slender .... ***C. pahangensis*** sp. nov.

27\. Lamella of antennomere 3 shorter than 1.3 times stem of antennomere, phallus slender in basal two thirds, widened apical part almost twice wider than basal part of phallus, widest close to mid of phallic length .... ***C. arribasae*** sp. nov.
– Lamella of antennomere 3 at least 1.5 longer than stem of antennomere, phallus slender in basal third, or gradually widened from base to middle part (Figs 67, 74–75) 28

28. Phallus gradually widened from base to middle part, with obtuse apex (Fig. 67) ... ***C. katarinae*** sp. nov.
– Phallus almost parallel sided at least in basal quarter of its length, with slender apex (Figs 74–75) ... 29

29. Phallus slightly constricted in middle of widest part .... ***C. renatae*** sp. nov.
– Phallus widest in middle of widened part (Fig. 75) .... ***C. reverandi*** Pic, 1925

Cautires alexae sp. nov.

urn:lsid:zoobank.org:act:9FAD9D3C-3443-41F8-83F6-D1F0860DAA4D

Figs 3, 21, 41, 59

Diagnosis

Cautires alexae sp. nov. is one of the species with a reddish humeral part of the elytra (Fig. 41), the pronotum with black pubescence (Fig. 21) and the medium size of the male eyes. It differs from the similar species in the widened apical third of the phallus and its obtuse apex (Fig. 59).

Etymology

The specific epithet *alexae* is a matronym in honour of Alex Crampton-Platt, a colleague from the Natural History Museum in London.

Type material

Holotype

MALAYSIA: ♂, Perak, Banjaran Titiwangsa, Ringlet, 900 m, 29 Mar.–15 Apr. 2004 (Voucher number VK0433).

Paratype

MALAYSIA: ♂, same locality data (VK0432).

Measurements

BL 7.2 mm, PL 1.1 mm, PW 1.6 mm, HW 0.95 mm, Edist 0.58 mm, Ediam 0.42 mm, LP 0.92 mm.

Description of the male

Body slender, black, only basal half of primary and secondary elytral costae with reddish pubescence (Fig. 41). Head small, eyes large, hemispherically prominent, eye diameter 0.72 times interocular distance. Antennae flabellate (Fig. 3). Pronotum with 5 areolae, posterior costae sharp in lateral parts and obtuse in middle part of pronotum, median areola complete, median areola attached directly to basal margin; anterior angles obtuse, lateral margins slightly concave, elevated, posterior angles prominent, pronotum with black pubescence (Fig. 21). Elytra parallel-sided, secondary costae well developed in humeral part and week apically, transverse costae dense (Fig. 41). Phallus wide in apical third, obtuse at apex (Fig. 59).

Distribution

Peninsular Malaysia: Perak. *Cautires alexae* sp. nov. is known only from the type locality.

Cautires andujari sp. nov.

urn:lsid:zoobank.org:act:2C5A1461-1A75-43F3-856C-E3C5437A0264

Figs 4, 22, 39, 42, 60

Diagnosis

Cautires andujari sp. nov. belongs to a group of mountain species with a uniformly black upper side of the body. The species is similar in general appearance to *Cautires maseki* sp. nov., but differs in the length of the male antennal lamellae (Figs 4, 15) and the shape of the phallus (Figs 60, 71).

Etymology

The specific epithet is honour of Carmelo Andújar Fernandéz, a specialist in the ecology of ground beetles.

Figs 21–38. Male pronotum. **21**. *Cautires alexae* sp. nov. **22**. *C. andujari* sp. nov. **23**. *C. arribasae* sp. nov. **24**. *C. berembanensis* sp. nov. **25**. *C. campestris* sp. nov. **26**. *C. communis* sp. nov. **27**. *C. griseus* Kleine, 1930. **28**. *C. jasarensis* sp. nov. **29**. *C. katarinae* sp. nov. **30**. *C. kirstenae* sp. nov. **31**. *C. kotatinggensis* sp. nov. **32**. *C. linardi* sp. nov. **33**. *C. maseki* sp. nov. **34**. *C. pahangensis* sp. nov. **35**. *C. nervosus* Kleine, 1926. **36**. *C. renatae* sp. nov. **37**. *C. reverandi* Pic, 1925. **38**. *C. simillimus* Kleine, 1926. — **39–40**. Male elytra costae, detail: **39**. *C. andujari* sp. nov. **40**. *C. campestris* sp. nov. Scale bars = 0.5 mm.

Type material

Holotype

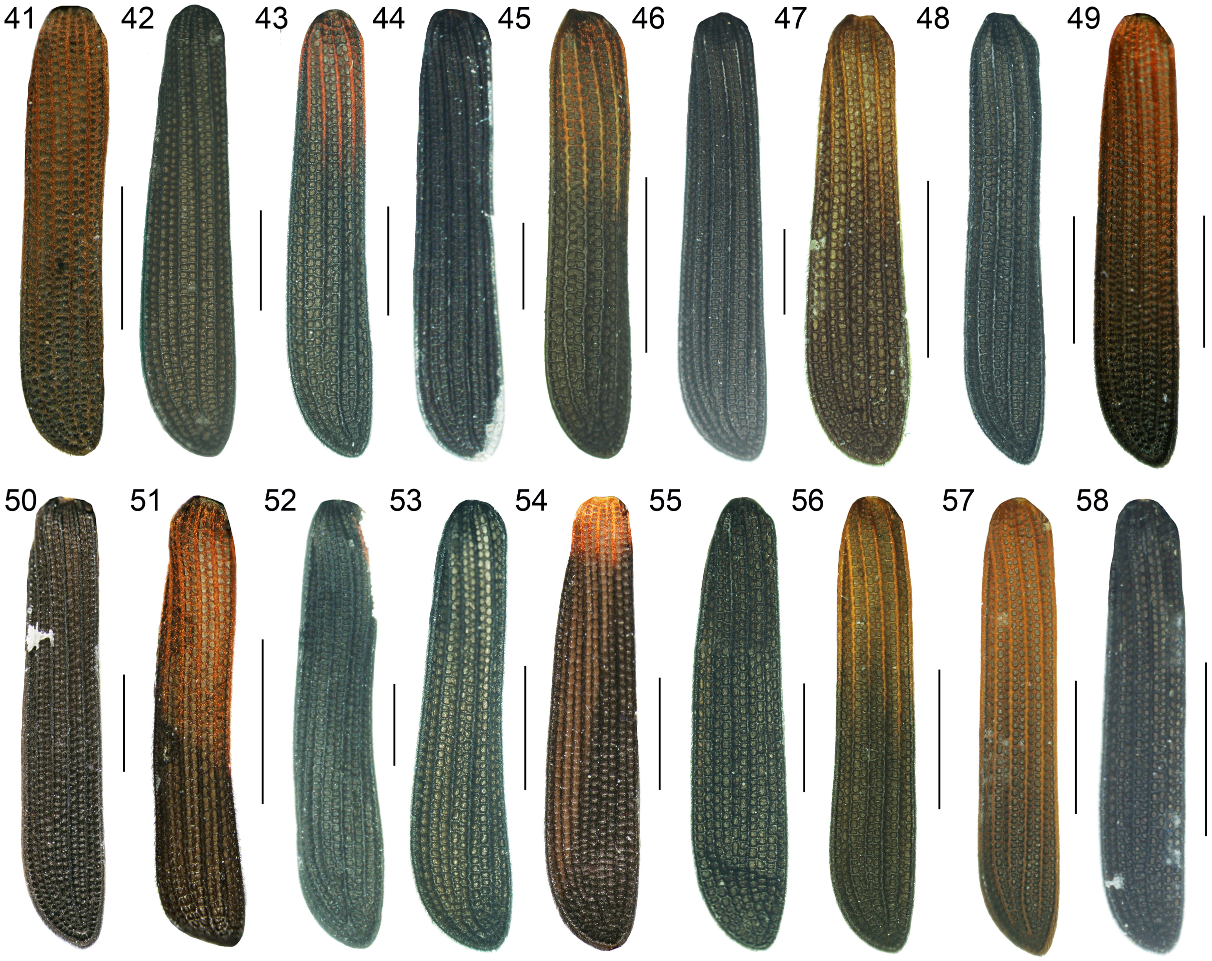
MALAYSIA: ♂, Pahang, Gn. Brinchang, 1800 m, 4°30'34" N, 101°23'09" E, 12–16 Apr. 2013 (AJ0082).

Paratypes

MALAYSIA: 1 ♀, same locality data (AJ0083); 1 ♂, 3 ♀♀, Pahang, Tanah Rata, 1500–1800 m, 2–26 Feb. 2004 (VK0272, VK0312, VK0322, VK0519); 2 ♂♂, 1 ♀, Pahang, Tanah Rata, 1600 m, Gn. Jasar, 3–9 Feb. 2005, Bolm leg. (VK0251, VK0426, VK0564).

Measurements

BL 10.7 mm, PL 1.5 mm, PW 2.25 mm, HW 1.2 mm, Edist 0.61 mm, Ediam 0.58 mm, LP 1.8 mm.



Figs 41–58. Male elytra. **41**. *Cautires alexae* sp. nov. **42**. *C. andujari* sp. nov. **43**. *C. arribasae* sp. nov. **44**. *C. berembanensis* sp. nov. **45**. *C. campestris* sp. nov. **46**. *C. communis* sp. nov. **47**. *C. griseus* Kleine, 1930. **48**. *C. jasarensis* sp. nov. **49**. *C. katarinae* sp. nov. **50**. *C. kirstenae* sp. nov. **51**. *C. kotatinggensis* sp. nov. **52**. *C. linardi* sp. nov. **53**. *C. maseki* sp. nov. **54**. *C. pahangensis* sp. nov. **55**. *C. nervosus* Kleine, 1926. **56**. *C. renatae* sp. nov. **57**. *C. reverandi* Pic, 1925. **58**. *C. simillimus* Kleine, 1926. Scale bars = 1.0 mm.

Description of the male

Body uniformly black (Figs 22, 42). Head small, eyes hemispherically prominent, eye diameter 0.95 times interocular distance. Antennae flabellate with short, slender lamella of antennomere 3 (Fig. 4). Pronotum with 7 areolae, but postero-lateral costae inconspicuous, median areola complete, sharp ridges, median areola attached directly to basal margin; anterior angles obtuse, lateral margins concave, strongly elevated, posterior angles acutely prominent (Fig. 22). Elytra slightly widened apically, primary and secondary costae well developed (Fig. 39), transverse costae dense (Fig. 42). Phallus robust, slender basally, apical part obtuse (Fig. 60).

Distribution

Peninsular Malaysia: Pahang. *Cautires andujari* sp. nov. is known only form the highest elevations of the Cameron Highlands.

Cautires arribasae sp. nov.

urn:lsid:zoobank.org:act:F77DC4A6-0363-4131-A8AA-B9334D4198CE

Figs 5, 23, 43, 61

Diagnosis

Cautires arribasae sp. nov. is one of the species with a brightly coloured humeral part of elytra and black pronotum. The species resembles *C. alexae* sp. nov. and *C. kotatinggensis* sp. nov. in general appearance and differs in the large eyes, the shape of the pronotum (Figs 21, 23, 31), and phallus (Figs 59, 61, 69).

Etymology

The specific epithet is proposed in honour of Paula Arribas, a colleague studying beetle soil communities.

Type material

Holotype

MALAYSIA: ♂, Pahang, Gn. Beremban, 1480 m, 4°27'51" N, 101°23'26" E, 6–28 Apr. 2013 (AJ0079).

Paratypes

MALAYSIA: 3 ♂♂, 3 ♀♀, same locality data (AJ0058, AJ0059, AJ0062, AJ0064, AJ0066, AJ0078).

Measurements

BL 9.8 mm, PL 1.5 mm, PW 2.05 mm, HW 1.15 mm, Edist 0.5 mm, Ediam 0.68 mm, LP 1.67 mm.

Description of the male

Body slender, black, only basal fourth of primary and fifth of secondary elytral costae with reddish pubescence (Fig. 43). Head small, hemispherically prominent, eyes large, eye diameter 1.36 times interocular distance. Antennae flabellate (Fig. 5). Pronotum with 7 areolae, median areola complete, marked by sharp ridges, attached directly to basal margin of pronotum; anterior angles obtuse, lateral margins slightly concave, lateral part of pronotum strongly elevated, posterior angles acutely prominent, pronotal margins and costae covered with brown, dense pubescence (Fig. 23). Elytra parallel-sided, secondary costae well developed, transverse costae dense (Fig. 43). Phallus robust, slender in basal part, its apex obtuse (Fig. 61).

Distribution

Peninsular Malaysia: Pahang. *Cautires arribasae* sp. nov. is known only from the mountain forests in the Cameron Highlands.

Cautires berembanensis sp. nov.

urn:lsid:zoobank.org:act:35C6DBC0-52EF-49A9-BDEF-9E8C4EADEE40

Figs 6, 24, 44, 62

Diagnosis

Cautires berembanensis sp. nov. belongs to a group of the species with the black body and very small eyes. The species is characteristic in the very wide, flat male antennomeres 3–10 (Fig. 6), which is unknown in other Malay species and in the extremely slender phallus (Fig. 62).

Etymology

The specific epithet refers to the type locality of the holotype.

Type material

Holotype

MALAYSIA: ♂, Pahang, Gn. Beremban, 1480 m, 4°27'51" N, 101°23'26" E, 6–28 Apr. 2013 (AJ0092).

Paratypes

MALAYSIA: 1 ♂, 2 ♀♀, Pahang, Tanah Rata, 1500–1800 m, 2–26 Feb. 2004 (VK0254, VK0275, VK0278).

Measurements

BL 12.1 mm, PL 1.65 mm, PW 2.1 mm, HW 1.5 mm, Edist 0.77 mm, Ediam 0.33 mm, LP 1.21 mm.

Description of the male

Body uniformly black (Fig. 44). Head small, eyes hemispherically prominent, but small, eye diameter 0.42 times interocular distance. Antennae acutely serrate (Fig. 6). Pronotum with 7 areolae, fronto-lateral costae vestigial in proximity to pronotal margin, median areola complete, attached basally directly to pronotal margin; anterior angles obtuse, lateral margins only slightly elevated, straight in whole length (Fig. 24). Elytra parallel-sided, secondary costae well developed, transverse costae dense (Fig. 44). Phallus extremely slender, stick-shaped, only very slightly wider in apical fourth, slightly pointed at apex (Fig. 62).

Distribution

Peninsular Malaysia: Pahang.

Cautires campestris sp. nov.

urn:lsid:zoobank.org:act:6F1955CA-3699-4BBC-8673-5DC0D1718774

Figs 7, 25, 40, 45, 63

Diagnosis

Cautires campestris sp. nov. is one of the species with a brightly coloured humeral part of the elytra, reddish pubescence on the disc of the pronotum and large eyes. This species has very long, slender antennal lamellae (Fig. 7), which resemble very closely those of the black coloured species *C. jasarensis* sp. nov. Additionally, *C. campestris* sp. nov. differs from other species in the robust phallus and the pronotum with vestigial postero-lateral ridges.

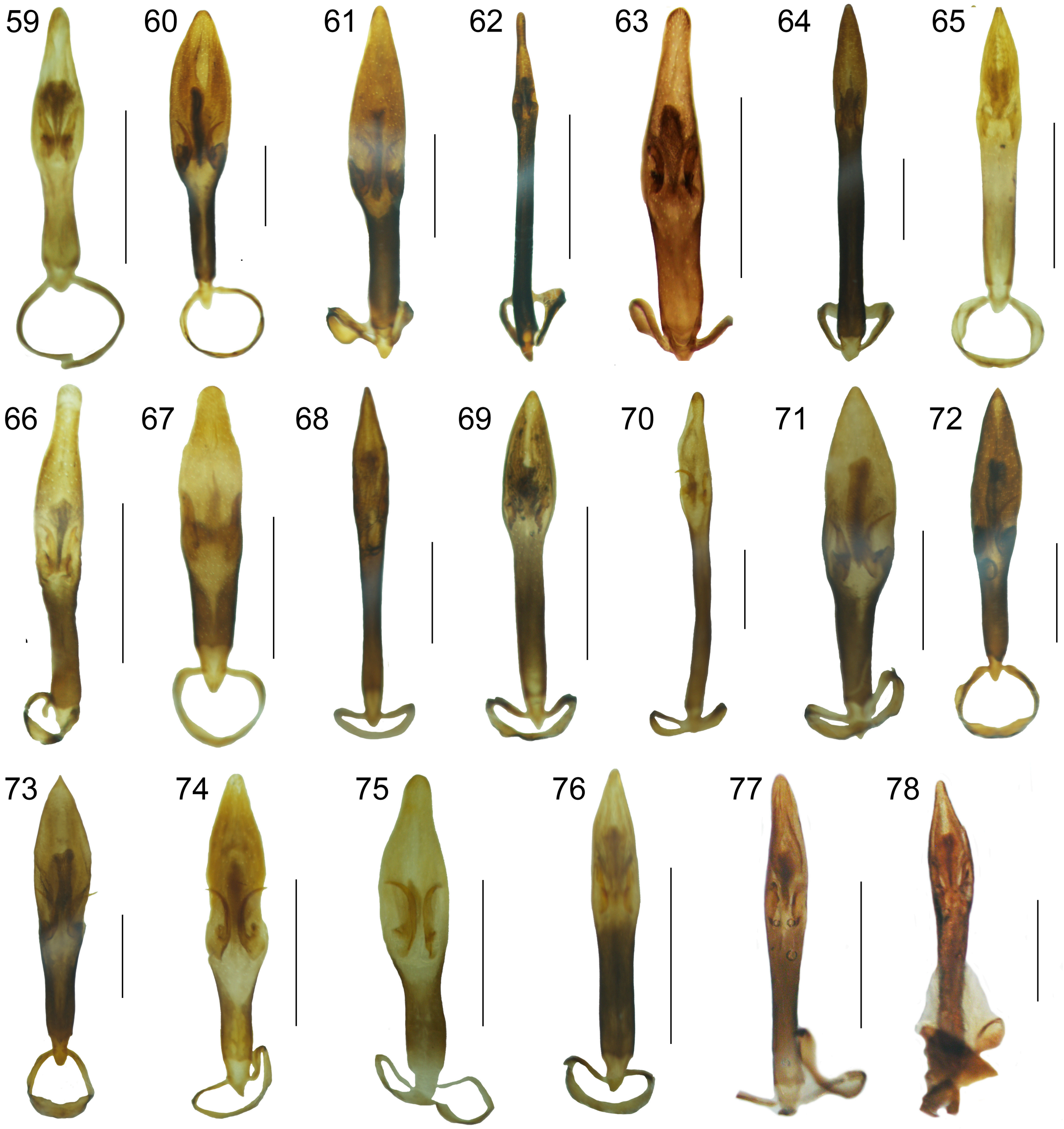
Etymology

The specific epithet refers to the lowland distribution of the species.

Type material

Holotype

MALAYSIA: ♂, Perak, km 24, Road Tapah-Ringlet, 350 m, 4°18'39" N, 101°19'52" E, 19 Apr. 2013 (AJ0039).



Figs 59–78. Phallus. **59**. *Cautires alexae* sp. nov. **60**. *C. andujari* sp. nov. **61**. *C. arribasae* sp. nov. **62**. *C. berembanensis* sp. nov. **63**. *C. campestris* sp. nov. **64**. *C. communis* sp. nov. **65**. *C. griseus* Kleine, 1930. **66**. *C. jasarensis* sp. nov. **67**. *C. katarinae* sp. nov. **68**. *C. kirstenae* sp. nov. **69**. *C. kotatinggensis* sp. nov. **70**. *C. linardi* sp. nov. **71**. *C. maseki* sp. nov. **72**. *C. pahangensis* sp. nov. **73**. *C. nervosus* Kleine, 1926. **74**. *C. renatae* sp. nov. **75**. *C. reverandi* Pic, 1925. **76**. *C. simillimus* Kleine, 1926. **77**. *C. selangorensis* Kleine, 1930. **78**. *C. tenebricus* Kleine, 1926. Scale bar = 0.5 mm.

Paratypes

MALAYSIA: 2 ♀♀, same locality data (AJ0040–AJ0041); 2 ♀♀, Kelantan, km 12, Road Kg. Raja–Gua Musang, 780 m, 4°38'15" N, 101°30'11" E, 20 Apr. 2013 (AJ0032, AJ0096).

Measurements

BL 6.5 mm, PL 1.0 mm, PW 1.55 mm, HW 0.9 mm, Edist 0.5 mm, Ediam 0.57 mm, LP 1.0 mm.

Description of the male

Body slender, black, only basal third of primary and secondary elytral costae with reddish pubescence (Fig. 45). Head small, eyes hemispherically prominent, moderately large, eye diameter 1.14 times interocular distance. Antennae flabellate, lamellae very long, slender, attached to base of antennomere (Fig. 7). Pronotum flat, with 7 areolae, median areola well-developed, ridges sharp, median areola attached directly to basal margin of pronotum; anterior pronotal angles obtuse, lateral margins concave, lateral part of pronotum strongly elevated, posterior angles only weakly prominent, rounded apically, pronotum with orange pubescence on edges (Fig. 25). Elytra parallel-sided, secondary costae week (Fig. 40), transverse costae dense (Fig. 45). Phallus moderately robust, widest in the middle part, obtuse at apex (Fig. 63).

Distribution

Peninsular Malaysia: Perak, Kelantan. The species is widely distributed in low elevations of the Cameron Highlands region.

Cautires communis sp. nov.

urn:lsid:zoobank.org:act:B24A79EF-21BA-450A-BB56-D19D7F613EED

Figs 8, 26, 46, 64

Diagnosis

Cautires communis sp. nov. belongs to the group of species with a black body and large male eyes. The species resembles *C. kirstenae* sp. nov. in the relatively slender phallus (Figs 64, 68), but these species differs in the relative length of antennal lamellae (Figs 8, 12). The antennal lamellae of *C. communis* sp. nov. are wide at the base and slightly short.

Etymology

The specific epithet refers to the abundance of the species. Altogether 52 specimens were identified in the available material and it makes *C. communis* sp. nov. the most common species in the Cameron Highlands.

Type material

Holotype

MALAYSIA: ♂, Pahang, Gn. Beremban, 1480 m, 4°27'51" N, 101°23'26"E, 6–28 Apr. 2013 (AJ0091).

Paratypes

MALAYSIA: 1 ♂, 4 ♀♀, Pahang, Tanah Rata, 1600 m, Gn. Jasar, 3–9 Feb. 2005 (VK0563, VK0568, VK0619, VK0622, VK00623); 1 ♂, 1 ♀, Pahang, Tanah Rata, 24–31 Jan. 2003 (VK0268, VK0450); 2 ♀♀, Pahang, Tanah Rata, 1600 m, 3–20 Feb. 2005 (VK0361, VK0418, VK0421, VK0526, VK0572); 1 ♀, Pahang, Tanah Rata, 1400–1650 m, 4–11 Apr. 2005 (VK0310); 2 ♀♀, Pahang, Brinchang, Gn. Brinchang, 1800 m, 4°30'34" N, 101°23'09" E, 12–16 Apr. 2013 (AJ0084, AJ0087); 4 ♂♂, Pahang, Gn. Beremban, 1480 m, 4°27'51" N 101°23'26" E, 6–28 Apr. 2013 (AJ0013, AJ0061, AJ0068, AJ0093); 1 ♂, 1 ♀, Pahang, Gn Jasar, N slope, 1550 m, 4°28'56" N, 101°21'55" E, 11 Apr. 2013 (AJ0004, AJ0006);

23 ♂♂, 11 ♀♀, Pahang, Tanah Rata, 1500–1800 m, 2–26 Feb. 2004 (VK0242, VK0244, VK0245, VK0246, VK0255, VK0260, VK0261, VK0262, VK0263, VK0264, VK02605, VK0267, VK0271, VK0274, VK0276, VK0277, VK0278, VK0279, VK0311, VK0313, VK00314, VK0316, VK0317, VK0321, VK0323, VK0324, VK0325, VK0512, VK0513, VK0514, VK0515, VK0520, VK0521, VK0523, VK0524).

Measurements

BL 12.2 mm, PL 1.75 mm, PW 2.35 mm, HW 1.4 mm, Edist 0.75 mm, Ediam 0.55 mm, LP 2.2 mm.

Description of the male

Body uniformly black (Fig. 46). Head small, eyes hemispherically prominent, eye diameter 0.73 times interocular distance. Antennae flabellate with moderately long lamellae widely attached to stem of antennomere (Fig. 8). Pronotum with 7 well developed areolae, median areola complete, marked by sharp ridges, attached directly to basal margin of pronotum; anterior angles obtuse, lateral margins slightly concave, strongly elevated, posterior angles acutely prominent (Fig. 26). Elytra almost parallel-sided, only very slightly widened posteriorly, primary and secondary costae well developed, transverse costae dense (Fig. 46). Phallus slender, stick-shaped, only slightly widened in apical part, obtusely pointed at apex (Fig. 64).

Distribution

Peninsular Malaysia: Pahang. *Cautires communis* sp. nov. was collected only in the highest part of the Cameron Highlands and does not occur on the northern slopes in lower elevations.

Cautires griseus Kleine, 1930

Figs 9, 27, 47, 65

Cautires griseus Kleine, 1930a: 96.

Diagnosis

Cautires griseus belongs to the group of species with a bright humeral part of the elytra (Fig. 47) and brown pubescence in the disc of the pronotum (Fig. 27). It differs from similarly coloured species in the length of antennal lamellae (Fig. 9) and in the relatively robust, shorter, parallel-sided phallus (Fig. 65).

Type material

Holotype

MALAYSIA: ♂, Perak, Doherty (BMNH).

Additional material examined

MALAYSIA: 1 ♂, Pahang, Tanah Rata, 1600 m, Cameron Highlands, 3–20 Feb. 2005 (VK0575); 1 ♀, Kelantan, Road Ipoh-Kg. Raja, 35 km E of Ipoh, 980 m, 8 Feb. 2005 (VK0308).

Measurements

BL 6.7 mm, PL 1.10 mm, PW 1.15 mm, HW 1.0 mm, Edist 0.34 mm, Ediam 0.61 mm, LP 1.07 mm.

Distribution

Peninsular Malaysia: Perak, Pahang, Kelantan.

Cautires jasarensis sp. nov.

urn:lsid:zoobank.org:act:7E53ED05-01B4-40F4-869B-AF04B3B9CAD9

Figs 10, 28, 48, 66

Diagnosis

Cautires jasarensis sp. nov. is similar to *C. kirstenae* sp. nov. Both species share the uniformly black body, pronotum and elytra, the relatively small, hemispherically prominent eyes and the long antennal lamellae (Figs 28, 30, 48, 50). *C. kirstenae* sp. nov. and the similarly coloured *C. communis* sp. nov. have a slender phallus pointed at the apex (Figs 64, 68), but the phallus of *C. jasarensis* sp. nov. is much wider in its apical third and its apical part is parallel-sided. The phallic apex of *C. jasarensis* sp. nov. is widely rounded in contrast with other species in the region (Fig. 66).

Etymology

The specific epithet refers to the Mt. Jasar, the locality where a part of the type series was collected.

Type material

Holotype

MALAYSIA: ♂, Pahang, Gn. Beremban, 1480 m, 4°27'51" N, 101°23'26"E, 6–28 Apr. 2013 (AJ0067).

Paratypes

MALAYSIA: 1 ♂, 1 ♀, Pahang, Gn. Beremban, 1480 m, 4°27'51" N, 101°23'26" E, 6–28 Apr. 2013 (AJ0070); 1 ♂, 2 ♀♀, Pahang, Tanah Rata, Gn. Jasar, 1600 m, 3–20 Feb. 2005 (VK0425, VK0362, VK0569); 1 ♂, Kelantan, km 12, Road Kg. Raja–Gua Musang, 980 m, 4°38'15" N, 101°30'11" E, 20 Apr. 2013 (AJ0034); 2 ♀♀, Pahang, Tanah Rata, Gn. Jasar, 1600 m, 3 Jan. 2005 (VK0252, VK0253); 1 ♂, Pahang, Tanah Rata, 1600 m, Gn. Jasar, 3–9 Feb. 2005, Bolm leg. (VK0565); 1 ♀, Pahang, km 51, Road Ipoh – Kg. Raja, 1100 m, 4 Feb. 2005 (VK0437).

Measurements

BL 8.7 mm, PL 1.5 mm, PW 1.7 mm, HW 1.1 mm, Edist 0.68 mm, Ediam 0.50 mm, LP 1.08 mm.

Description of the male

Body black (Fig. 48). Head small, eyes hemispherically prominent, relatively small, eye diameter 0.73 times interocular distance. Antennae flabellate, lamellae very slender, including their bases, attached to basal part of antennomeres (Fig. 10). Pronotum with 7 well developed areolae, posterior costae obtuse, inconspicuous, median areola complete, marked with complete ridges, attached directly to basal margin; anterior angles obtuse, lateral margins strongly elevated, very slightly concave in anterior part of pronotum, straight and divergent in posterior part (Fig. 28), posterior angles sharp, but not acutely projected. Elytra parallel-sided, primary and secondary costae well developed, transverse costae dense (Fig. 48). Phallus moderately slender, widest in apical third, obtuse at apex (Fig. 66).

Distribution

Peninsular Malaysia: Pahang, Kelantan. This species is widely distributed in the Cameron Highlands.

Cautires katarinae sp. nov.

urn:lsid:zoobank.org:act:98428C4C-91DD-4AB8-9B4F-397A9083D5BC

Figs 11, 29, 49, 67

Diagnosis

Cautires katarinae sp. nov. is similar to *C. griseus* in the reddish pubescence on the humeral part of the elytra and the shape of the pronotum. It differs in the shape of antennal lamellae (Figs 9, 11). Additionally, *C. katarinae* sp. nov. has the robust phallus with the obtuse apex (Fig. 67).

Etymology

The specific epithet is in honour of Katerina Sklenarova, a colleague from the laboratory.

Type material

Holotype

MALAYSIA: ♂, Kelantan, km 12, Road Kg. Raja–Gua Musang, 980 m, 4°38'15" N, 101°30'11" E, 20 Apr. 2013 (AJ0028).

Measurements

BL 8.1 mm, PL 1.5 mm, PW 1.65 mm, HW 1.05 mm, Edist 0.51 mm, Ediam 0.66 mm, LP 1.1 mm.

Description of the male

Body slender, mostly black, primary and secondary elytral costae with reddish pubescence, only posterior part of costae black (Fig. 49). Head small, eyes hemispherically prominent, large, eye diameter 1.29 times interocular distance. Antennae robust, flabellate, lamellae wide and flat (Fig. 11). Pronotum with 7 areolae, median areola well developed, marked by sharp ridges, median areola attached directly to basal margin of pronotum; anterior pronotal angles obtuse, lateral margins straight, lateral part of pronotum elevated, only slightly divergent, posterior angles prominent, but not acutely projected, pronotum with red pubescence (Fig. 29). Elytra parallel-sided, very slightly widened apically, primary and secondary costae well developed, transverse costae dense (Fig. 49). Phallus robust, widened from basal to apical fifth, slightly constricted in middle of widened part, widely rounded at apex (Fig. 67).

Distribution

Peninsular Malaysia: Kelantan. The species is known only from the type locality.

Cautires kirstenae sp. nov.

urn:lsid:zoobank.org:act:82953FF5-3CB3-40FB-8E92-4454E29C5A15

Figs 12, 30, 50, 68

Diagnosis

Cautires kirstenae sp. nov. belongs to the species with a uniformly black body. It is similar to *C. communis* sp. nov. and *C. jasarensis* sp. nov., but differs from *C. communis* sp. nov. in the long and slender male antennal lamellae (Figs 8, 12) and from *C. jasarensis* sp. nov. in the more slender phallus (Figs 66, 68).

Etymology

The specific epithet *kirstenae* is a matronym in honour of Kirsten Miller, a colleague from the Natural History Museum in London.

Type material

Holotype

MALAYSIA: ♂, Pahang, Tanah Rata, 1600 m, 3–20 Feb. 2005 (VK0419).

Measurements

BL 11.7 mm, PL 1.5 mm, PW 2.2 mm, HW 1.2 mm, Edist 0.72 mm, Ediam 0.59 mm, LP 1.66 mm.

Description of the male

Body uniformly black (Fig. 50). Head small, eyes hemispherically prominent, eye diameter 0.82 times interocular distance. Antennae flabellate, lamella of antennomere 3 about 2.5 longer than stem of antennomere (Fig. 12). Pronotum with 7 areolae, fronto- and postero-lateral ridges obtuse, inconspicuous, only median areola complete, marked by well developed ridges, median areola attached directly to basal margin; anterior angles obtuse, lateral margins slightly concave, lateral part of pronotum elevated, posterior angles sharply prominent (Fig. 30). Elytra parallel-sided, primary and secondary costae well developed, transverse costae dense, reticulate cells regular (Fig. 50). Phallus very slender, only slightly widened in apical fourth, pointed at apex (Fig. 68).

Distribution

Peninsular Malaysia: Pahang. The species is known only from the type locality.

Cautires kotatinggensis sp. nov.

urn:lsid:zoobank.org:act:5586C104-301B-4C4A-A772-9849A7E3E2A2

Figs 13, 31, 51, 69

Diagnosis

Cautires kotatinggensis sp. nov. resembles *C. alexae* sp. nov. and *C. arribasae* sp. nov. in the bright humeral part of the elytra and the black pronotum. Additionally, all these species differ in the shape of the pronotum (Figs 21, 23, 31) and the shape of their phalli (Figs 59, 61, 69).

Etymology

The specific epithet refers to the town Kota Tinggi, a place close to the locality where the paratype was collected.

Type material

Holotype

MALAYSIA: ♂, Perak, km 24, Road Tapah–Ringlet, 350 m, 4°18'39" N, 101°19'52" E, 19 Apr. 2013 (AJ0048).

Paratypes

MALAYSIA: 1 ♂, 1 ♀, same data as the holotype (AJ0042, AJ0048).

Measurements

BL 6.5 mm, PL 1.1 mm, PW 1.5 mm, HW 0.85 mm, Edist 0.44 mm, Ediam 0.44 mm, LP 1.1 mm.

Description of the male

Body slender, black, except basal half of primary and secondary elytral costae bearing reddish pubescence (Fig. 51). Head small, eyes hemispherically prominent, quite large, eye diameter 1.0 times interocular distance. Antennae flabellate, with moderately long antennae (Fig. 13). Pronotum with 5 areolae, postero-lateral ridges absent, median areola complete, well developed, attached directly to basal margin of pronotum; anterior angles obtuse, lateral margins straight, strongly elevated, posterior angles prominent, pronotal margins and costae with brown pubescence (Fig. 31). Elytra parallel-sided, primary and secondary costae well developed, transverse costae dense, minute (Fig. 51). Phallus slender, wide, spoon-shaped in apical part, obtuse apically (Fig. 69).

Distribution

Peninsular Malaysia: Perak, Johor. *Cautires kotatinggensis* sp. nov. is one of a few widely distributed *Cautires* species in the Malay Peninsula.

Cautires linardi sp. nov.

urn:lsid:zoobank.org:act:30D4C7CB-4F8D-4176-A2D0-8E3050A8CB32

Figs 14, 32, 52, 70

Diagnosis

Cautires linardi sp. nov. belongs to the group with the uniformly black body and large eyes. This species has the characteristic shape of the pronotum with the very wide basal part and acutely projected posterior angles (Fig. 32).

Etymology

The specific epithet *linardi* is a patronym in honour of Benjamin Linard, a colleague from the Natural History Museum in London.

Type material

Holotype

MALAYSIA: ♂, Pahang, Mt. Jasar, N slope, 1550 m, 4°28'56" N, 101°21'55" E, 11 Apr. 2013 (AJ0005).

Paratypes

MALAYSIA: 1 ♀, Pahang, Tanah Rata, 24–31 Jan. 2003 (VK0451); 1 ♀, Malaysia, Pahang, Tanah Rata, 1–13 Feb. 2003 (VK0625).

Measurements

BL 11.6 mm, PL 1.7 mm, PW 2.5 mm, HW 1.15 mm, Edist 0.66 mm, Ediam 0.71 mm, LP 2.12 mm.

Description of the male

Body uniformly black (Fig. 52). Head small, eyes hemispherically prominent, quite large, eye diameter 1.08 times interocular distance. Antennae flabellate with lamella of antennomere 6 about three times longer than stem of antennomere (Fig. 14). Pronotum transverse, about twice wider than long at midline, with 7 areolae, only postero-lateral ridges weaker, obtuse; median areola complete, well developed, attached directly to basal margin; anterior angles obtuse, lateral margins concave, lateral part of pronotum strongly elevated, posterior angles slender, acutely prominent (Fig. 32). Elytra parallel-sided, primary and secondary costae well developed, transverse costae dense, irregular (Fig. 52). Phallus very slender, only slightly wider in apical part, obtuse at apex (Fig. 70).

Distribution

Peninsular Malaysia: Pahang.

Cautires maseki sp. nov.

urn:lsid:zoobank.org:act:653D5519-1C19-4526-ABC2-373B1484A6F2

Figs 15, 33, 53, 71

Diagnosis

Cautires maseki sp. nov. is one of numerous species with a uniformly black body. It is very similar to *C. nervosus* and *C simillimus* sp. nov. in general appearance and these species differ only in the shape of the phallus, which is extremely robust in *C. maseki* sp. nov. (Figs 71, 73, 76).

Etymology

The specific name is in honour of Michal Masek, a colleague from the laboratory.

Type material

Holotype

MALAYSIA: ♂, Pahang, Gn. Beremban, 1480 m, 4°27'51" N, 101°23'26" E, 6–28 Apr. 2013 (AJ0069).

Additional material examined

MALAYSIA: 1 ♀, Pahang, Tanah Rata, 1500–1800 m, 2–26 Feb. 2004 (VK0280); 1 ♂, Pahang, Tanah Rata, 1–13 Feb. 2003 (VK0628).

Measurements

BL 9.8 mm, PL 1.25 mm, PW 1.75 mm, HW 1.0 mm, Edist 0.57 mm, Ediam 0.44 mm, LP 1.45 mm.

Description of the male

Body uniformly black (Fig. 53). Head small, eyes hemispherically prominent, small, eye diameter 0.77 times interocular distance. Antennae flabellate, with lamella of antennomere 6 about twice longer than stem of antennomere (Fig. 15). Pronotum with shining disc and with 7 well developed areolae, median areola complete, well marked, attached directly to basal margin of pronotum; anterior angles obtuse, lateral margins concave, almost parallel-sided in anterior half of pronotum, lateral part of pronotum strongly elevated, posterior angles slender, acutely prominent (Fig. 33). Elytra apparently widened apically, primary and secondary costae well developed, transverse costae dense, slightly irregular (Fig. 53). Phallus very robust, slender only at basal third, apex rather obtuse (Fig. 71).

Distribution

Peninsular Malaysia: Pahang.

Cautires pahangensis sp. nov.

urn:lsid:zoobank.org:act:2616E587-EEC1-4C9E-90CD-F5D5F85793DB

Figs 16, 34, 54, 72

Diagnosis

Cautires pahangensis sp. nov. is a mountain species with a bright pubescent humeral part of the elytra and a reddish pubescence on the pronotum. It has moderately long antennal lamellae (Fig. 16) and a slender phallus with a gradually widened part and a pointed apex (Fig. 72).

Etymology

The specific epithet refers to the Malay state Pahang where the holotype of *C. pahangensis* sp. nov. was collected.

Type material

Holotype

MALAYSIA: ♂, Pahang, Tanah Rata, 1600 m, 3–20 Feb. 2005 (VK0527).

Measurements

BL 9.3 mm, PL 1.15 mm, PW 1.75 mm, HW 1.0 mm, Edist 0.53 mm, Ediam 0.58 mm, LP 1.49 mm.

Description of the male

Body quite slender, black, upper side bicoloured, pronotum orange, elytra black except basal fifth of primary and secondary elytral costae bearing orange pubescence (Fig. 54). Head small, eyes hemispherically prominent, quite large, eye diameter 1.09 times interocular distance. Antennae flabellate with moderately long lamellae (Fig. 16). Pronotal disc mat, with 7 areolae, median areola complete, but ridges forming median areola obtuse similarly to postero-lateral ridges, median areola attached directly to basal margin of pronotum; anterior angles obtuse, lateral margins slightly concave, lateral part of pronotum strongly elevated, posterior angles robust but prominent (Fig. 34). Elytra apparently widened apically, primary and secondary costae well developed, transverse costae dense (Fig. 54). Phallus moderately robust, widest in apical third, slightly pointed at apex (Fig. 72).

Distribution

Peninsular Malaysia: Pahang. This species is known in a single specimen only.

Cautires nervosus Kleine, 1926

Figs 17, 35, 55, 73

Cautires nervosus Kleine, 1926: 187.

Diagnosis

Cautires nervosus is one of the uniformly black coloured species (Figs 35, 55). The species has extremely small male eyes, their diameter only 0.54 times the interocular distance, and a very short antennal lamella of antennomere 3 (Fig. 17). The phallus of *C. nervosus* is moderately wide (Fig. 73) and differs from the similar phalli of *C. maseki* sp. nov. and *C. simillimus* sp. nov. (Figs 71, 76).

Type material

Syntypes

MALAYSIA:1 ♂, Pahang, Cameron Highlands, Tanah Rata, 4800 ft., 13 Mar. 1924; 1 ♂, same locality, Rhododendron Hill, 5200 ft., 22 Jun. 1923; 1 ♂, Lubok Tamang, 3500 ft., 11 Mar. 1924, all specimens H.M. Pendlebury leg. (BMNH).

Additional material examined

MALAYSIA: 2 ♂♂, Pahang, Tanah Rata, 1500–1800 m, 2–26 Feb. 2004 (VK0516, VK0517); 12 ♀♀, Pahang, Tanah Rata, 1500–1800 m, 2–26 Feb. 2004 (VK0241, VK0243, VK0257, VK0258, VK0266, VK0273, VK0281, VK0282, VK0318, VK0319, VK0518, VK0525); 3 ♀♀, Pahang, Tanah Rata, 1600 m, Cameron Highl., 3–20 Feb. 2005 (VK0570, VK0573, VK0576); 1 ♂, 3 ♀♀, Pahang, Tanah Rata, 1600 m, Cameron Highl., 3–20 Feb. 2005 (VK0360, VK0422, VK0533, VK0571); 1 ♀, Pahang, Gn. Jasar, E slope, 1500 m, 4°28'23" N, 101°22'06" E, 8 Apr. 2013 (AJ0076); 1 ♂, 1 ♀, Pahang, Tanah Rata, 1600 m, Gn. Jasar, 3–9 Feb. 2005 (VK0618, VK0621); 1 ♀, Pahang, Tanah Rata, 24–31 Jan. 2003 (VK0269, VK0270, VK0453); 1 ♂, 2 ♀♀, Pahang, Gn. Beremban, 1480 m, 4°27'51" N, 101°23'26" E, 6–28 Apr. 2013 (AJ0010, AJ0065, AJ0080); 1 ♂, Pahang, Brinchang, Gn. Brinchang, 1800 m, 4°30'34" N, 101°23'09" E, 12–16 Apr. 2013 (AJ0085, AJ0086); 2 ♀♀, Pahang, Tanah Rata, 1600 m, Gn. Jasar, 3–9

Feb. 2005, Bolm leg. (VK0566, VK0567); 1 ♂, Pahang, Tanah Rata, Gn. Jasar, 1600 m, 3 Jan. 2005 (VK0250).

Measurements

BL 8.9 mm, PL 1.5 mm, PW 1.75 mm, HW 1.1 mm, Edist 0.61 mm, Ediam 0.33 mm, LP 1.76 mm.

Distribution

Peninsular Malaysia: Pahang. *Cautires nervosus* is a very common species in the Cameron Highlands area, but no specimens were recorded outside the Cameron Highlands plateau and adjacent mountain tops with elevation over 1400 m a.s.l.

Cautires renatae sp. nov.

urn:lsid:zoobank.org:act:FC371A58-9CB9-4581-9A86-AB6DF50B8BB9

Figs 18, 36, 56, 74

Diagnosis

Cautires renatae sp. nov. resembles *C. reverandi* in the bright humeral part of elytra and the reddish pubescence on the pronotum (Figs 36–37). Additionally, *C. renatae* sp. nov. has a different shape of the phallus (Figs 74–75).

Etymology

The specific name is in honour of Renata Bilkova, a colleague from the laboratory.

Type material

Holotype

MALAYSIA: ♂, Kelantan, km 12, Road Kg. Raja–Gua Musang, 980 m, 4°38'15" N, 101°30'11" E, 20 Apr. 2013 (AJ0035).

Paratype

MALAYSIA: 1 ♂, same locality data as the holotype (AJ0027).

Measurements

BL 7.6 mm, PL 1.2 mm, PW 1.55 mm, HW 0.85 mm, Edist 0.41 mm, Ediam 0.55 mm, LP 1.1 mm.

Description of the male

Body slender, black, pronotum with orange pubescence, elytra mostly black, only basal third of primary and one fourth of secondary elytral costae with orange pubescence (Fig. 56). Head small, eyes hemispherically prominent, large, eye diameter 1.34 times interocular distance. Antennae flabellate, lamella of antennomere 3 slightly more that 1.5 length of antennomere length (Fig. 18). Pronotum with seven areolae, posterior costae sharp in lateral part and obtuse in middle of pronotum, median areola complete, well-marked, attached directly to basal margin; anterior angles obtuse, lateral margins concave, strongly elevated, posterior angles strongly prominent, (Fig. 36). Elytra parallel-sided, secondary costae developed, transverse costae dense (Fig. 56). Phallus robust, constricted in middle part, obtuse at apex (Fig. 74).

Distribution

Peninsular Malaysia: Kelantan. *Cautires renatae* sp. nov. is known only from the type locality in the Kelantan state.

Cautires reverandi Pic, 1925

Figs 19, 37, 57, 75

Cautires reverandi Pic, 1925: 9.

Diagnosis

Cautires reverandi belongs to a group of species with a bright humeral part of the elytra (Fig. 57), a reddish pubescence on the pronotum (Fig. 37) and big eyes. It differs from the superficially similar species *C. renatae* sp. nov. in the shorter lamella of the antennomere 3 (Figs 18–19) and in the very wide phallus (Figs 74–75).

Type material

Holotype

MALAYSIA: ♀, Penang (without further data, MHNP).

Additional material examined

MALAYSIA: 2 ♂♂, 1 ♀, Kelantan, km 12, Road Kg. Raja–Gua Musang, 980 m, 4°38'15" N, 101°30'11" E, 20 Apr. 2013 (AJ0029–31); 2 ♀♀, Pahang, Kg Kuala Boh, 1040 m, 4°26'25" N, 101°28'14" E, 18 Apr. 2013 (AJ0018, 24); 1 ♂, Perak, Banjaran Titiwangsa, Ringlet, 900 m, 29 Mar.–15 Apr. 2004 (VK0430); 1 ♂, Pahang, 30 km NE of Raub, 600 m (LB0178).

Measurements

BL 8.3 mm, PL 1.4 mm, PW 1.7 mm, HW 1.0 mm, Edist 0.5 mm, Ediam 0.6 mm, LP 1.1 mm.

Distribution

Peninsular Malaysia: Perak, Pahang, Kelantan. *Cautires reverandi* is a widely distributed species in the Cameron Highlands region.

Remark

The holotype of *C. reverandi* is a female and the comparison with other species is limited to the general appearance. We identified a series of very similar specimens from several localities in the lowlands and lower mountain forests in the region, which we identified as *C. reverandi*. Our association of the female type and the newly collected individual from Malay inland as the same species is additionally supported by a common occurrence in the region.

Cautires simillimus Kleine, 1926

Figs 20, 38, 58, 76

Cautires simillimus Kleine, 1926: 187.

Diagnosis

Cautires simillimus belongs to a group of mountain species with a uniformly black body (Figs 38, 58). This species resembles *C. nervosus* and *C. maseki* sp. nov. in the general appearance, but the males of *C. simillimus* have long and slender antennal lamellae (Fig. 20) and additionally they differ in the relatively robust, parallel-sided phallus (Fig. 76).

Type material

Holotype

MALAYSIA: ♀, Pahang, Lubok Tamang, 3500 ft., 10 Jun. 1923, H.M. Pendlebury (BMNH).

Additional material examined

MALAYSIA: 2 ♂♂, Pahang, Gn. Beremban, 1480 m, 4°27'51" N, 101°23'26" E, 6–28 Apr. 2013 (AJ0011, AJ0073); 1 ♂, Pahang, Gn. Beremban, N slope, 1580 m, 4°29'12" N, 101°23'27" E, 12 Apr. 2013 (AJ0090); 2 ♂♂, 1 ♀, Pahang, Tanah Rata, 1500–1800 m, 2–26 Feb. 2004 (VK0247, VK0259, VK0283); 1 ♂, Pahang, Tanah Rata, 1400–1650 m, 4–11 Apr. 2005 (VK0309); 2 ♀♀, Pahang, Tanah Rata, 1600 m, Cameron Highlands, 3–20 Feb. 2005 (VK0574, VK0620); 1 ♂, Ringlet (MM0005).

Measurements

BL 7.0 mm, PL 1.1 mm, PW 1.5 mm, HW 1.0 mm, Edist 0.50 mm, Ediam 0.45 mm, LP 0.9 mm.

Distribution

Peninsular Malaysia: Pahang. The species occurs exclusively in the high mountains in the Cameron Highlands.

Remark

The identity of this species is based on the general appearance, which might be misleading in some cases, but with a female designated as the holotype we do not have any other possibility for identification. The newly identified specimens were collected in the type locality and the species is common in the Cameron Highlands.

Cautires selangorensis Kleine, 1930

Fig. 77

Cautires selangorensis Kleine, 1930b: 170.

Diagnosis

Cautires selangorensis belongs to a group of species with at least the basal part of the elytra covered with a red pubescence. It differs from the similarly coloured species in the relatively slender phallus, which is widest in the apical two fifths of its length (Fig. 77).

Type material

Holotype

MALAYSIA: ♂, Malay Peninsula, Selangor, Kuala Lumpur, 21 Jul. 1929, H.M. Pendlebury leg. (BMNH).

Redescription of the male

Body slender, black, only basal third elytral costae with reddish pubescence. Head small, antennae flabellate, with lamellae of antennomeres 7–9 about twice longer than respective stems. Pronotum with 7 areolae, postero-lateral costae sharp, well-developed, conspicuous, median areola complete, sharp with elevated margins, areola attached directly to basal margin; anterior angles obtuse, lateral margins concave in the posterior part, posterior angles sharply prominent, pronotum covered with black pubescence. Elytra parallel-sided, secondary costae developed, transverse costae dense. Phallus slender, widest in apical two fifths, apex slender, long 1.2 mm (Fig. 77).

Distribution

This species is known only from the type locality in the Selangor state. Although a wide distribution is expected as in other lowland species, these habitats are heavily affected by urban development and palm oil production and the species has not been recorded since its description.

Cautires tenebricus Kleine, 1926

Fig. 78

Cautires tenebricus Kleine, 1926: 96.

Diagnosis

Cautires tenebricus belongs to a group of mountain species with a uniformly black body. This species resembles *C. nervosus* and *C. maseki* sp. nov. in general appearance, but the male genitalia are characteristic in the slender phallus with the widened apical third (Fig. 78).

Type material

Holotype

MALAYSIA: ♂, Perak, Doherty (BMNH).

Measurements

BL 7.0 mm, PL 1.05 mm, PW 1.35 mm, HW 1.0 mm, LP 0.9 mm.

Distribution

Peninsular Malaysia: Perak.

Remark

Cautires tenebricus has not been found in the recently collected material from the Malay Peninsula and the only known specimen is the holotype deposited in the Museum of Natural History in London.

Cautires congener Waterhouse, 1879

Cautires congener Waterhouse, 1879: 36.

Type material

Holotype

INDONESIA: ♂, Java (BMNH); no further data available.

Remark

Kleine (1926) reported *C. congener* from several localities in the Malay Peninsula and illustrated the apical part of the phallus of a specimen. We studied the holotype of *C. congener*, deposited in the BMNH collection, and found that Kleine's identification was incorrect. The holotype has the apical part of the phallus much wider and the species is yellowish orange coloured unlike all Malay *Cautires* species. Kleine (1926) reported several specimens from various localities from the lowlands to the lower mountain elevations in the Cameron Highlands. These specimens were not available for our study, but they probably do not represent *C. congener*, which is known only from Java.

Discussion

Tropical mountains have been identified as regions with high diversity and endemism (e.g., Toussaint *et al.* 2014; Merckx *et al.* 2015), and in our study we also demonstrate the occurrence of a high number of *Cautires* species in the limited mountain area of the Main Range of the Malaysian Peninsula. We suppose that these species evolved in the region as they do not occur anywhere else. Altogether, fourteen new *Cautires* species have been added in this contribution to the seven species originally known from the Malay Peninsula and the ten species of the *Cautires obsoletus* group reviewed earlier (Jiruskova &

Bocak 2015). The total number of *Cautires* in the Malay Peninsula has reached 30 species (Fig. 79). The altitudinal distribution shows a very high diversity in the Main Range and twenty-one species have been reported from the humid and relatively cold mountain forests in the Cameron Highlands plateau and the adjacent mountain tops with altitudes > 1000 m a.s.l. Only two species were collected in the intermediate elevations 600–1000 m a.s.l. and they overlap in distribution with the mountain species from elevations around 1000 m a.s.l. Additionally, six species were collected in the lowlands of the Malay Peninsula, i.e., elevations under 400 m a.s.l., and, finally, only a single species, *C. indus*, has a wide altitudinal distribution and this is the only species which was also reported from Sumatra. The proportion of lowland species is higher in the *C. obsoletus* species group as defined by Dudkova & Bocak (2010). The fauna of the mountain regions is mostly represented by species with a fully developed pattern of seven areolae in the pronotum. We noted that none of the species occurs in the wide span of different ecosystems from the lowlands to the high mountains and that a low number of species have been recorded from the intermediate to lower mountain elevations 600–800 m a.s.l. (Fig. 79).

Numerous black coloured species occur in the mountain forest at elevation over 1000 m a.s.l. (Fig. 79). Although some species with bright colour pattern have been collected in the mountain habitats, we noted that the black individuals dominated the mountain ecosystem and the brightly coloured individuals were only rarely collected from among them. The black species are restricted to elevations over 1000 m a.s.l. and we suggest that differences in mimicry patterns might play a role in the evolution of the mountain species. Membership in different aposematic rings has been found to be a factor limiting the gene flow in other organisms (e.g., Merrill *et al.* 2014; Twomey *et al.* 2014).

The favourable wet conditions are another factor which potentially contributes to the observed diversity in the higher elevations. The larvae of net-winged beetles have unique mandibles adapted for sucking liquids from decaying organic material (Bocak & Matsuda 2003) and they need very moist organic material to be able to feed throughout the year. The mountain area has a similar amount of precipitation to the lowlands west of the range, around 2600 mm per year, but further moisture occurs in mountain forests through condensation from clouds and lower evaporation. This is because the roughly 10ºC lower temperature results in the absence of a clear dry season in the high elevations (data from the www.worldclimate.com database). The amount of organic debris on the soil surface is higher and the net-winged beetles are very common in these mountain localities. The larvae of *Cautires* have been collected from decaying twigs in the mountains of Sumatra (Bocak & Matsuda 2003) and sifted from soil surface wood debris in the Cameron Highland area (unpublished data).

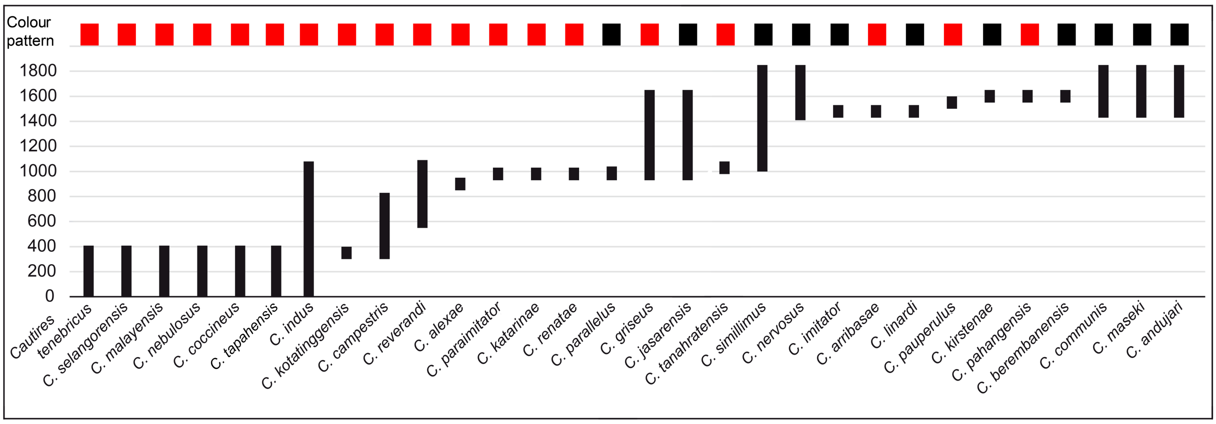


Fig. 79. The altitudinal zonation of the *Cautires* species occurring in the Malay Peninsula.

The comparison of a relatively high number of Cautirina sequences reported in the previous study on phylogeny of Metriorrhynchini (Sklenarova *et al.* 2013) indicates that the Oriental species of *Cautires* have small ranges. The uniqueness of the Malay fauna was confirmed by the extensive search in the historical collections of the Oriental region in the museums of Paris, Warsaw and London, where the most important collections are deposited. We noted during this study that only a single species, *C. indus*, has been recorded in the Malay Peninsula and simultaneously in neighbouring Sumatra and Borneo. The other species was reported from Malaysia and Java due to incorrect identification (Kleine 1926; *C. congener*). This finding agrees with the low dispersal propensity of net-winged beetles. In contrast with them, the fauna of many beetle families is similar on both sides of the shallow Malacca Strait which was dry for the substantial part of the Quaternary (Sathiamurthy & Voris 2006). The described high diversity, almost complete turnover between major regions and high level of endemism call for the protection of the unique faunas in the Malay mountains.

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Part 2

IS THE MALACCA STRAIT AN EFFECTIVE ISOLATING BARRIER TO POORLY FLYING *CAUTIRES* NET-WINGED BEETLES?

(Under review)

Is the Malacca Strait an effective isolating barrier to poorly flying *Cautires* net-winged beetles?

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We investigated the spatial and temporal patterns of *Cautires* diversification on the Malay Peninsula and Sumatra to understand the role of the narrow and frequently subaerial Malacca Strait as a geographic barrier. Moreover, we analysed the origin of *Cautires* mountain faunas. We sampled 18 localities and present the mtDNA molecular phylogeny of 76 species as represented by 388 individuals. The phylogenetic tree was dated using three mtDNA evolution rates and the ancestral ranges were estimated using the Bayesian approach. The phylogeny identifies multiple lineages on the Malay Peninsula since the mid-Eocene (35 mya) and a delayed evolution of diversity in Sumatra since the upper Oligocene (26 mya). A limited number of dispersal events across the Malacca Strait were identified up to the Pliocene and the more intensive faunal exchanges which have taken place since the Pleistocene. The colonization of an area across the Strait regularly resulted in speciation and the species adopted local aposematic patterns. The colonization events were commonly followed by *in situ* diversification. As a result, the Malacca Strait now separates two faunas with a high species-level turnover. Only two species were present in both regions. The mountain fauna diversified in a limited space and seldom took part in dispersals across the Strait. Besides isolation by open sea or a savannah corridor, mimetic patterns are hypothesized as a potential factor in decreasing the dispersal propensity of *Cautires*. The Malay fauna is phylogenetically more diverse and has a higher value if conservation priorities should be defined.

Is the Malacca Strait an effective isolating barrier to poorly flying *Cautires* net-winged beetles?

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Abstract

We investigated the spatial and temporal patterns of *Cautires* diversification on the Malay Peninsula and Sumatra to understand the role of the narrow and frequently subaerial Malacca Strait as a geographic barrier. Moreover, we analysed the origin of *Cautires* mountain faunas. We sampled 18 localities and present the mtDNA molecular phylogeny of 76 species as represented by 388 individuals. The phylogenetic tree was dated using three mtDNA evolution rates and the ancestral ranges were estimated using the Bayesian approach. The phylogeny identifies multiple lineages on the Malay Peninsula since the mid-Eocene (35 mya) and a delayed evolution of diversity in Sumatra since the upper Oligocene (26 mya). A limited number of dispersal events across the Malacca Strait were identified up to the Pliocene and the more intensive faunal exchanges which have taken place since the Pleistocene. The colonization of an area across the Strait regularly resulted in speciation and the species adopted local aposematic patterns. The colonization events were commonly followed by *in situ* diversification. As a result, the Malacca Strait now separates two faunas with a high species-level turnover. Only two species were present in both regions. The mountain fauna diversified in a limited space and seldom took part in dispersals across the Strait. Besides isolation by open sea or a savannah corridor, mimetic patterns are hypothesized as a potential factor in decreasing the dispersal propensity of *Cautires*. The Malay fauna is phylogenetically more diverse and has a higher value if conservation priorities should be defined.

Keywords Molecular phylogeny, Oriental region, Phylogeny, Mimicry, Dispersal

Introduction

Geographic isolation is an important factor in the high diversity observed in most insect groups (Barraclough & Vogler, 2008). Recent studies have shown that poor dispersers have a tendency to produce a higher number of species in a small area (Ikeda *et al*., 2011; Bray & Bocak 2016). The effectiveness of geographical barriers depends on the dispersal propensity of the animals under consideration (Emerson *et al*., 2000; Yoder & Nowak, 2006; Lohman *et al*., 2011; Huseman *et al*., 2014; Toussaint *et al*., 2015, 2017). Most beetles are considered to be effective dispersers and their ability to cross sea straits or open seas has been demonstrated in numerous phylogeographic studies (e.g., Balke *et al*., 2009; Bocak & Yagi, 2010; Toussaint *et al*., 2015; Tseng *et al*., 2018). Nevertheless, the frequency and timing of successful dispersal events have seldom been evaluated in detail for a high number of closely related species.

Our study area is located on the Sunda Shelf (Hall, 2002; Cottam, 2013) which includes Sumatra, Java, Borneo and the Malay Peninsula. The South China Sea is shallow and the continental shelf was subaerial during cold periods in the Tertiary and Quaternary when the sea level dropped by 50 m or more (Voris, 2000; Lohman *et al*., 2011). We focus our study on the isolation role of the Malacca Strait separating the Malay Peninsula and Sumatra. Compared to widely accepted zoogeographical barriers such as Wallace's, Weber's and Lyddeker's lines (Mayr, 1944), the Malacca Strait is very shallow and narrow and has never been considered to be a zoogeographic barrier. The width of the open sea in the southern part of the Malacca Strait is 38–46 km, but the southernmost area is packed with a number of small islands separated by maximum distance under 10 km at the present sea level and with extensive emerged dry-land areas if the sea level drops by 10 m (Fig. 1; http://maps.ngdc.noaa.gov/viewers/bathymetry/; Voris, 2000). The northern part of the Strait was completely subaerial when the sea level dropped by 100 m or more (Voris, 2000). The tectonic history of the landmasses on each side of the Malacca Strait differs. Unlike the tectonically very stable Malay Peninsula, Sumatra was at least partly submerged in the late Oligocene and Lower Miocene and became predominantly subaerial 15 million years ago (mya) (Hall, 2002). There is no information about the extent of dry land left when Sumatra was submerged, but the presence of old endemic lineages of neotenic net-winged beetles indicates that at least some parts of Sumatra were not inundated (Malohlava & Bocak, 2010; Masek *et al*., 2014).

The predominant ecosystems in the Sundaland are humid monsoon rainforests. It is supposed that there has been an uninterrupted presence of wet highly productive ecosystems in the area since the origin of the Asian monsoon system caused by the collision of the Indian and Asian cratons ~50 mya, and by the closed access of humid sea air masses to Central Asia (Heaney, 1991; Royden *et al*., 2008), but their extent strongly depends on climatic fluctuations. Knowledge of the detailed distribution of rainforest ecosystems is limited for earlier periods, but the recent cold periods are known for their dry climate. During the Pleistocene glacial maxima, tropical forests shrank and mostly persisted in the mountains along the western coast of Sumatra and on the Malay Peninsula. Internal lowland regions were covered by savannah and rainforests persisted only in refuges along rivers (Gathorne–Hardy *et al*., 2002; Lohman *et al*., 2011). The savannah ecosystems are supposed to be a significant barrier to rainforest taxa (Heaney, 1991; Lohman *et al*., 2011).

The Malay Peninsula and Sumatra represent a single zoogeographic region with a high number of widespread species and no zoogeographic subregions with high endemism (Myers *et al*., 2000). Nevertheless, numerous species are endemic to a limited part of the Sunda Shelf and it is worth investigating their evolutionary history and distribution in detail, as was demonstrated in recent study of the great apes (Nater *et al*., 2017). As a model system we use the genus *Cautires* Waterhouse, 1879 (Metriorrhynchini: Cautirina), net-winged beetles which were supposedly brought to Asia with drifting India 35–55 mya (Sklenarova *et al*., 2013, 2014). Altogether 35 species were known in Sumatra and the Malay Peninsula until a further 18 species were described in recent taxonomic reviews (Kleine, 1933; Bocak, 2002; Dudkova & Bocak, 2010; Jiruskova & Bocak, 2015; Jiruskova *et al*., 2016). Taxonomic studies have already identified high diversity, especially in the mountain forests where *Cautires* are more common compared to seasonally dry lowland ecosystems. Most species are endemic to restricted areas and they do not occur across a wide range of elevations (Jiruskova & Bocak, 2015; Jiruskova *et al*., 2016). The adults of net-winged beetles are poor fliers and are inactive of the most time, remaining on leaves in the lowest forest stratum. Their dispersal capacity has not been studied in detail, but previous phylogenies have shown that endemic faunas are often separated by narrow sea straits (Malohlava & Bocak, 2010; Li *et al.*, 2015a, 2015b, 2017). Some flower-visiting net-winged beetles have a higher dispersal propensity, but even in those cases, only a few dispersal events led to the current distribution (Motyka *et al.*, 2017). *Cautires*, as with all net-winged beetles, are protected by smelly and bitter compounds in their haemolymph and they are usually aposematically coloured (Eisner *et al*., 2008; Bocak & Yagi, 2010). Most aposematic patterns only occur in clearly defined ranges and potentially prevent easy dispersal to areas with different aposematic signals (Chouteau & Angers, 2011; Motyka *et al*., 2018).

The aim of this study is to test the Malacca Strait barrier hypothesis using the phylogeny and distribution of *Cautires* on the Malay Peninsula and Sumatra. We estimate the origin of respective faunas separated by the Malacca Strait and discuss the effects of ecosystem distribution and the presence of mimetic patterns on the diversification process. Although biodiversity hotspots are often defined as homogeneous regions (Myers *et al*., 2000), a much finer identification of areas with long-term stable habitats and a high phylogenetic diversity is necessary in order to understand the evolution the tropical biodiversity and to set priorities for conservation management.

Methods

Sampling and sequencing

Altogether, ~80 species of *Cautires* net-winged beetles (Lycidae: Metriorrhynchini: Cautirina) from the Malay Peninsula and Sumatra were included in the dataset. The available material contained 140 samples from Sumatra and 248 samples from the Malay Peninsula. The samples were collected in 18 localities representing the western part of the Sunda Shelf. The sampled localities cover forest ecosystems from the sea level to 2400 m above sea level (Fig. 1, Tab. S1).

The total DNA was extracted from metathoracic muscles using a DNeasy tissue kit (Qiagen). Three mitochondrial fragments were amplified: *rrnL*–tRNA-Leu–*nad1* (~817 bp), the

3'end of *cox1*–tRNA-Leu–*cox2* (~1104 bp), and *nad5*–tRNA-Phe–tRNA-Glu–tRNA-Ser (~1322 bp). The individual fragments are further referred as *rrnL*, *cox1*, and *nad5*, only. The primers and PCR conditions follow Sklenarova *et al*. (2013). The PCR products were purified using PCRμ96 Plates (Millipore) and sequenced by an ABI 3130 automated sequencer using the Big Dye Sequencing Kit 1.1 (Life Technologies Inc.). The chromatograms produced by Sanger sequencing were edited using Sequencher 4.8 (Gene Codes Inc.) and the new data (GenBank accession codes AB123456–AB123456, Tab. S1) were merged with the previously published sequences representing several Metriorrhynchini genera (Sklenarova *et al*., 2013, 2014).

Phylogenetic analyses, species delimitation, reconstruction of ancestral areas and dating

Mitochondrial DNA fragments were separately aligned with MAFFT 7.017 plug-in (Katoh & Standley, 2013) in Geneious R7.1.9 (Biomatters Inc., Newark, NJ, USA) and G-Ins-i algorithm. The alignments of the protein-coding genes *cox1*, *cox2*, *nad1*, and *nad5* were checked by amino acid reading frames and manually corrected where necessary. The concatenated supermatrix was partitioned using PartitionFinder2 for all fragments and codon positions where appropriate (Lanfear *et al*., 2014, 2016). The best partitioning scheme contained 14 subsets for individual genes and codon positions where appropriate. The model GTR+I+G was proposed for all subsets and was applied in the maximum-likelihood analyses (Stamatakis, 2014). We conducted ML phylogenetic analyses using RAxML-HPC2 8.2.9 (Stamatakis, 2014) as implemented in the CIPRES web server (Miller *et al*., 2010). The analysis was performed using 100 searches for the best tree under a model identified by the PartitionFinder, with bootstrap (BS) values calculated using the rapid algorithm with 500 bootstrap iterations under the GTRCAT model (Stamatakis *et al*., 2008).

The taxonomy of *Cautires* has not been revised and original descriptions are uninformative, therefore we combined morphology and DNA data to delimit putative biological species. The DNA-based species delimitation was conducted with the Bayesian implementation of the Poisson Tree Processes model (bPTP) using the PTP server (URL: http://species.h-its.org/, Zhang *et. al*, 2013). Outgroups were omitted from the analysis and 500 000 MCMC generations were evaluated; other parameters were set to defaults. Furthermore, with putative species delimited, we counted uncorrected pairwise genetic distances using Species Identifier 1.8 (Meier *et al*., 2006). The clades of closely related individuals were studied in detail using external morphology and the structure of male genitalia. Genitalia were dissected, and cleaned from muscles and fat bodies. The species identifications were partly based on previously published taxonomic studies (Jiruskova & Bocak, 2015; Jiruskova *et al*., 2016). Additionally, the colouration of pronotum and elytra was recorded for each individual (Tab. S2).

The dataset for subsequent analyses was pruned to a single representative of each species and population if these were available from distant areas (Fig. 1). The reduced dataset contained 89 terminals with *Xylobanus* sp. as a single outgroup and was analysed using RAxML-HPC2 8.2.9 as implemented in the CIPRES web server using settings as above to produce a guiding tree for dating analyses. The splits between species and/or populations were dated in Beast 1.8.1 using the fixed topology inferred from the analysis of the pruned dataset (Drummond & Rambaut, 2007, Suchard & Rambaut, 2009). The HKY model, Yule Process and Lognormal Uncorrelated Relaxed Clock, as proposed in the Beast manual, were set in the Beast analysis (Drummond *et al.*, 2012, Drummond & Bouckaert, 2015). As no fossils of Metriorrhynchini are available, the 0.0115 substitutions/site/my/lineage for *cox1* fragment (Brower, 1994), the 0.0054 subs/s/my/l for *rrnL* fragment (Papadopoulou *et al*., 2010) and the 0.0167 subs/s/my/l for *nad5* fragment (Pons *et al*., 2006) were used for calibration. The MCMC parameters were set to 50 million generations with sampling every 5,000 generations and the Effective Sample Size values (ESS) and the pre-stationary phase were identified in Tracer 1.6 (Rambaut *et al*., 2014). The initial 12.5 million generations were discarded as burn-in.

Additionally, the ancestral areas were inferred in Beast 1.8.1 using the HKY model as above, the Coalescent Model: Constant Population Size, Strict Clock and constrained topology gained from the ML analysis of the same dataset. The parameters of the analysis follow the recommendations in the Beast manual. The localities were coded as in Fig. S1: general geographic origin (a) Sumatra and (b) Malaya; specific geographic origin: (a) Cameron Highlands, (b) Malay lowlands and lower elevation forest <1000 a. s. l., (c) Sumatra Barat (Merapi, Maninjau, Talamau), Sumatra Jambi (Tujuh and Kerinci) and Sumatra Utara (Sibayak and Sinabung).

RESULTS

Sanger sequencing, alignment, phylogenetic analyses

Three mtDNA fragments, *rrnL*, *cox1*, and *nad5* were assembled in the dataset of 388 ingroup and 18 outgroup taxa. The ingroup was represented by 369 *cox1* fragments (95% completeness, 817 homologous positions in the Mafft alignment)), 178 *rrnL* (45%, 1104 positions) and 368 *nad5* (95%, 1322 positions) (Tab. S1). The ML analysis of pruned and complete datasets produced similar topologies (Figs. 2 and S1). *Cautires* was retrieved as a monophyletic albeit with low support BS 64 %, similar to the relationships among the deepest clades. The shallower splits had mostly high bootstrap (BS >85%). The robustly supported split separates the *C. pauper* species group and the *Cautires* s. str. clade (i.e., all *Cautires* including *C. obsoletus* species group as defined by Dudkova & Bocak 2010, Jiruskova & Bocak 2015). The tree with collapsed species-level clades is shown in Fig. 2, the full resolution tree in Fig. S1.

Species delimitation and distribution

We identified 76 species when the results of algorithmic delimitations were compared with morphology (Fig. S1, Tab. S2). The bPTP analysis suggested 82 species (Tab. S2) and six species were split into two putative species: *C. paraimitator* (in two species-rank clades with posterior probabilities, PP=93.3%), *Cautires* sp. AD (PP=78.4%), *Cautires* sp. AB (PP=59.1%), *Cautires* sp. AU (PP=50.4%), *Cautires* sp. B (PP=100%), and *C. pauper* (PP=100 %) (Tab. S3). In contrast with this over-splitting, two species were merged into one species rank entity: *C. rianganus* + *C. tapahensis* (PP=98.4%) and *Cautires* sp. AN + *C. pauperulus* with (PP=78.5%) (Tab. S2). The uncorrected pairwise distance analysis of the *cox1* fragment (available for 74 of 76 species) proposed 70 putative species rank clusters under 2 % genetic distance as a threshold (Tab. S2).

Altogether 39 species were recorded on the Malay Peninsula and 39 species in Sumatra. Only two species (*Cautires* sp. G and *C. rianganus*) were simultaneously recorded on the Malay Peninsula and Sumatra (Fig. 3C). The highest local diversity was identified in the lower mountain forests of both regions: the Cameron Highlands (24 spp.), the Sinabung and Sibayak volcanoes (10 spp.) and the Kerinci massif (22 spp.) (Fig. 3A–B). About two-thirds of species were recorded only in a single locality (Fig. 3D).

Ancestral distribution and dating of diversification events

We included 88 *Cautires* terminals in the dating analyses and a single terminal, *Xylobanus* sp., was used as an outgroup. We identified two deeply split clades designated as *Cautires* s. str. and *C. pauper* group (Fig. 4). The *C. pauper* group diversified in six species. Five species were recorded from Sumatra and only *C. pauper* from the lowlands of the Malay Peninsula split from *Cautires* sp. E from Sumatra about 1.4 mya (Fig. 4). The Malay clade started its diversification early and 16 splits were identified from 49 to 26 mya. A single deeply rooted species colonized Sumatra (*Cautires* sp. U), but as it is a single species we cannot exactly date this dispersal event. Further dispersal events leading to the origin of the clades dominantly occurring in Sumatra were identified at 26.1 mya, 16.5 mya and 5.9 mya. In all these cases an ancestor was the origin of a group of species which diversified within Sumatra (Figs. 4–5). Some re-colonization events back to the Malaya were identified within these clades, but we are not able to date them more precisely as in all cases they represent a single species (Fig. 4). We identified 11 dispersal events from Malaya to Sumatra, 10 dispersal events in the opposite direction. Additionally, we identified five transfers between the Malay lowlands and the Cameron Highlands (Figs. 4–5).

Aposematic patterns

Further, we investigated the origins of colour patterns of *Cautires*. Multiple origins of similar aposematic colouration were identified in unrelated taxa: e.g. orange and black colour patterns in *Cautires* sp. K, *Cautires* sp. AH, and an additional 19 species (Figs. 2, 6, S4, Table S4). The Malay *Cautires* are less brightly coloured and most species in lower elevations have brown to orange-brown pronotum and humeral part of elytra with a gradual transition between bright and dark coloured parts (Fig. 6). Further species are dark brown to black with parts of their elytral costae coloured red. The mountain species are either uniformly black (13 spp.) or they have a red coloured pronotum, humeri or both (Fig. S4). The Sumatran low elevation species are uniformly black, have a red coloured pronotum and black elytra, or they have a brown to orange-brown pronotum and humeral part of the elytra (Figs 6, S4).

The Sumatran mountain species are brightly coloured and they usually have a high-contrast border between dark and bright parts: 21 species are orange and black, further species are uniformly bright coloured or black. The populations of a single species were generally uniform in colour pattern and the observed differences were subtle (Fig. S4). The variability in colour pattern was identified in some geographically distant populations (*C. rianganus* and *C. jasarensis*) and within a single population (*Cautires* spp. AH and T).

DISCUSSION

Species delimitation

We identified 76 species and most of them are clearly separated by DNA divergence and morphological uniqueness (Fig. S1; Jiruskova & Bocak 2015; Jiruskova *et al*., 2016). We delimited a separate biological species when, apart from genetic difference, we are able to define clear morphological diagnostic characters (e.g., male genitalia of *C. tapahensis* and *C. rianganus*, Fig. S1). Although more species that have been formally described were included in the current analysis (76 versus 53 spp.), we suppose that further species will be discovered in the future.

Origins of Cautires and their diversification

We suggest that deep *Cautires* lineages originated in drifting India or in a contact zone between India and continental Asia at the time of their collision (55–35 mya, Sklenarova *et al*., 2013). They subsequently dispersed eastwards to the Sundaland, including Malaya and Sumatra, starting their diversification in the region in approximately the Lower Oligocene 35 mya (Fig. 4). The *C. pauper* group contains species limited in their distribution to Sumatra prior to the lower Pleistocene and only 1.4 mya a single species colonized Malaya (Figs 2, S1). As at least one additional species, *C. malayensis,* is known from the Malay Peninsula (Dudkova & Bocak, 2010), further sampling is needed for robust identification of the ancestral region of this clade.

Cautires s. str. is a lineage of Malay origins and almost all species only occurred on the Malay Peninsula prior to the Upper Oligocene (26.2 mya). We identified ten lineages of *Cautires* s. str. on the Malay Peninsula and a single one in Sumatra (Fig. 5B). The Sumatran fauna consists mostly of terminal subclades nested in older, more inclusive Malay groups (Fig. 5AB). The first Sumatran highly diverse lineage originated from dispersal out of Malaya in the upper Oligocene (Figs. 4, 5). Further dispersal events from Malaya to Sumatra are dated to the Miocene (16.5 and 5.9 mya) and later in the Pliocene (three events, 4.4, 4.1 and 3.4 mya). The dispersal to Sumatra was regularly followed by diversification which lead to the origin of a high number of species in the newly colonized range. The Sumatran *Cautires* diversified with an apparent delay compared to the Malay fauna. Sumatra was submerged 15–25 Ma (Hall, 2002) and, in accord with tectonic history, the origin of most lineages of Sumatran *Cautires* were dated to the last 17 my (Fig. 3). The oldest Sumatran clade pre-dates the period of submerged Sumatra and supports the existence of an island chain in the region throughout the lower Miocene (Hall, 2002; Malohlava & Bocak, 2010). The dispersal direction was asymmetrical from the Upper Oligocene until the end of the Pliocene. In this period, we identified several dispersal events from the Malay

Peninsula to Sumatra which gave origin to multi-species clades, and only three species (*C. pauper*, *C. berembanensis*, and *C. tanahratensis*) recolonized Malaya from Sumatra (Fig. 4). The Pleistocene connection between Sumatra and the Malay Peninsula resulted in several dispersal events in both directions and this faunal exchange is in line with paleoclimatic reconstructions which suggest at land connection between Malaya and Sumatra due to low sea levels (Voris, 2000). Except for two species recorded from both regions, all dispersal events resulted in the origin of a different species or a whole local clade (Figs 4, 5). Although the sampling is apparently incomplete, we can conclude that most *Cautires* have small ranges and due to the limited dispersal propensity faunal exchange is uncommon and the geographic speciation mode of speciation is frequent between Sumatra and the Malay Peninsula (Barraclough & Vogler, 2000). We suppose that intensive exchange between these regions would prevent the observed allopatric speciation.

Further aspects of the dispersal and diversification history are the origin and uniqueness of the mountain faunas. We identified 19 *Cautires* with distribution limited to the mountain forests in the Malay Central Mountains and none of them are distributed in a wide range of elevations (Table S1, Jiruskova *et al*., 2016). We identified the early origin of three clades containing a total of 13 species of Malayan mountain fauna (26.4, 17.8 and 11.4 mya). These species represent 68 % of the diversity reported from the Malay mountains. Only an additional 6 species were found in the Malay mountains and the time of their split from their sister species cannot be exactly estimated. Despite the limited extent of mountain regions on the Malay Peninsula and a turbulent climatic history which could have potentially caused complex range shifts over such long periods, these three specious clades are dominantly mountainous and only a single species, *Cautires* sp. S, was inferred to be a member of the mountain clade yet was also distributed in lower elevations (Fig. 5B). The Malay Central Range is a biodiversity hotspot with ancient and diverse fauna similar to other tropical mountains (Merckx *et al*., 2015). Additionally, we found a high turnover between Sumatran Mountains and lowlands and only three species were recorded simultaneously in two mountain regions of Sumatra – *Cautires* spp. B, N, and AN.

Mimetic patterns

The colouration of the pronotum and elytra is highly variable in *Cautires* and ranges from uniformly black to combinations of bright red and black body parts (Figs 6, S4). Although not brightly coloured, we suggest that the body shape and black colouration serve as a salient aposematic signal and these beetles can be very conspicuous on leaves under a forest canopy where predators can observe them against a clear sky (Bocak & Yagi, 2010; Bray & Bocak, 2016; Motyka *et al*., 2018). The Malay and Sumatran species from lower elevations are less brightly coloured and are often widely distributed (e.g., dark brown forms with red elytral costae; Fig. 4, S4A, J); some patterns are known only from Sumatra (Fig. S4K). The Malay mountain fauna is dominantly uniformly black or the pronotum and humeral parts of elytra are dark red. Although more patterns are present in the Cameron Highlands, the uniformly black individuals predominate (Fig. 4, Table S4). Unlike the Malay fauna, the Sumatran mountain species are mostly brightly coloured (Figs 6, S4) and occur typically in a single mountain range (Figs S4L, M, Q and R). In many cases the dispersing individuals have to enter regions where their aposematic signal is uncommon or absent and they are supposedly under the antiapostatic selection which can wipe out rare prey (Beatty *et al*., 2004; Sherratt, 2008). Such selection explains intraspecific polymorphism in *C. rianganus* (the forms with black, brown or brightly red pronotum, Tab. S4) and *Cautires sp.* T (Figs S4G, H). The current sampling cannot discriminate between microhabitat and large-range differences, but in both cases, the polymorphism indicates divergent selection for resemblance to different co-mimics.

The dispersal barriers

The Malacca Strait is shallow and, especially in the southern part, very narrow, so it should not represent a major dispersal barrier for flying insects as numerous beetles lineages easily cross open see straits several hundred kilometres wide (Fig. 1; Balke *et al*., 2009, Tänzler *et al*., 2014, Touissant *et al*., 2017). Additionally, very similar ecosystems are currently present on the Malay Peninsula and Sumatra and we suppose that the narrow Malacca Strait never separated different ecosystems (Morley et al. 2000). Nevertheless, we identified a high species turnover between the Malay and Sumatran *Cautires* faunas. Hence, we discuss the potential factors which might be responsible for the observed distribution. The inundated shelf and geographic distance are the first factors separating the Malay and Sumatran faunas. In contrast with most beetles, *Cautires* are poor dispersers, because they occur only under a canopy in tropical rainforests and seldom fly outside the forest canopy. Their low dispersal capability has been repeatedly documented where single origins were inferred for Madagascar and Afrotropical *Cautires* faunas and for the Sundaland fauna of *Metriorrhynchus* (Yagi & Bocak, 2010; Sklenarova *et al*., 2013). Furthermore, the reconstruction of the climate during recent glacial maxima indicates that the temporarily subaerial Sunda Shelf was covered by semi-dry savannah instead of the lowland rain forest known in the region during interglacial periods (Voris, 2000, Cannon *et al*., 2009; DiNiezo & Tierney, 2013). We identified a lower abundance and diversity of *Cautires* in lowland localities characterized by a more pronounced dry season than in mountain ecosystems. The semi-dry conditions in the subaerial Shelf represent another obstacle for intensive faunal exchange between Malaya and Sumatra. When *Cautires* populations disperse, it is highly probable from the observed distribution of aposematic patterns that most of them will be different colours than local species and predators will not be familiar with their allochthonous aposematic signal. The negative selection against unfamiliar aposematic pattern can be hypothesized as an additional factor decreasing the chances that the new range is successfully colonized (Beaty *et al*., 2004; Sherratt, 2008).

Conclusions

The current analysis of the mtDNA *Cautires* dataset with a representative sampling of the Malay and Sumatran fauna provides evidence for the effective isolation of respective net-winged beetle faunas, even by the shallow and commonly subaerial Malacca Strait. The faunas have a high level of endemism and a different diversification history. The ancestral area reconstructions indicate that most deeply rooted lineages evolved on the Malay Peninsula and some species dispersed to Sumatra where they subsequently diversified. Surprisingly, dispersals to Sumatra were uncommon despite the close geographic position and similar ecosystems in both regions. Even the relatively recent dispersal events across the Malacca Strait in the Upper Pliocene and Pleistocene were commonly followed by speciation. The species colonizing the new range adopted local mimetic patterns and we suppose that the selection against rare aposematic patterns limits the dispersal propensity of unpalatable *Cautires*, but simultaneously it may enhance speciation (Bocak & Yagi, 2010; Bray & Bocak, 2016). The mountain faunas, especially in Malaya, are of ancient origin, contain a high proportion of endemic species and represent biodiversity islands. The survival of South East Asian fauna is under ever increasing human pressure (Sodhi *et al*., 2004) and we demonstrate that the Malay fauna contains all deep lineages, i.e., it has higher phylogenetic diversity, and therefore has much higher value for conservation if priorities are to be set in this region.

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Figure 1. The sampled localities with the samples included in the analysis of the pruned dataset.

Figure 2. The maximum likelihood tree for *Cautires* recovered from the complete dataset. The species level terminals are collapsed. The general appearance of samples illustrates the multiple origins of similar aposematic patterns.

Figure 3. The diversity of *Cautires* in the region: A – the number of species recorded in Malay localities; B – ditto in Sumatran localities; C – the number od species recorded only in Sumatra, Malaya and both regions. D – the number of species recorded from a single or multiple localities.

Figure 4. The reconstruction of ancestral distribution of *Cautires*.

Figure 5. The dated tree of *Cautires* with estimated dispersal events from Malaya to Sumatra (green), from Sumatra to Malaya (bright red) and from lower elevations in Malaya to the Malay Highlands (dark red).

Figure 6. The aposematic patterns of *Cautires* and their distribution in the region.

Supplementary material.

Supplementary Table S1. The list of sequenced specimens with geographic origin and GenBank Accession Numbers.

Supplementary Table S2. Uncorrected genetic distances in *Cautires cox1* mitochondrial DNA fragment.

Supplementary Table S3. The best supported species partitions found by simple heuristic search

Supplementary Table S4. The list of sequenced ingroup terminals with description of dorsal colour patters.

Supplementary Figure S1.The maximum likelihood tree for *Cautires* recovered from the full dataset with morphology of closely related species.

Supplementary Figure S2. Aposematic patterns of *Cautires* net-winged beetles in the Malay Peninsula and Sumatra. A–*Cautires indus* (Kirsch) (Voucher number AJ0046, Malaya: Tapah); B–*C. rianganus* (Pic) (LB0297, Sumatra: Talamau); C–ditto (MM0020, Sumatra: Maninjau): Rd Gua Musang); D – *C. reverandi* Pic (AJ0029:

Rd Gua Musang); E–*C. katarinae* Jiruskova *et al*. (AJ0028, Malaya: Rd K. Raja to Gua Musang, 980 m); F–*C. arribasae* Jiruskova *et al*. (AJ0066, Malaya: Gunung Beremban); G–*Cautires* sp. T (LB0070, Malaya: Tanah Rata); H–ditto (AJ0074, Malaya: Tanah Rata); I–*C. communis* Jiruskova *et al*. (AJ0091, Malaya: Gunung Beremban); J–*C. pauperulus* Bourgeois (MM0043, Malaya: Tapah); K–*Cautires* sp. AK (MM0014, Sumatra: Maninjau); L–*Cautires* sp. AA (VK0228, Sumatra: Gunung Tujuh); M–*Cautires* sp. AE (VK0230, Sumatra: Gunung Tujuh); N–*Cautires* sp. K (VK0219, Sumatra: Gunung Sinabung); O–*Cautires* sp. AD (VK0222, Sumatra: Gunung Sinabung); P–*Cautires* sp. AH (MM060, Sumatra: Gunung Kerinci); Q–ditto (VK0210, Sumatra: Gunung Kerinci); R–*Cautires* sp. U (VK0214, Sumatra: Gunung Kerinci).

Dataset. The full dataset used in the ML analysis.

Figure 1

Study Area

The sampled localities with the samples included in the analysis of the pruned dataset.

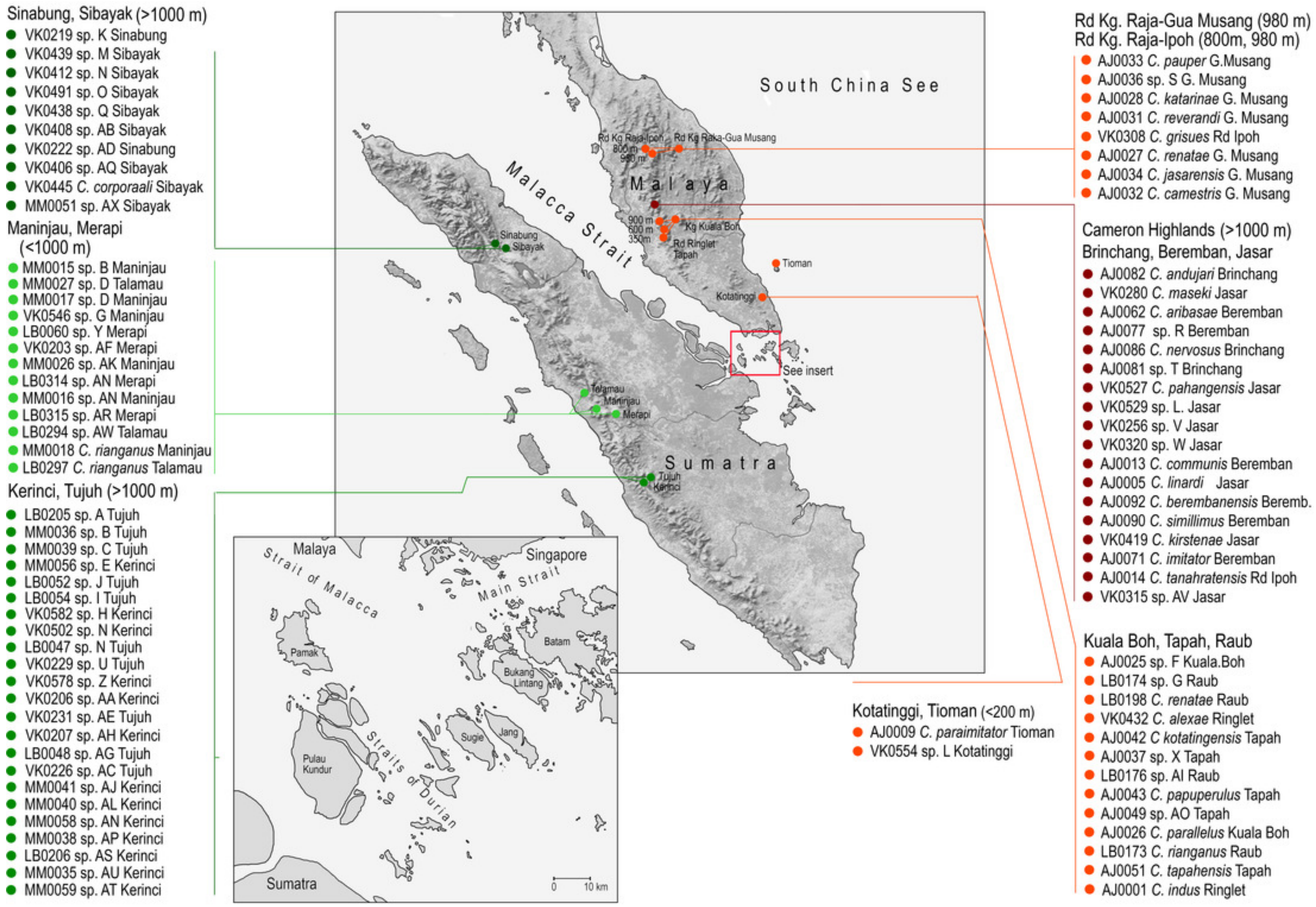


Figure 2

Phylogenetic hypothesis

The maximum likelihood tree for *Cautires* recovered from the complete dataset. The species level terminals are collapsed. The general appearance of samples illustrates the multiple origins of similar aposematic patterns.

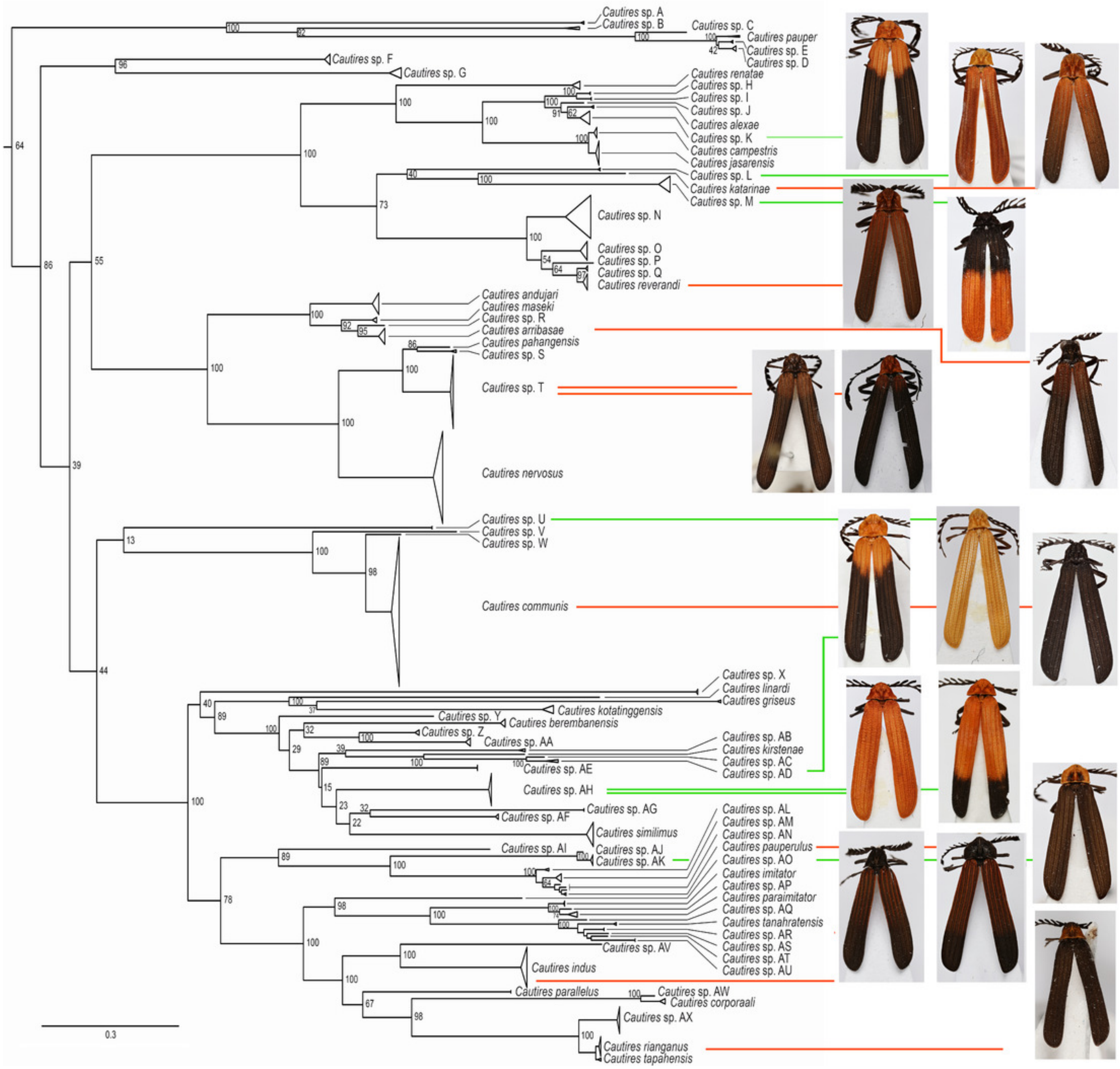


Figure 3

The diversity of *Cautires* in the region

A – the number of species recorded in Malay localities; B – ditto in Sumatran localities; C – the number od species recorded only in Sumatra, Malaya and both regions. D – the number of species recorded from a single or multiple localities.

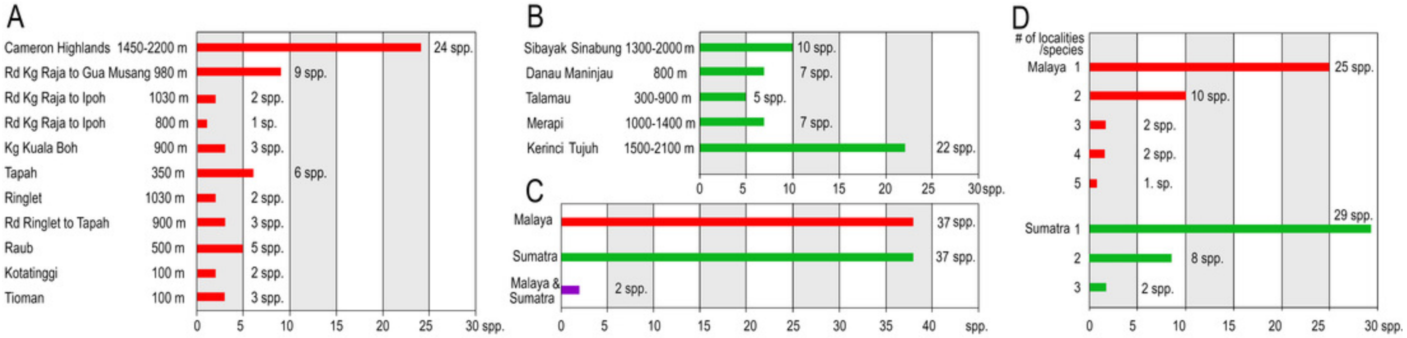


Figure 4

The reconstruction of ancestral distribution of *Cautires*.

The pies represent probabilities for respective nodes.

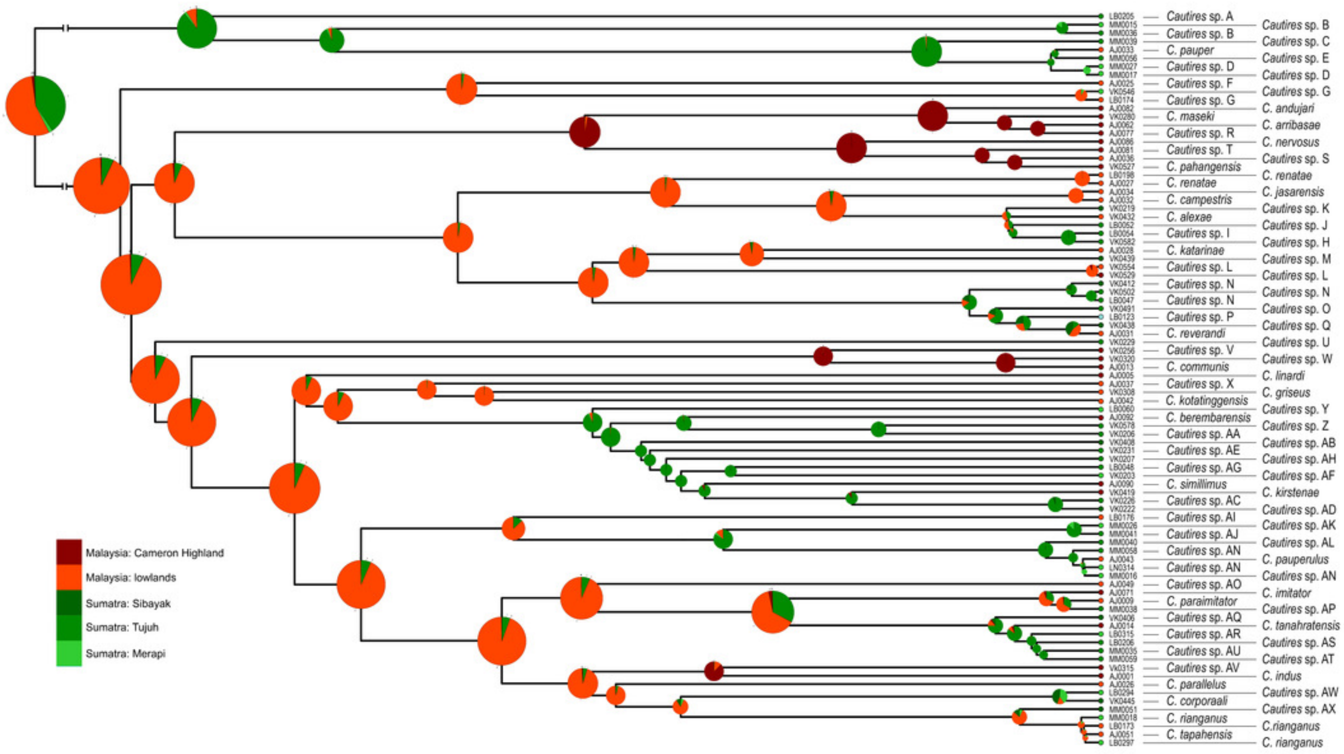


Figure 5

The dated tree of *Cautires.*

The codes designate estimated dispersal events from Malaya to Sumatra (green), from Sumatra to Malaya (bright red) and from lower elevations in Malaya to the Malay Highlands (dark red).

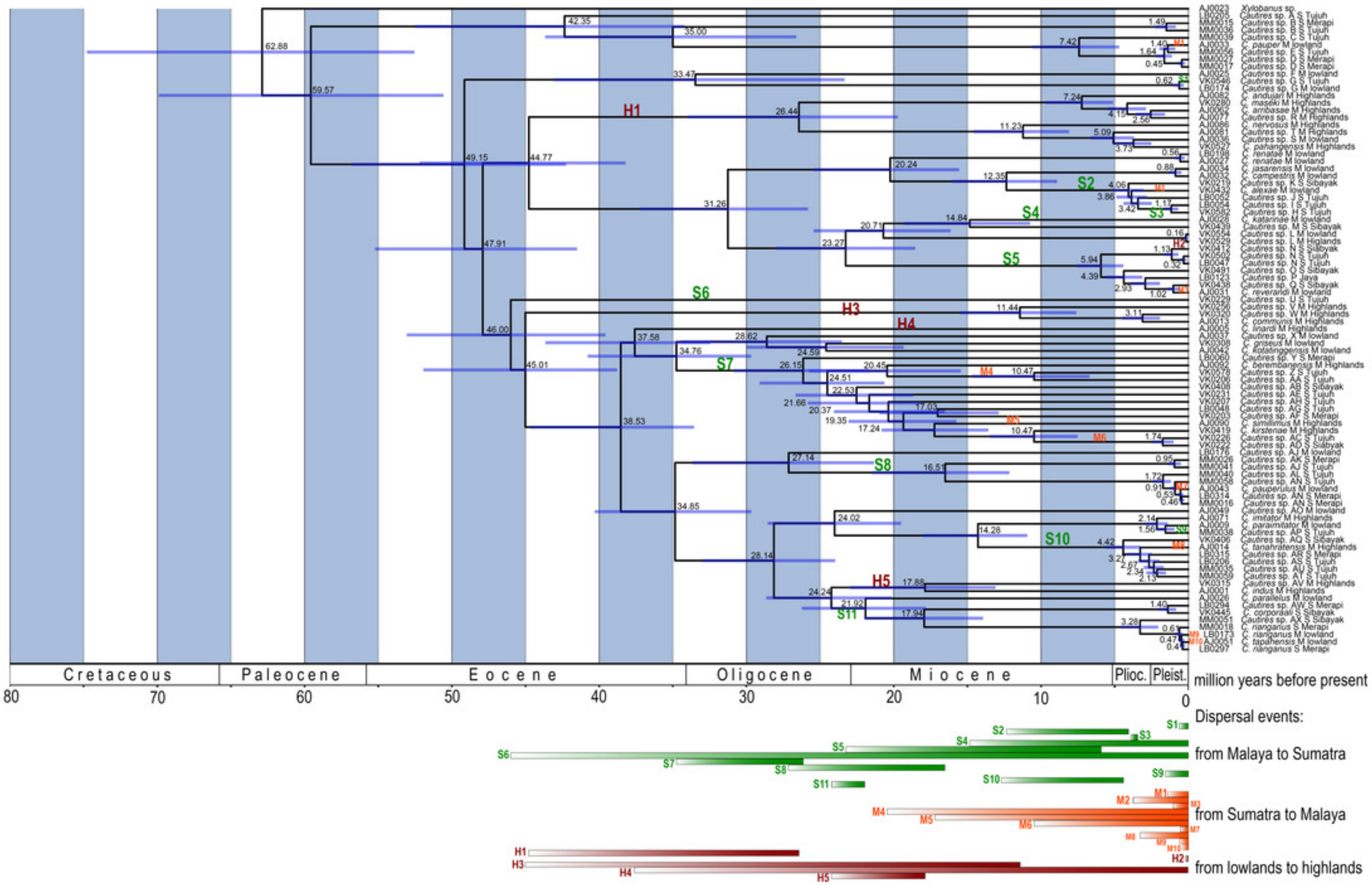
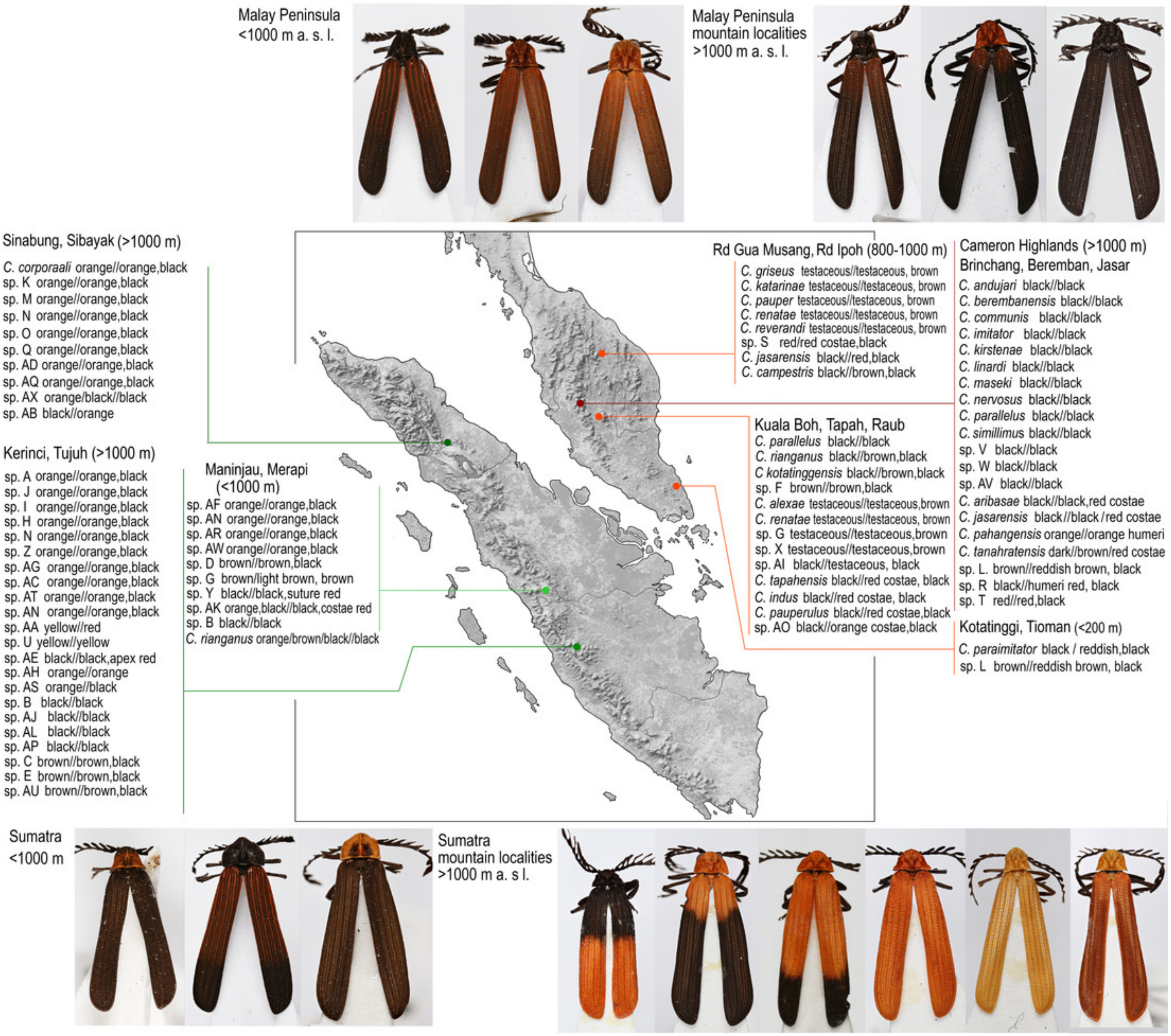


Figure 6

The aposematic patterns.

The distribution of *Cautires* aposematic patterns in the region.



Part 3

CAN A WORLD-WIDE DIVERSITY SEQUENCING IDENTIFY THE RANGES OF NATURAL TAXA? AN EXAMPLE OF POORLY DEFINED GENERA OF METRIORRHYNCHINI (COLEOPTERA: LYCIDAE)

(Unpublished manuscript)

Can a world-wide diversity sequencing identify the ranges of natural taxa? An example of poorly defined genera of Metriorrhynchini (Coleoptera: Lycidae)

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Abstract

Taxonomy should provide an information-rich phylogenetic classification for all biological disciplines. In contrast with its goal, the current classification contains often polyphyletic higher taxa which contain unrelated species. Here, the molecular phylogeny of Metriorrhynchini is investigated based on earlier published sequences and the monophyletic genus-group taxa are delimited. Then, the distribution of selected species-rich genera based on catalogues and original descriptions is compared with the distribution of these taxa included in the molecular analysis. The inferred ranges differ in numerous aspects. *Xylobanus* does not occur in the Afrotropical region, *Cautires* does not occur east of Weber's line, *Cladophorus* is an endemic to New Guinea, and *Procautires* is a Metriorrhynchina genus distributed only in New Guinea and Buru island. About a quarter of species classified in considered genera was misplaced in the wrong genus. The critical revision of traditional classification is necessary before any data are used for zoogeographical and evolutionary studies.

Introduction

The ultimate goal of taxonomy is to recognize and name the biological diversity on Earth and to group all taxa in the relationship-based hierarchical structure of higher taxa which have a predictive power for morphology, biology, ecology, and distribution (Quicke 1993, Wiley and Lieberman 2011). The phylogeny of many groups, such as vertebrates, is intensively studied and their classification is well-founded (Prum *et al.* 2015). These groups are commonly used for delimitation of zoogeographical regions or the biodiversity hotspots (Myers *et al.* 2000; Holt *et al.* 2013). Conversely, the insects are much less known and especially the classification of the enormous tropical diversity is inadequate and only a fraction of the extant diversity has been described and robustly classified. We face the burden of uninformative descriptions (e.g. the studies by the French entomologist M. Pic in the first half of the 20th century), the careless classification of newly described species based on poor knowledge of the group (often a single new species described in a very diverse, poorly known genus without a reference to earlier described species), inaccessibility of type-holding collections or their poor organization, e.g. due to shortage of funding and staff. Recently, further obstacles have been raised from unwillingness of collection curators to locate and send types for a loan, the shortage of experts in many groups and legal limits set for bona-fide taxonomic research, e.g. the laws implementing the Nagoya Protocol in national legislations (Nijar *et al.* 2017).

Here, I investigate the delimitation of several tropical net-winged beetle genera as an example of the current state of beetle systematics. There were five Metriorrhynchine genera which housed the majority of about 1200 described species: *Trichalus* Waterhouse, 1879 (~130 spp.), *Metriorrhynchus* Gemminger and Harold, 1869 (~180 spp.), *Xylobanus* Waterhouse, 1879 (~230 spp.), *Cautires* Waterhouse, 1879 (~200 spp.), and *Cladophorus* Guerin Méneville, 1830 (~190 spp.; Kleine 1926, 1933, Calder 1995, Bocak 2002, 2012, Bocak and Bocakova 2008, Dudkova and Bocak 2010). *Trichalus* was recovered as a much smaller clade than *Microtrichalus* Pic, 1921, originally, a monotypic genus from Java, in which have been transferred many *Trichalus* species whenever their types become available for study (Bocak 1998a, b, 1999, 2002, Bocek and Bocak 2017). *Metriorrhynchus* diversity was split between genera *Porrostoma* Laporte, 1838 and the proper *Metriorrhynchus* (Bocak 1998c), but all Australian *Metriorrhynchus* were incorrectly transferred to *Porrostoma* Castelnau, 1838 by Calder (1995). The revision of this species complex is beyond the scope of this study as most type specimens are inaccessible due to legal regulations of Australian museums and all Australian fauna of *Metriorrhynchus* remains formally placed in *Porrostoma* (Calder 1995). *Xylobanus* was recovered as a monophyletic clade which contains all Oriental species with four primary costae, but available Afrotropical *Xylobanus* species were recovered as a terminal clade within Afrotropical *Cautires* in the molecular phylogeny (Sklenarova *et al.* 2013, 2014) and some species earlier considered related to *Xylobanus* turned to be Metanoeina (Kubecek *et al.* 2015). *Cautires* was recovered as a lineage which colonized Madagascar and continental Africa during the drift of Indian northwards and after accretion of India to the Asian craton it colonized the Oriental and eastern Palearctic regions (Sklenarova *et al.* 2013, 2014). Additional genus, *Procautires* Kleine, 1925, was reported from various disjunctive ranges in Asia, Africa and Australasia (Kleine 1933).

Here, I present a result of the world-wide molecular biodiversity screening of the Metriorrhynchini, the most species-rich tribe of the net-winged beetles. Although many types have been inaccessible for various reasons and I am not able to provide taxonomic reviews for individual genera, the relatively dense sampling provides sufficient information to revise the distribution of the genera *Cladophorus*, *Procautires* (both Metriorrhynchina), *Xylobanus*, and *Cautires* (both Cautirina, Sklenarova *et al.* 2014). As a result, I can indicate a proportion of species which have been very probably incorrectly classified in the respective genera and provide some proposals for the further studies, such as geographically restricted taxonomic revision, reviews and catalogues.

Material and Methods

I assembled a three-marker dataset from multiple earlier publications dealing with various taxonomic, phylogeographic and evolutionary topics (Kubecek *et al.* 2011, 2015, Sklenarova *et al.* 2013, 2014, Jiruskova and Bocak 2015, Jiruskova *et al.* 2016, under review, Motyka unpublished dataset.). The dataset consisted of three mtDNA fragments for 832 terminals and about 500 species representing faunas of Palearctic, Afrotropical, Oriental, and Australian regions (Fig. 1, Supplementary Table S1). The dataset contained 233 sequences for SSU rRNA, 230 sequences for LSU rRNA, 512 sequences for rrnL+tRNA-Leu+nad2 mtDNA fragment, and 749 for cox1-tRNA-Leu-cox2 mtDNA and 745 nad5+tRNAs mtDNA, all mtDNA fragments are referred further as *rrnL*, *cox1*, and *nad5* only). The sequences were aligned separately using default parameters of MAFFT 7.2 and Q-INS-I algorithm (Katoh *et al.* 2002) and the concatenate aligned dataset had 5876 homologous positions (Table 1). IQ-TREE 1.5.5 (Nguyen *et al.* 2015) was used to calculate best maximum likelihood (ML) tree topology with partition identified by the ModelFinder tool implemented in IQ-TREE which recognizes the best fit models using the Bayesian Information Criterion (Kalyaanamoorthy *et al.* 2017, Chernomor *et al.* 2016). The partitions, models and parameters are listed in the Table 2. The ultrafast bootstrap option was set with 1000 bootstrap repetitions and 1000 bootstrap iterations (Hoang *et al.* 2017).

Results

The DNA sequences for five fragments produced an alignment with a relatively low number of indels. The non-coding fragments represented closely related species, all ingroup taxa belonging to a single tribe, and especially the *SSU* and *LSU* sequences were conservative (Tab. 1). The alignment algorithm produced the datasets of 5867 characters. The numbers of characters are given in Tab. 1. The phylogenetic reconstruction inferred by ML resulted in the topology with a high bootstrap support in the lower level branches (Fig. 1). The trees had fully resolved basal branches, although the arrangement of subtribes was in conflict with previous analyses and obtained a lower support. All trees recovered Metriorrhynchini as a monophylum. The Metriorrhynchina clade was well supported and included also Metanoeina as defined by Kubecek *et al.* (2015). The Cautirina clade was consistently found with basal split of *Xylobanus* and *Cautires* and both genera were inferred as monophyla. The species earlier classified in *Bulenides* were found as terminal branches in *Cautires* as well as the Afrotropical species with only four primary costae and therefore typologically belonging to *Xylobanus*.

The evaluation of geographic distribution of the genus level clades was assessed with information from primary descriptions and catalogues and with geographic information inferred from randomly sampled representatives of the local faunas of Metriorrhynchini in the molecular phylogenetic analysis. The results are summarized in the Table S1 and in Figures 2–6). The tribe Metriorrhynchini has a Gondwanan distribution and the range expands in the Palearctic East Asia (Russian Far East). Additionally the tribe is well represented in the Sino-Japanese realm (China, Japan) and in the Oriental realm (most of India, Sri Lanka, the lower elevation Himalayas, Indo-Burma, Malaya, the Great Sundas, Lesser Sundas, Philippines). Further the tribe is widespread in the Oceania realm, its western part: the Moluccas, New Guinea, the Solomon Islands and a few islands further west, e.g. Samoa) and the Australian realm (Australia, Tasmania, and one introduced species in New Zealand). The Afrotropical realm houses relatively diversified fauna in forest and savannah habitats.

The subtribes differ in their distribution. Metriorrhynchina are mostly Oceanian and Australian, relatively rich Metriorrhynchina fauna is known from the Sulawesi but differs in the generic composition from the New Guinea fauna, much less species occur in the Philippines and only a few species of *Diatrichalus*, *Leptotrichalus*, *Microtrichalus* and *Metriorrhynchus* occur in the eastern part of the Oriental realm, i.e. Indo-Burma, Malaya and the Sundaland (Bocak 1999, 2000a, b, 2007, Bocak *et al.* 2006, Bocak and Yagi 2010). The Cautirina occur in the Afrotropical, Oriental, Palearctic and Sino-Japanese realm, but they do not cross Weber's line which was proposed as a border between Oriental and Oceanian realm (Holt *et al.* 2013).

To sum up some distributions: *Xylobanus* does not occur in the Afrotropical and Australian realms (Fig. 3), *Cautires* does not occur in the Oceanian realm (Fig. 4), *Cladophorus* is endemic to New Guinea and does not occur in any further region (Fig. 5) and *Procautires* is present only in the islands Buru and New Guinea (Fig. 6). The list of evaluated species, their original generic placement and the placement based on the distribution of the monophyla inferred from the molecular phylogeny are listed in Table S1. The maps with ranges based on original descriptions and catalogue information and ranges derived from molecular phylogeny are shown in Figs 3–6.

Discussion

Systematics provides for other biologists not only names, but also hypotheses on relationships which gives a sense to names used in studies dealing with phylogenetic biodiversity, endemism, zoogeography and biodiversity conservation (Myers *et al.* 2000, Sodhi *et al.* 2004). The regional catalogues are published (e.g., Loebl and Smetana 2007, Calder 1995) and the online databases strive to provide the overview of local or taxon based faunas (Fauna Europea-https://fauna-eu.org, Tree of Life project-http://tolIb.org/tree/, etc.).

Recently, the databases such as GenBank and the methods of next-gen barcoding and environmental sequencing produce a high volume of data and extensive phylogenies for meta-analyses (Peters *et al.* 2013, Bocak *et al.* 2014, Linard *et al.* in press). As the link between a specimen and the sequence is often lost, the taxonomic backbones provided by identified specimens and reflecting the correct phylogenetic classification are extremely important. The studies dealing with data of various origins depend on the robustness of the classification and especially on the monophyly of delimited genera, families and eventually higher taxa. If the taxonomic backbone is poor, the results would be hardly interpretable.

Here, I demonstrate with four genera of net-winged beetles as a model, that a large part of information which can be inferred from the classification of tropical beetles and extracted from catalogues, databases and primary descriptions might be misleading. The primary data based on original classification and the ranges of monophyla recovered from the molecular phylogeny differ in numerous aspects. Most earlier and some recent taxonomic studies provide information in conflict with results based on sequencing and phylogenetic analysis of the dataset which represents almost 400 species and it means about a third compared to the number of formally described species (Kleine 1933, Bocak 2002).

The first genus for which I analyzed distribution and phylogeny is *Xylobanus*. Morphological definition of this genus provides basically a single character: the presence of only four primary costae in each elytron, all costae well-developed in the whole length. As a result, numerous taxa, often belonging to unrelated lineages have been placed in *Xylobanus*. e.g., almost all Metriorrhynchini species with four costae in Sulawesi belong to *Sulabanus* Dvorak and Bocak, 2007, *Mangkutanus* Kubecek *et al.*, 2011 or eventually *Wakarumbia* Bocak, 1999 (all Metriorrhynchina), but not to *Xylobanus* (Cautirina) as was shown by Kubecek *et al.* 2011, Dvorak and Bocak 2007, 2009) and is apparent in the presented phylogenetic analysis (Fig. 1 part 1). *Sulabanus* occurs also in the Philippines as is demonstrated in the current phylogeny and therefore, also the Philippine fauna of *Xylobanus* should be critically revised (Fig. 1 part 1). Additionally, Sklenarova *et al.* (2014) showed that the Afrotropical species, all until that time classified in *Xylobanus* are in fact representatives of a single terminal clade of Afrotropical *Cautires* which dispersed only a single time to the Afrotropical region (Fig. 1 part 2, Sklenarova *et al.* 2013). Similarly, the "*Xylobanus*" species from Australia, all of them listed by Calder (1995), belong to various Metriorrhynchina lineages, but not to Cautirina where real *Xylobanus* belongs (https://bie.ala.org.au/search?q=*Xylobanus*andfq =imageAvailable:%22true%22) and also the Australia fauna should be revised and the generic classification modified. Recently, Kazantsev (2015) described several species of Metriorrhynchina in *Xylobanus* which belongs to Cautirina when he applied the typological assignment of all Metriorrhynchines with four costae to *Xylobanus*. Also the position of these species needs revision.

Further genus containing some unrelated taxa is *Cautires*. About 230 sequenced species were recorded only from the Oriental, Palearctic and Afrotropical regions. Although, similarly to *Xylobanus* the occurrence in Sulawesi can be expected, no species east of the Wallace's line, eventually Weber's line has been reported. In contrast with the inferred distribution, there had been described before the World War II *Cautires* species from New Guinea (Kleine 1926) and recently some species from the Moluccas (Kazantsev 2010). The additional taxonomical uncertainty represent species classified in *Cladophorus*, but occurring in the range of *Cautires*, i.e., in the Palearctic, Oriental and Afrotropical regions. Nakane (1969) transferred all Japanese *Cladophorus* correctly to *Cautires*. He based this study on the type material in the Paris Natural History Museum. Later, Bocak (2002) noted that *Cladophorus* is a solely Papuan genus and that about 200 species placed in *Cladophorus* should be revised as they cannot be related to the typical *Cladophorus*. Recently Kazantsev (2012) listed all Afrotropical *Cladophorus* under *Cautires* without any reference to the type material. Additionally, Kazantsev (2006, 2012) described further three genera, *Tricautires* Kazantsev, 2006, *Paracautires* Kazantsev, 2012 and *Spartoides* Kazantsev, 2012. All these genera are defined based on the structure of elytral costae which have been proven as a very plastic character by Sklenarova *et al.* (2014). Concerning the fact, that I recovered a single proved dispersal event giving the origin to Afrotropical Metriorrhynchini until now (Fig. 1 part 3, Sklenarova *et al.* 2013), the occurrence of additional three genera delimited using a dubious traits needs revision.

Cladophorus is further all-in-one basket Metriorrhynchine genus and some 200 species have been incorrectly placed in this genus (Kleine 1933). *Cladophorus* has been delimited using the basally attached antennal lamellae, but this character cannot be used as many real *Cladophorus* have variable position of lamellae (Kalousova and Bocak 2017). Some *Cladophorus* species have already been transferred to *Cautires* (see above), but the Oriental species have never been revised and many still remain formally placed in *Cladophorus*. The phylogeny presented in the Fig. 1 contains number of Indo-Burman species and no species except two *Metriorrhynchus*, which is the type genus of Metriorrhynchina, all belong to Cautirina. The occurrence of *Cladophorus* is limited to New Guinea and the close biologically interconnected islands and all records outside this region are false.

Procautires is the last Metriorrhynchina genus which has been reported from the Oriental and Afrotropical regions. Similarly to *Cautires* and *Xylobanus*, *Procautires* has been defined based using the structure of elytral costae. In this case, the middle part of the elytron has only four primary costae and some short secondary costae are present in the humeri and the apical part of the elytron. My revision of all available material shows that *Procautires* surely belongs to Metriorrhynchina and that all reports from the Oriental and Afrotropical regions are false.

The classification of Metriorrhynchini is an example which very probably does not represent exception, but might be in fact similar to the taxonomic situation in other tropical insect lineages which are too diverse, too widely distributed and poorly defined that a good part of the classification is in fact incorrect and cannot be used for biogeographic or evolutionary studies. The overview of several Metriorrhynchini genera demonstrates that about a 45 % of *Cautires* species were originally placed in some other genus (187 of 417 spp.). The combination with *Cautires* has been already proposed for 82 spp., additional 105 species are still placed in various unrelated Metriorrhynchina genera and they need the taxonomic revision of their classification. As a result of the combination of earlier and now hypothesized changes, the number of *Cautires* species may rise to 417 spp. Altogether 45 species of Afrotropical "*Xylobanus*" are very probably just representatives of a terminal lineage of *Cautires* (Fig. 1 part 3) and additional 40 species of Australian "*Xylobanus*" should be transferred to *Metriorrhynchus*. With 85 species excluded, only 168 species should remain in *Xylobanus* and their range shrinks to the Oriental and Palearctic regions (Fig. 3). The widely disjunctive range of *Procautires* was an artifact of an incorrect classification and the genus is an endemic of the New Guinea and Buru. Other records of this genus are false.

In summary, the classification of Metriorrhynchini and very probably also other groups, as was demonstrated by Bocek and Bocak (2017), contains a number of genera containing unrelated taxa. The polyphyly makes such taxa inacceptable for any evolutionary studies. The world-wide sequencing of a single group can easily identify discrepancies between the formal classification and relationships and focus the taxonomist on critical taxa and lineages which need taxonomic revision. The correctly identified entries in databases, including GenBank, are critical for the placement of samples in diversity monitoring studies which depend on environmental sequencing and are not voucher-specimen based.

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Table 1. The characteristics of the dataset

832 taxa with 10 partitions and 5866 total sites

Gene	Type	#Seq.	Site	Unique	Infor.	Invar.	Model
cox1	DNA	749	780	581	450	281	SYM+R8
cox tRNA(cox)	DNA	719	61	35	21	38	TVMe+I+G4
cox2	DNA	716	255	231	187	54	SYM+R7
nad5	DNA	745	1014	934	767	176	SYM+R9
tRNAs (nad5)	DNA	713	334	297	208	83	TVM+F+R5
rrnL	DNA	512	676	533	347	246	GTR+F+R6
tRNA-Leu(rrnL)	DNA	488	71	55	24	37	TIM+F+R3
nd1	DNA	489	127	125	84	22	SYM+R6
SSU	DNA	233	1897	381	211	1592	TIM2e+R4
LSU	DNA	230	651	154	93	528	K3P+R4

Column meanings:

Unique: Number of unique site patterns

Infor: Number of parsimony-informative sites

Invar: Number of invariant sites

Table 2. List of best-fit models per partition:

ID	Model	LogL	AIC	AICc	BIC
cox1	SYM+R8	-105182.1405	210404.2810	210405.3877	210497.4669
tRNA-Leu (cox)	TVMe+I+G4	-1918.9377	3851.8753	3853.9885	3866.6514
cox2	SYM+R7	-36725.1687	73486.3374	73489.2357	73550.0802
nad5	SYM+R9	-163873.4249	327790.8498	327791.8710	327899.1263
tRNAs (nad5)	TVM+F+R5	-19173.7471	38379.4942	38381.2103	38440.4725
rrnL	GTR+F+R6	-41273.0728	82584.1455	82585.3041	82669.9532
tRNA-Leu (rrnL)	TIM+F+R3	-1817.7705	3657.5409	3662.0155	3682.4304
nad1	SYM+R6	-14147.2290	28326.4580	28331.4035	28371.9650
SSU	TIM2e+R4	-11700.2367	23420.4734	23420.5900	23475.9537
LSU	K3P+R4	-5271.2916	10560.5832	10560.8640	10600.8898

AIC, w-AIC: Akaike information criterion scores and weights.

AICc, w-AICc: Corrected AIC scores and weights.

BIC, w-BIC: Bayesian information criterion scores and weights.

Plus signs denote the 95% confidence sets; minus signs denote significant exclusion.

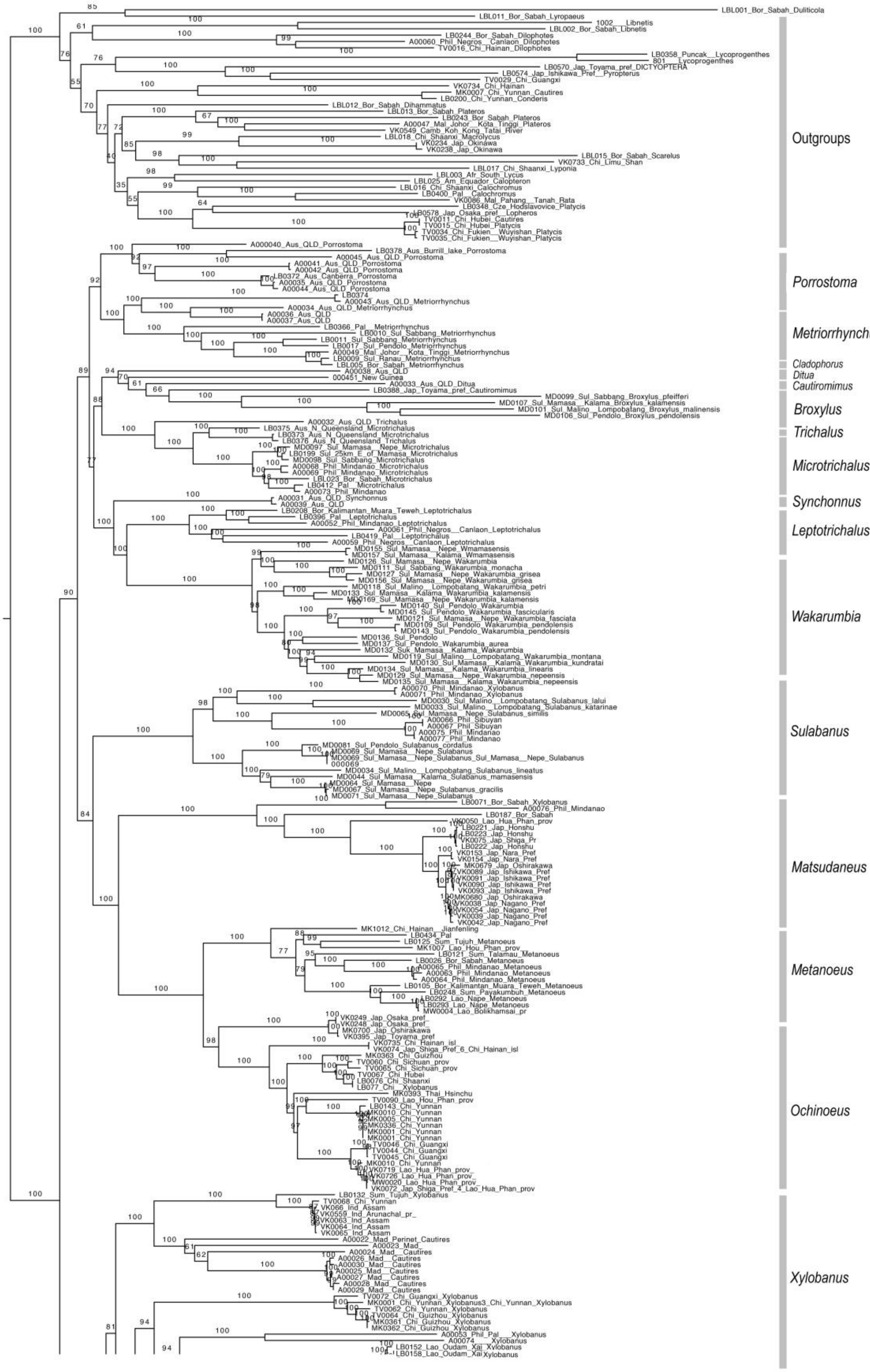

Figure 1. The maximum likelihood tree recovered from the five-gene alignment of Metriorrhynchini Kleine (part 1).

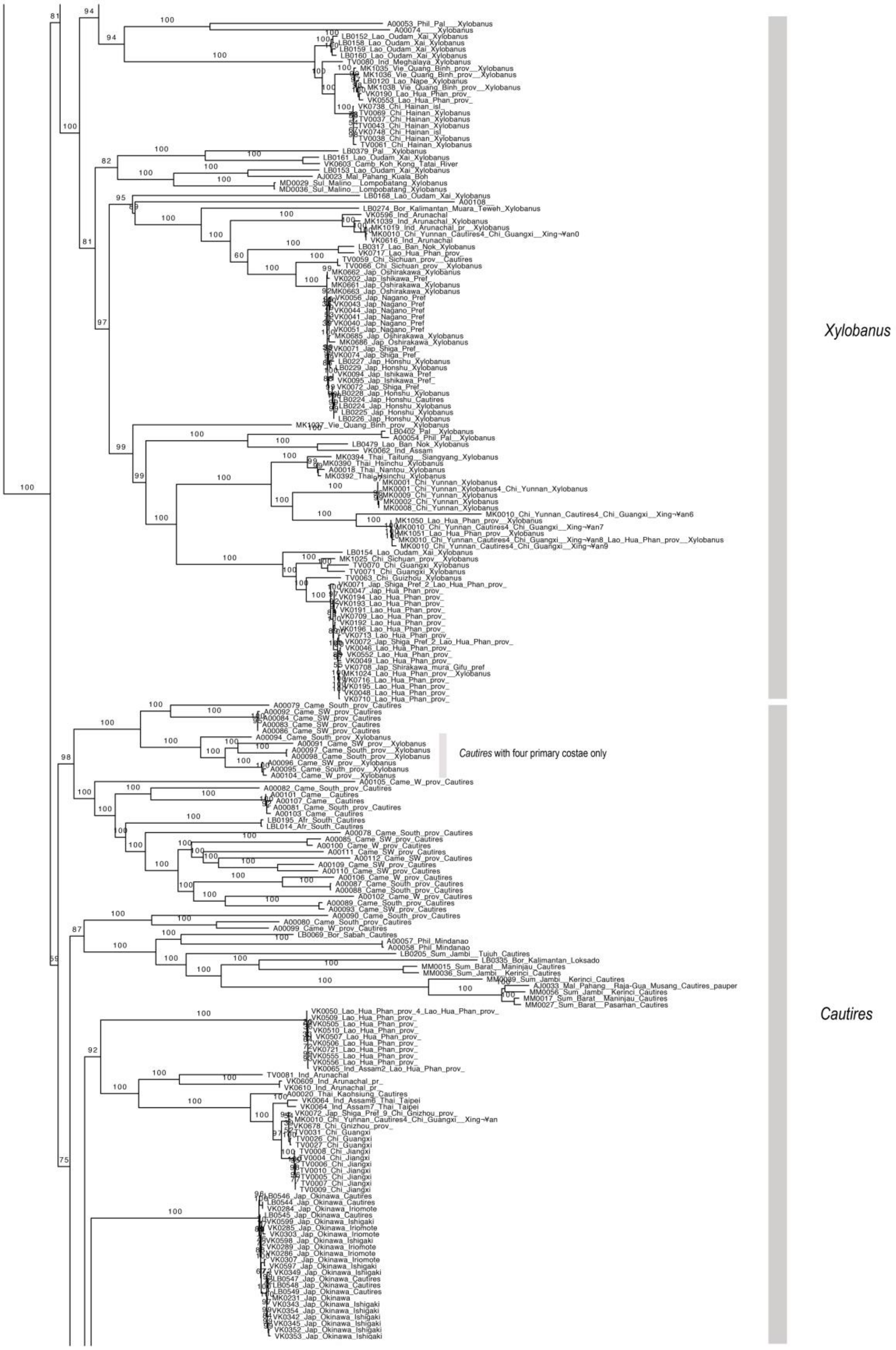

Figure 1. The maximum likelihood tree recovered from the five-gene alignment of Metriorrhynchini Kleine (part 2)

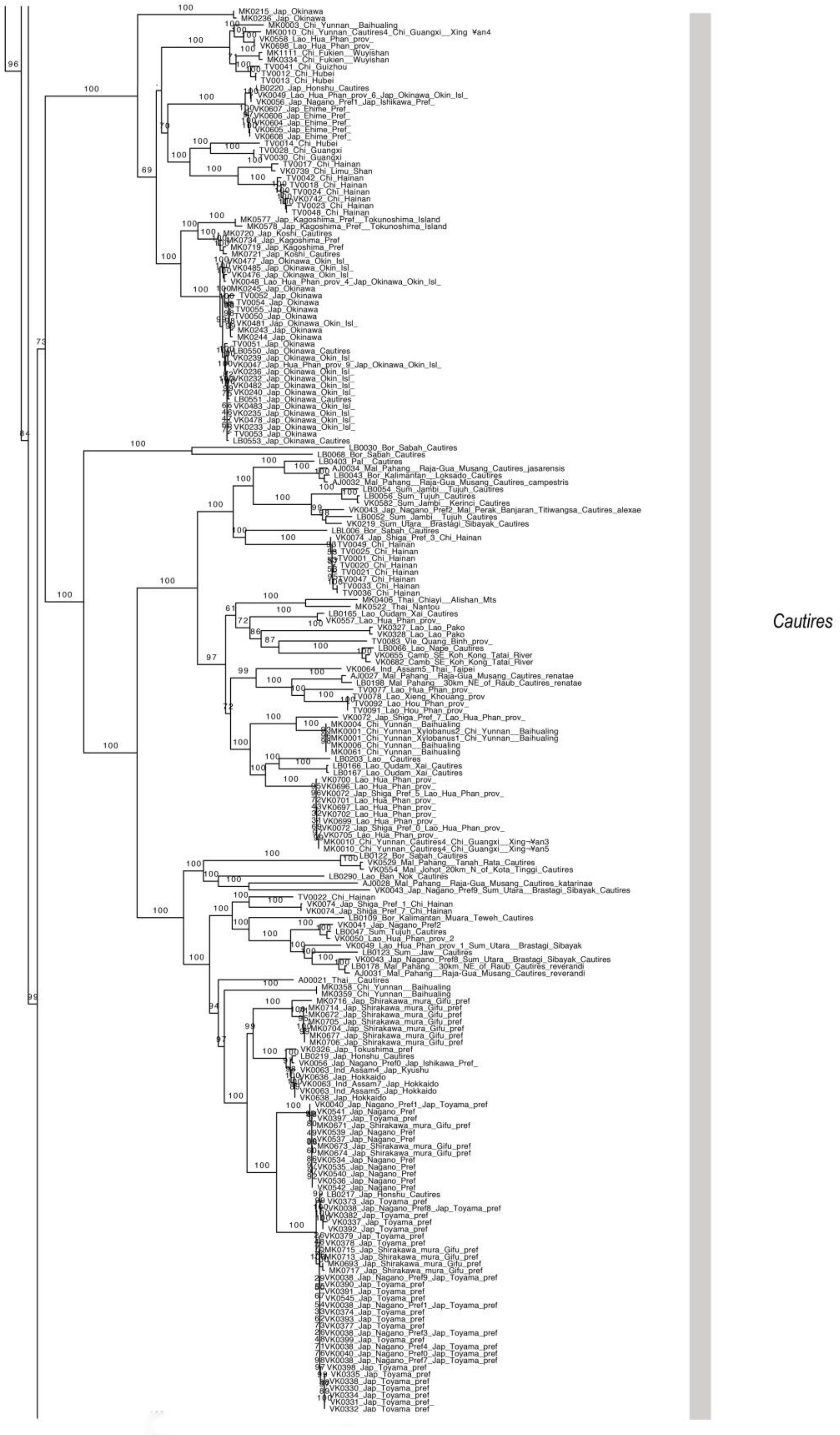

Figure 1. The maximum likelihood tree recovered from the five-gene alignment of Metriorrhynchini Kleine (part 3).

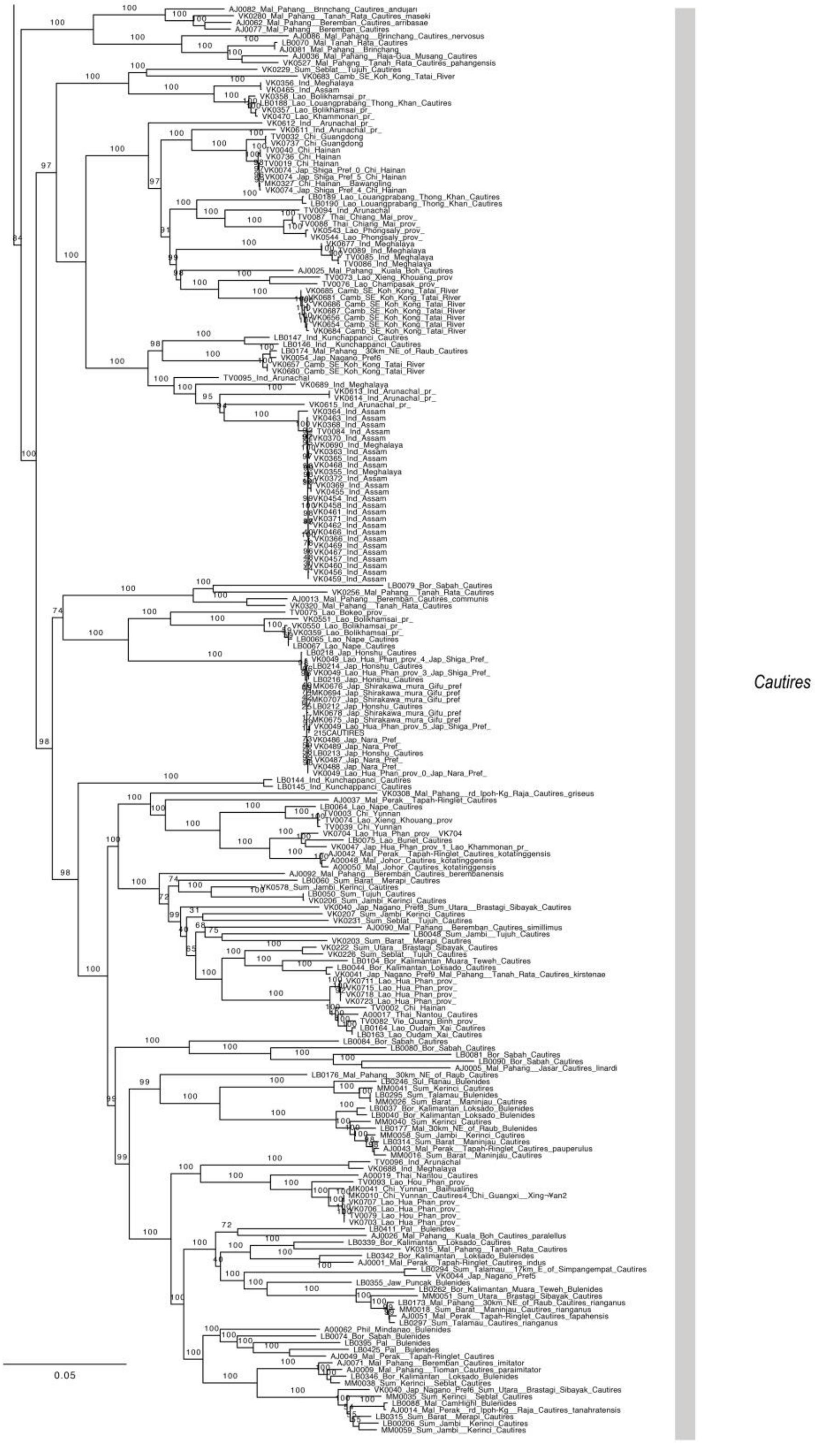

Figure 1. The maximum likelihood tree recovered from the five-gene alignment of Metriorrhynchini Kleine (part 4).

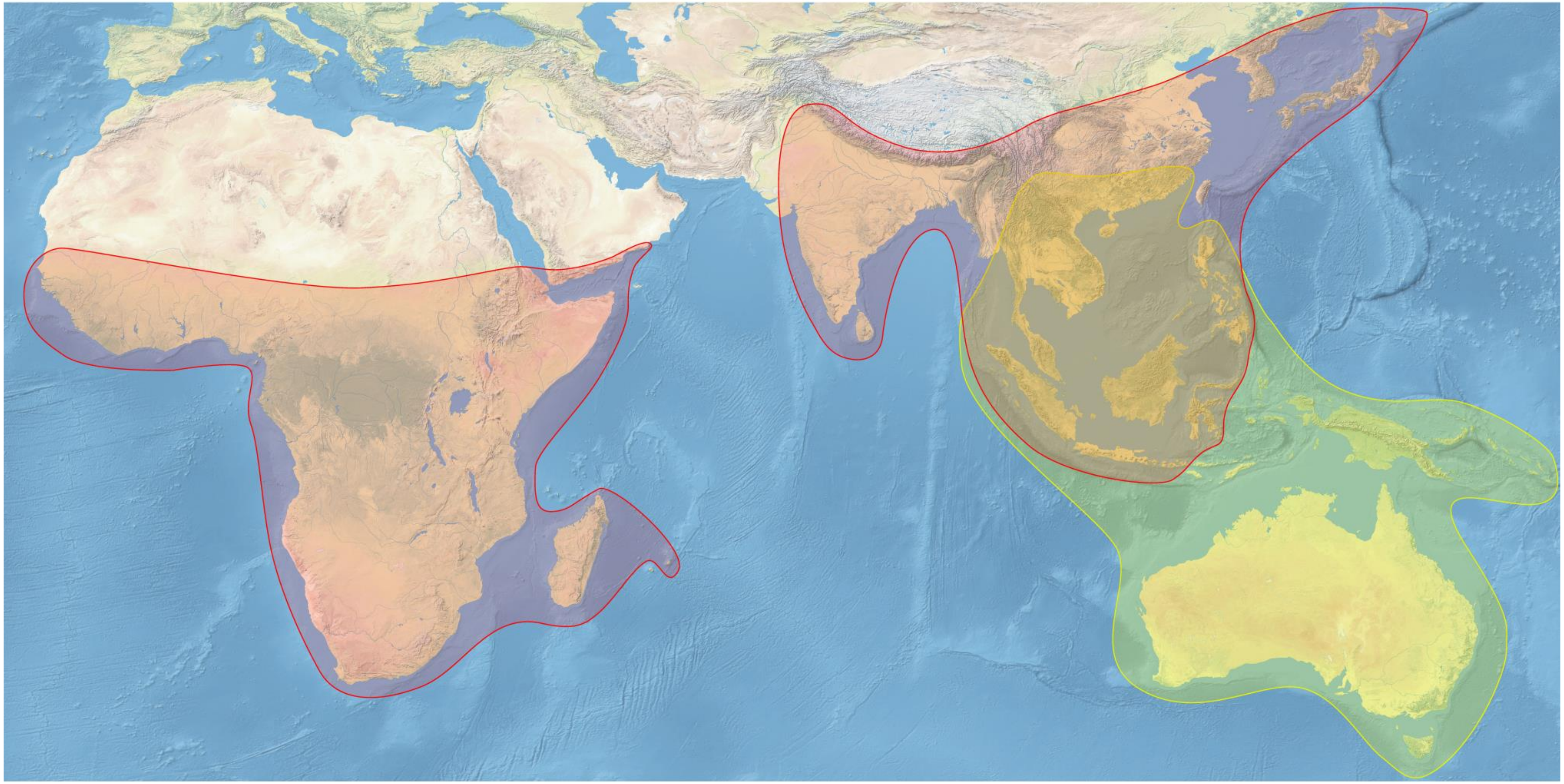

Figure 2. Distribution of Metriorrhynchina Kleine (yellow) and Cautirina Sklenarova et al. 2014 (reddish).

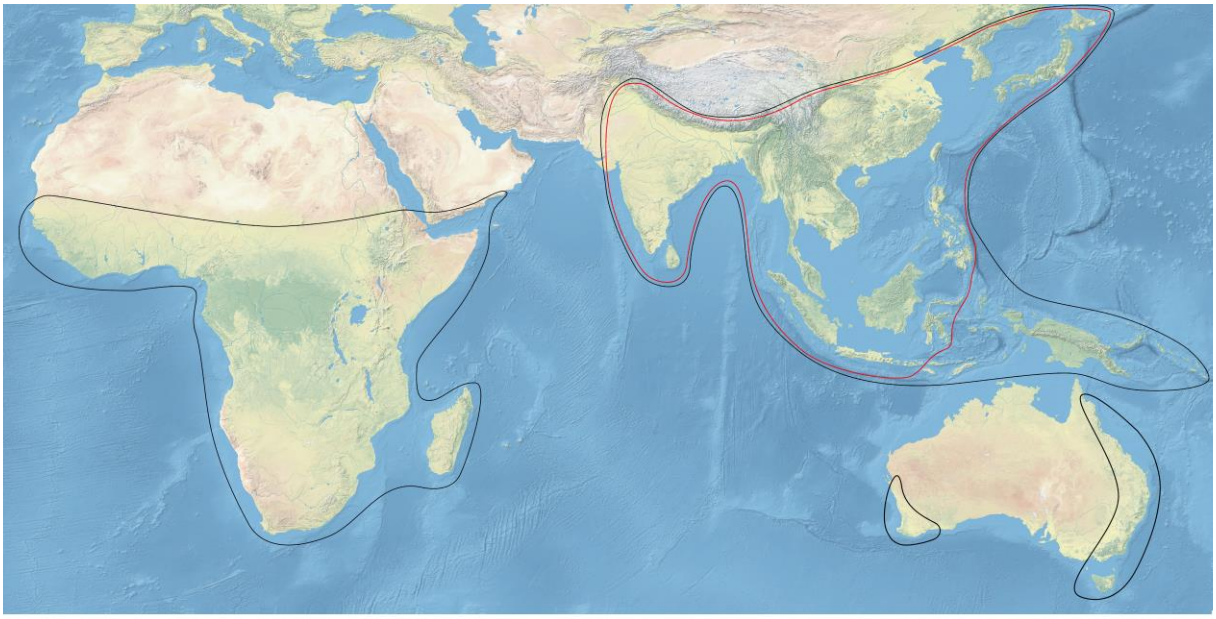

Figure 3. Distribution of *Xylobanus* Waterhouse recovered from catalogues and primary descriptions (black line) and from the analyzed molecular dataset (red line).

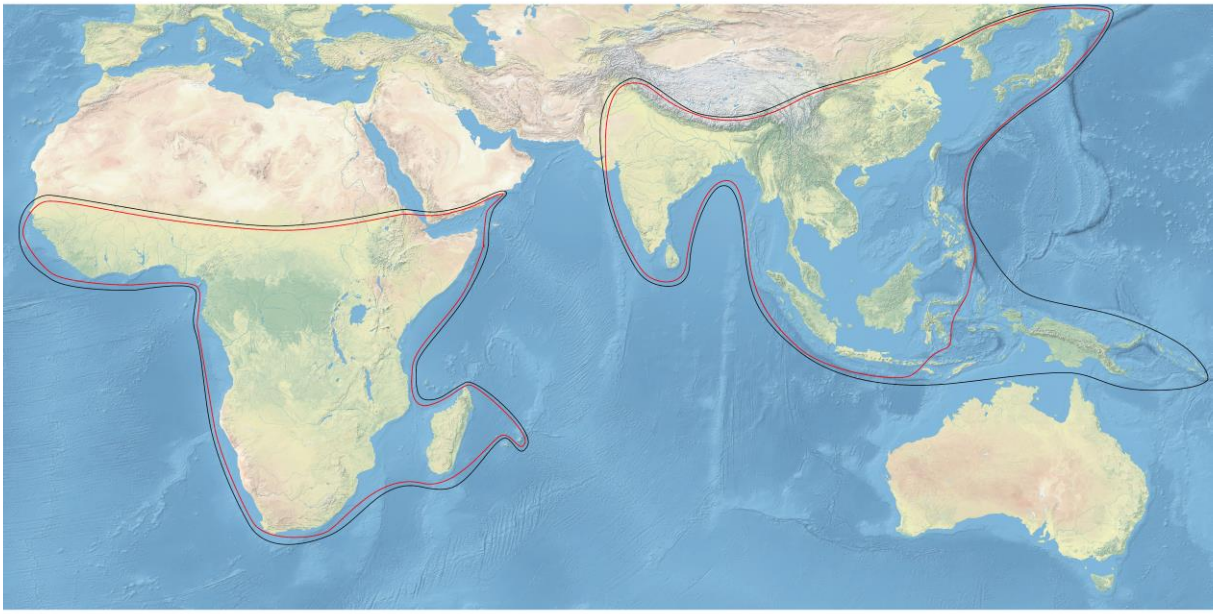

Figure 4. Distribution of *Cautires* Waterhouse recovered from catalogues and primary descriptions (black line) and from the analyzed molecular dataset (red line).

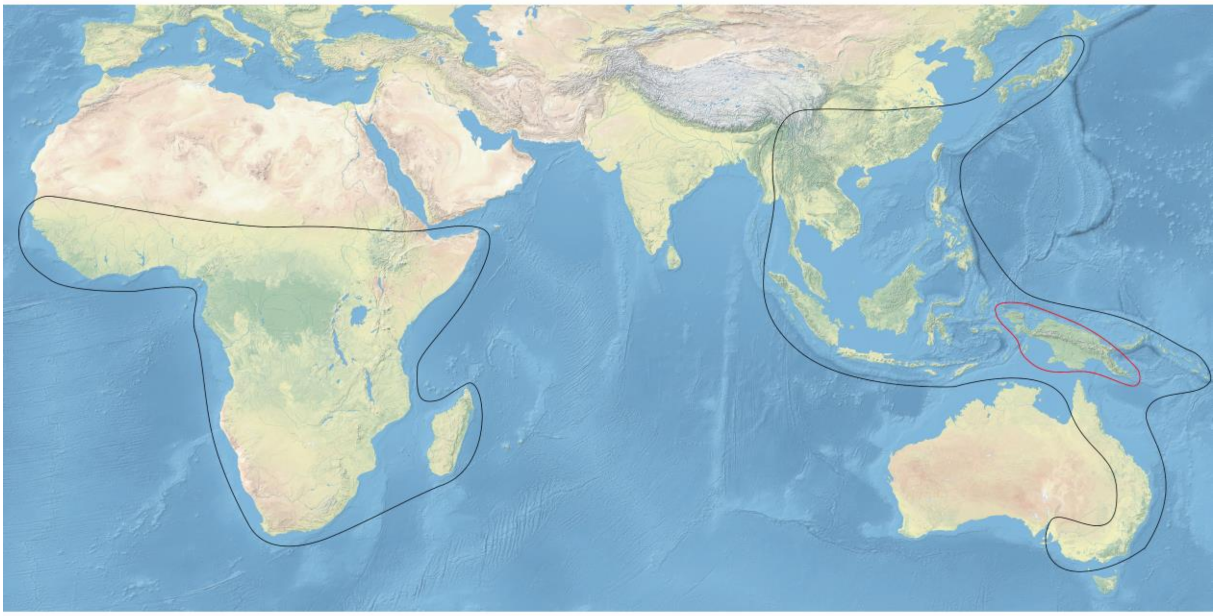

Figure 5. Distribution of *Cladophorus* Castelnau recovered from catalogues and primary descriptions (black line) and from the analyzed molecular dataset (red line).

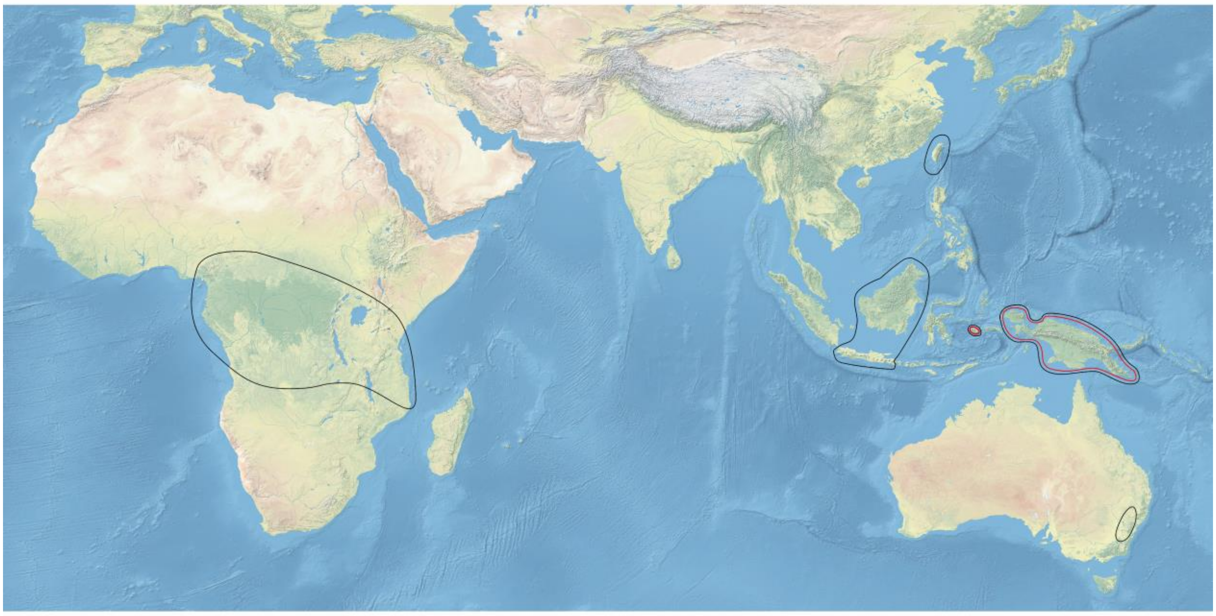

Figure 6. Distribution of *Procautires* Kleine recovered from catalogues and primary descriptions (black line) and from the analyzed molecular dataset (red line).

Supplementary Table S1. An overview of species classified in the genera *Cautire*s Waterhouse, *Xylobanus* Waterhouse and *Procautires* Kleine.
The original combinations rejected in the current study are given in **bold.**

Subtribe/genus	Species	Author, year	Distribution	Original classification
Cautirina Sklenarova *et al.* 2014				
Cautires Waterhouse, 1878				
Cautires	*adumbratus*	Kleine, 1926	Philippines	*Bulenides*
Cautires	*adventicius*	Kleine, 1926	Philippines	*Bulenides*
Cautires	*aethiops*	Kleine, 1933	Uganda	***Procautires***
Cautires	*aethiops*	Kleine, 1933	Tanganyika	*Cladophorus*
Cautires	*aethiops*	Kleine, 1930	DR Congo	
Cautires	*africaans*	Kazantsev, 2012	South Africa	
Cautires	*africaensis*	Bourgeois, 1902	South Africa	*Cladophorus*
Cautires	*africanus*	Pic, 1928	Cameroon	***Procautires***
Cautires	*africanus*	Kleine, 1930	DR Congo	
Cautires	*agrillosus*	Kleine, 1926	Borneo	*Bulenides*
Cautires	*alexae*	Jiruskova *et al*., 2016	Malaya	
Cautires	*alluaudi*	Bourgeois, 1902	Madagascar	***Xylobanus***
Cautires	*amamiensis*	Nakane, 1961	Japan	
Cautires	*ambrensis*	Pic, 1922	Madagascar	***Xylobanus***
Cautires	*anceyi*	Pic, 1928	West Africa	***Xylobanus***
Cautires	*andujari*	Jiruskova *et al*., 2016	Malaya	
Cautires	*angulatus*	Kluge, 1833	Madagascar	
Cautires	*angulicollis*	Pic, 1922	Madagascar	
Cautires	*angustatus*	Pic, 1922	Madagascar	***Xylobanus***
Cautires	*angustoareolatus*	Pic, 1942	Vietnam	***Cladophorus***
Cautires	*annulipes*	Pic, 1933	Congo	*Cladophorus*
Cautires	*anomalis*	Pic, 1928	Uganda	*Cladophorus*
Cautires	*apicalis*	Pic, 1928	Vietnam	
Cautires	*apicalis*	Kleine, 1926	Sierra Leone	
Cautires	*arcuatithorax*	Pic, 1922	Madagascar	***Xylobanus***
Cautires	*arens*	Kleine, 1926	Borneo	*Bulenides*
Cautires	*areolatus*	Pic, 1950	Madagascar	
Cautires	*aridus*	Kleine, 1926	Malaya	*Bulenides*
Cautires	*arribasae*	Jiruskova *et al*., 2016	Malaya	
Cautires	*asper*	Kleine, 1928	Borneo	
Cautires	*asperoides*	Kleine, 1932	Borneo	
Cautires	*astutus*	Walker, 1858	Sri Lanka	
Cautires	*ater*	Pic, 1921	Sumatra	*Bulenides*
Cautires	*aterrimus*	Kleine, 1926	Philippines	*Bulenides*
Cautires	*atricollis*	Pic, 1922	Congo	
Cautires	*atricolor*	Pic, 1922	Madagascar	***Xylobanus***
Cautires	*atricolor*	Pic, 1923	Vietnam	***Cladophorus***
Cautires	*atricornis*	Pic, 1922	Central Africa	***Xylobanus***
Cautires	*atrimembris*	Pic, 1928	Malawi	***Xylobanus***
Cautires	*atrimembris*	Pic, 1931	DR Congo	
Cautires	*atrithorax*	Pic, 1925	Ost-India	***Cladophorus***
Cautires	*atroapicalis*	Pic, 1939	Vietnam	***Cladophorus***
Cautires	*atrodiversus*	Pic, 1929	Vietnam	
Cautires	*atronotatus*	Pic, 1923	Vietnam	***Cladophorus***

Cautires	*atropunctatus*	Pic, 1921	Sumatra	***Cladophorus***
Cautires	*atropunctatus*	Pic, 1925	Palawan	*Bulenides*
Cautires	*baillyi*	Fairmaire, 1880	Madagascar	
Cautires	*bambesanus*	Kleine, 1940	DR Congo	***Procautires***
Cautires	*bannanus*	Nakane, 1980	Japan	
Cautires	*basalis*	Pic, 1925	Sumatra	*Bulenides*
Cautires	*basicornis*	Fairmaire, 1887	South Africa	
Cautires	*basilanus*	Pic, 1925	Philippines	*Bulenides*
Cautires	*basilewskii*	Pic, 1955	Rwanda	
Cautires	*basilewskyi*	Pic, 1955	Rwanda	***Xylobanus***
Cautires	*basilewskyi gitarama*	Pic, 1955	Rwanda	***Xylobanus***
Cautires	*basimaculatus*	Kleine, 1939	Burma	***Cladophorus***
Cautires	*berembanensis*	Jiruskova *et al*., 2016	Malaya	
Cautires	*biafrensis*	Bourgeois, 1905	Equatorial Guinea	
Cautires	*bicoloratus*	Kleine, 1930	Sumatra	*Bulenides*
Cautires	*bicoloratus*	Kleine, 1932	Borneo	
Cautires	*bidentatus*	Pic, 1925	Luzon	***Cladophorus***
Cautires	*binaluanus*	Pic, 1925	Palawan	***Cladophorus***
Cautires	*binhanus*	Pic, 1926	Vietnam	***Cladophorus***
Cautires	*binotatus*	Pic, 1922	Tropical Africa	
Cautires	*bogorensis*	Pic, 1922	Java	
Cautires	*bolivari*	Bourgeois, 1905	Equatorial Guinea	
Cautires	*bosanganus*	Pic, 1933	Congo	
Cautires	*bourgeoisi*	Nakane 1969	Japan	
Cautires	*bourgeoisi*	Fairmaire, 1901	Madagascar	
Cautires	*brazzai*	Pic, 1931	Congo	
Cautires	*brevenotatus*	Pic, 1922	Madagascar	
Cautires	*burgeoni*	Kleine, 1936	DR Congo	***Xylobanus***
Cautires	*calida*	Harold, 1879	South Africa	
Cautires	*cameroonus*	Kleine, 1930	West Africa	***Xylobanus***
Cautires	*campestris*	Jiruskova *et al*., 2016	Malaya	
Cautires	*carbonarius*	Bourgeois, 1898	Malaya	***Cladophorus***
Cautires	*carnoti*	Pic, 1922	Madagascar	
Cautires	*caroli*	Pic, 1925	East Africa	
Cautires	*castetsi*	Pic, 1925	Ost-India	***Cladophorus***
Cautires	*cautiroides*	Kleine, 1933	South Africa	*Cladophorus*
Cautires	*certus*	Kleine, 1926	Taiwan	***Cladophorus***
Cautires	*certus*	Kleine, 1930	DR Congo	
Cautires	*certus dahomeyensis*	Pic, 1952	Benin	
Cautires	*certus nigroapicalis*	Pic, 1953	Senegal	
Cautires	*chapuisi*	Kleine, 1935	Kenya	***Xylobanus***
Cautires	*chariensis*	Pic, 1931	Central Africa	
Cautires	*chatanayi*	Pic, 1922	Madagascar	
Cautires	*circamcinctus*	Bourgeois, 1902	Madagascar	
Cautires	*coarcticollis*	Bourgeois, 1908	East Africa	*Cladophorus*
Cautires	*coccineus*	Kleine, 1930	Malaya	*Bulenides*
Cautires	*cognatus*	Bourgeois, 1883	Java, Borneo	*Bulenides*
Cautires	*communis*	Jiruskova *et al*., 2016	Malaya	
Cautires	*concoloripennis*	Pic, 1933	Congo	
Cautires	*confusus*	Waterhouse, 1879	Congo	***Xylobanus***
Cautires	*congener*	Waterhouse, 1879	Malaya, Sumatra, Java, Timor	
Cautires	*congonus*	Kleine, 1930	DR Congo	
Cautires	*congruens*	Pic, 1929	Vietnam	***Cladophorus***

Cautires	*conicicollis*	Pic, 1922	Madagascar	
Cautires	*conicus*	Pic, 1922	Madagascar	***Xylobanus***
Cautires	*conradti*	Kleine, 1930	Cameroon	
Cautires	*constans*	Kleine, 1930	DR Congo	
Cautires	*coomani*	Pic, 1929	Vietnam	
Cautires	*coquereli*	Fairmaire, 1869	Madagascar	
Cautires	*cordicollis*	Pic, 1931	Uganda	*Cladophorus*
Cautires	*coronarius*	Kleine, 1926	Philippines	
Cautires	*corporaali*	Pic, 1921	Sumatra	***Cladophorus***
Cautires	*corporaali*	Pic, 1921	Java, Sumatra	*Bulenides*
Cautires	*costulatus*	Kleine, 1930	DR Congo	
Cautires	*curtenotatus*	Pic, 1924	Fernando Poo	
Cautires	*curticornis*	Pic, 1928	Erythrea	*Cladophorus*
Cautires	*cyaneiceps*	Pic, 1923	Jolo	***Cladophorus***
Cautires	*dalmani*	Bourgeois, 1908	Tanzania	
Cautires	*dembickyi*	Dudkova & Bocak, 2010	India	
Cautires	*destrictus*	Kleine, 1927	Madagascar	***Xylobanus***
Cautires	*devotus*	Kleine, 1927	East Africa	***Xylobanus***
Cautires	*dichrocerus*	Bourgeois, 1889	West Africa	
Cautires	*dichrous*	Fairmaire, 1893	Comores	
Cautires	*differens*	Kleine, 1929	Sri Lanka	
Cautires	*difficilis*	Kleine, 1927	Uganda	***Xylobanus***
Cautires	*diffusus*	Kleine, 1933	Uganda	***Xylobanus***
Cautires	*dilucidus*	Kleine, 1926	Tropical Africa	
Cautires	*dilucidus burgeoni*	Pic, 1933	Congo	
Cautires	*dimidius*	Kleine, 1926	South Africa	
Cautires	*discoidalis*	Kleine, 1926	Uganda	
Cautires	*discolor*	Kleine, 1926	Sumatra	*Bulenides*
Cautires	*discolor*	Kleine, 1926	South Africa	
Cautires	*discordans*	Kleine, 1929	India	
Cautires	*discors*	Kleine, 1926	Congo, Uganda	
Cautires	*disjunctus*	Kleine, 1926	Congo, Uganda	
Cautires	*dissentaneus*	Kleine, 1929	Borneo	
Cautires	*diversesculptus*	Pic, 1922	Cameroon	
Cautires	*diversipes*	Pic, 1931	Cameroon	
Cautires	*diversithorax*	Pic, 1922	Gabon	
Cautires	*dohrni*	Fairmaire, 1869	Madagascar	
Cautires	*dolens*	Bourgeois, 1902	Madagascar	
Cautires	*dolosus*	Kleine, 1929	Sri Lanka	
Cautires	*donckieri*	Pic, 1922	Congo	***Xylobanus***
Cautires	*dondonensis*	Harold, 1879	Tropical West Africa	
Cautires	*drescheri*	Kleine, 1931	Java	
Cautires	*dubiosus*	Kleine, 1933	Uganda	*Cladophorus*
Cautires	*dubius*	Waterhouse, 1879	Borneo	*Bulenides*
Cautires	*duplicatus*	Kleine, 1928	Borneo	*Bulenides*
Cautires	*egenus*	Kleine, 1939	Sumatra	
Cautires	*elongatissimus*	Kleine, 1935	Central Africa	
Cautires	*excellens*	Waterhouse, 1879	Borneo, Java, Sumatra	
Cautires	*exploratus*	Kleine, 1926	Philippines	
Cautires	*exsertus*	Kleine, 1926	Angola, Sierra Leone	
Cautires	*fainanensis*	Pic, 1925	Taiwan	
Cautires	*fairmairei*	Bourgeois, 1902	Madagascar	
Cautires	*favosus*	Gerst. 1871	East Africa	*Cladophorus*

Cautires	*feai*	Pic, 1924	Guinea	***Xylobanus***
Cautires	*feai*	Pic, 1924	Fernando Poo	
Cautires	*fehsei*	Kleine, 1939	Sumatra	
Cautires	*flabellatus*	Pic, 1953	Madagascar	***Xylobanus***
Cautires	*flabellatus*	Pic, 1932	Africa	***Procautires***
Cautires	*flavipennis*	Kleine, 1930	DR Congo	
Cautires	*flavofemoralis*	Kleine, 1930	DR Congo	
Cautires	*flavoreticulatus*	Kleine, 1932	Borneo	*Bulenides*
Cautires	*fortesculptus*	Pic, 1939	Laos	***Cladophorus***
Cautires	*fragilis*	Kleine, 1926	Philippines	***Cladophorus***
Cautires	*fratellus*	Bourgeois, 1902	Madagascar	***Xylobanus***
Cautires	*furcatus*	Bourgeois, 1900	Ghana	***Xylobanus***
Cautires	*fuscopubens*	Pic, 1922	Madagascar	
Cautires	*fuscoreticulatus*	Kleine, 1933	Borneo	***Procautires***
Cautires	*gestroi*	Pic, 1924	Fernando Poo	
Cautires	*gorhami*	Pic, 1922	Madagascar	
Cautires	*goudoti*	Bourgeois, 1908	Madagascar	***Xylobanus***
Cautires	*gowdeyi*	Kleine, 1926	Uganda	
Cautires	*gracilis*	Kleine, 1930	DR Congo	
Cautires	*grandissimus*	Kleine, 1926	Java	
Cautires	*granulosus*	Pic, 1922	Madagascar	
Cautires	*griseus*	Kleine, 1930	Malaya	
Cautires	*guttatus*	Kleine, 1931	Java	
Cautires	*hergovitsi*	Dudkova & Bocak, 2010	Laos	
Cautires	*hilaris*	Kleine, 1939	Sumatra	
Cautires	*hoanus*	Pic, 1926	Vietnam	***Cladophorus***
Cautires	*hoanus dallieri*	Pic, 1939	Vietnam	***Cladophorus***
Cautires	*holomelas*	Fairm. 1885	Madagascar	
Cautires	*hulstaerti*	Kleine, 1935	DR Congo	*Cladophorus*
Cautires	*hyonosen*	Nakane, 1969	Japan	
Cautires	*imitator*	Kleine, 1930	Malaya	*Bulenides*
Cautires	*impressicollis*	Kleine, 1926	Tanzania	
Cautires	*inaequalis*	Pic, 1928	Cameroon	*Cladophorus*
Cautires	*inapicalis*	Pic, 1928	Uganda	***Xylobanus***
Cautires	*inapicalis*	Pic, 1926	Vietnam	***Cladophorus***
Cautires	*inapicalis*	Pic, 1929	Vietnam	*Bulenides*
Cautires	*inapicalis*	Pic, 1922	Cameroon	
Cautires	*incompletus*	Pic, 1939	Yunnan	***Cladophorus***
Cautires	*incompositus*	Ohbayashi, 1954	Japan	***Cladophorus***
Cautires	*incorruptus*	Kleine, 1929	India, Burma, Thailand	
Cautires	*indus*	Kirsch 1875	Malaya, Sumatra, Borneo,	*Bulenides*
Cautires	*indus*	Kleine, 1929	India	
Cautires	*inflatellus*	Bourgeois, 1889	Ethiopia	
Cautires	*ingeniculatus*	Pic, 1922	Gabon	
Cautires	*inhumeralis*	Pic, 1925	Bogor	*Bulenides*
Cautires	*irregularis*	Pic, 1926	Fernando Poo	*Cladophorus*
Cautires	*irregularis*	Kleine, 1926	Cameroon	
Cautires	*ivoirensis*	Pic, 1947	Ivory Coast	***Xylobanus***
Cautires	*jacobsoni*	Kleine, 1926	Sumatra	
Cautires	*jasarensis*	Jiruskova *et al*., 2016	Malaya	
Cautires	*javanicus*	Bourgeois, 1883	Java	*Bulenides*
Cautires	*javanicus*	Kleine, 1926	Java	
Cautires	*jeanneli*	Kleine, 1935	Kenya	

Cautires	*jeanvoinei*	Pic, 1939	Vietnam	***Cladophorus***
Cautires	*jendeki*	Dudkova & Bocak, 2010	Laos	
Cautires	*jokoensis*	Pic, 1931	Cameroon	
Cautires	*karnyi*	Kleine, 1931	Sumatra	***Cladophorus***
Cautires	*katarinae*	Jiruskova *et al*., 2016	Malaya	
Cautires	*katoi*	Nakane, 1969	Taiwan	
Cautires	*kazuoi*	Sato & Ohbayashi, 1968	Loochoos	
Cautires	*kilimanus*	Bourgeois, 1908	Tanzania	
Cautires	*kinabalensis*	Kleine, 1932	Borneo	
Cautires	*kirstenae*	Jiruskova *et al*., 2016	Malaya	
Cautires	*kisibanus*	Pic, 1925	Uganda	***Xylobanus***
Cautires	*kleinei*	Pic, 1926	Sumatra, Halmahera	
Cautires	*klugi*	fairm. 1869	Mauritius, Madagascar	
Cautires	*kotatinggensis*	Jiruskova *et al*., 2016	Malaya	
Cautires	*kundratai*	Dudkova & Bocak, 2010	Thailand	
Cautires	*kurilensis*	Medvedev, 1966	Kuriles	***Cladophorus***
Cautires	*laboisieri*	Pic, 1925	Vietnam	***Cladophorus***
Cautires	*lamellatus*	Kleine, 1930	DR Congo	
Cautires	*laosensis*	Pic, 1926	Laos	***Cladophorus***
Cautires	*lateauxensis*	Pic, 1952	Benin	
Cautires	*latefenestratus*	Pic, 1939	Laos	***Cladophorus***
Cautires	*lateniger*	Pic, 1922	Tanzania	
Cautires	*laticollis*	Pic, 1926	Laos	***Cladophorus***
Cautires	*latior*	Pic, 1925	Sri Lanka	
Cautires	*latithorax*	Bourgeois, 1889	Cameroon, Nigeria	
Cautires	*legitimus*	Kleine, 1926	Thailand	
Cautires	*leonensis*	Pic, 1922	Sierra Leone	***Xylobanus***
Cautires	*leonensis*	Pic, 1928	Sierra Leone	*Cladophorus*
Cautires	*liberianus holasi*	Pic, 1949	Liberia	
Cautires	*linardi*	Jiruskova *et al*., 2016	Malaya	
Cautires	*lineatus*	Pic, 1921	Java	*Bulenides*
Cautires	*lineatus*	Hope, 1831	Sri Lanka	
Cautires	*longeareolatus*	Kleine, 1936	Java	*Bulenides*
Cautires	*longipennis*	Pic, 1931	Congo	***Xylobanus***
Cautires	*longissimus*	Pic, 1921	Sumatra	*Bulenides*
Cautires	*longithorax*	Kleine, 1926	Cameroon	
Cautires	*luchti*	Kleine, 1933	Java	
Cautires	*luteopubens*	Pic, 1955	Rwanda	***Procautires***
Cautires	*lyciformis*	Kleine, 1932	Borneo	*Bulenides*
Cautires	*lyciformis*	Pic, 1922	East Africa	
Cautires	*macer*	Bourgeois, 1889	Cameroon, Ethiopia	
Cautires	*maculatithorax*	Pic, 1924	Fernando Poo	
Cautires	*maculatithorax*	Kleine, 1930	DR Congo, Rwanda	
Cautires	*madecassus*	Pic, 1923	Madagascar	
Cautires	*maindroni*	Pic, 1925	India	***Cladophorus***
Cautires	*malayaensis*	Jiruskova *et al*., 2016	Malaya	
Cautires	*malayensis*	Kleine, 1930	Malaya	*Bulenides*
Cautires	*marshalli*	Kleine, 1933	South Africa	*Cladophorus*
Cautires	*maseki*	Jiruskova *et al*., 2016	Malaya	
Cautires	*matsudai*	Dudkova & Bocak, 2010	Thailand	
Cautires	*melanogaster*	Kleine, 1928	Borneo	
Cautires	*melanopteryx*	Kleine, 1926	Tanzania	
Cautires	*miniatipennis*	Bourgeois, 1888	India	

Cautires	*minimus*	Pic, 1928	Cameroon	
Cautires	*minor*	Pic, 1929	Vietnam	
Cautires	*minutus*	Pic, 1922	Madagascar	
Cautires	*mirandus*	Kleine, 1929	Burma	
Cautires	*mocquerysi*	Pic, 1922	Gabon	***Xylobanus***
Cautires	*mocquerysi*	Pic, 1931	Gabon	
Cautires	*modulatus*	Kleine, 1931	Java	
Cautires	*montanus*	Kleine, 1933	Uganda	***Procautires***
Cautires	*monticola*	Kleine, 1928	Borneo	***Cladophorus***
Cautires	*nakanei*	Winkler, 1953	Japan	***Cladophorus***
Cautires	*nakanei yakushimanus*	Nakane, 1969	Japan	
Cautires	*nanus*	Kleine, 1933	Cameroon	*Cladophorus*
Cautires	*nebulosus*	Kleine, 1930	Malaya	*Bulenides*
Cautires	*nepos*	Kleine, 1926	Java	
Cautires	*nervosus*	Kleine, 1926	Malaya	
Cautires	*nigricollis*	Bourgeois, 1906	Tanzania	***Xylobanus***
Cautires	*nigricollis*	Kleine, 1935	DR Congo	
Cautires	*nigricollis*	Pic, 1953	Fernando Poo	
Cautires	*nigricolor*	Pic, 1925	Sumatra	*Bulenides*
Cautires	*nigricolor*	Pic, 1922	Madagascar	
Cautires	*nigricornis*	Pic, 1928	Uganda	*Cladophorus*
Cautires	*nigripes*	Bourgeois, 1906	Tanzania	***Xylobanus***
Cautires	*nigrithorax*	Pic, 1928	South Africa	*Cladophorus*
Cautires	*nigroapicalis*	Kleine, 1931	Java	***Cladophorus***
Cautires	*nigroareolatus*	Pic, 1942	Vietnam	***Cladophorus***
Cautires	*nigrocarinatus*	Pic, 1922	Gabon	
Cautires	*nigromaculatus*	Pic, 1925	Java	*Bulenides*
Cautires	*nigronotatus*	Kleine, 1926	Uganda	
Cautires	*nigropallidus*	Kleine, 1928	Borneo	***Cladophorus***
Cautires	*nigrostriatus*	Kleine, 1929	Sikkim	
Cautires	*nodosus*	Kleine, 1926	Thailand	
Cautires	*notabilis*	Fahrens, 1833	South Africa	*Cladophorus*
Cautires	*notabllis*	Kleine, 1928	Thailand	
Cautires	*notaticeps*	Pic, 1928	Gabon	*Cladophorus*
Cautires	*notatithorax*	Pic, 1923	Vietnam	***Cladophorus***
Cautires	*nyassicus*	Kleine, 1933	Malawi	*Cladophorus*
Cautires	*obconicus*	Pic, 1922	Madagascar	
Cautires	*obliteratus*	Pic, 1925	Palawan	***Cladophorus***
Cautires	*obscurithorax*	Pic, 1931	Congo	
Cautires	*obsoletus*	Waterhouse, 1878	Sumatra, Borneo, Java	*Bulenides*
Cautires	*obsoletus*	Kleine, 1926	Java	
Cautires	*obtusatus*	Bourgeois, 1902	Madagascar	
Cautires	*ochraceipennis*	Kleine, 1930	DR Congo	
Cautires	*ocularis*	Bourgeois, 1882	Trop.s West Afrca	
Cautires	*opacicollis*	Kleine, 1930	DR Congo	
Cautires	*orientalis*	Waterhouse, 1878	Indochina	***Cladophorus***
Cautires	*ornaticollis*	Bourgeois, 1892	Thailand	***Cladophorus***
Cautires	*pajanicus*	Kleine, 1928	Borneo	
Cautires	*pallens*	Kleine, 1926	Cameroon	
Cautires	*pallidicolor*	Kleine, 1930	Cameroon	***Xylobanus***
Cautires	*paraimitator*	Jiruskova & Bocak, 2015	Malaya	
Cautires	*parallelipennis*	Pic, 1939	Vietnam	
Cautires	*parallelus*	Jiruskova & Bocak, 2015	Malaya	

Cautires	*particularis*	Pic, 1926	Vietnam	***Cladophorus***
Cautires	*particularithorax*	Pic, 1925	Vietnam	***Cladophorus***
Cautires	*parvulus*	Kleine, 1926	Philippines	*Bulenides*
Cautires	*patrizii*	Pic, 1926	Guinea-Bissau	***Xylobanus***
Cautires	*pauliani*	Pic, 1953	Madagascar	
Cautires	*pauper*	Waterhouse, 1879	Malaya, Sumatra	*Bulenides*
Cautires	*pauperulus*	Bourgeois, 1883	Great Sundas, Malaya	*Bulenides*
Cautires	*pectinatus*	Bourgeois, 1892	Tanzania	*Cladophorus*
Cautires	*pentagonus*	Bourgeois, 1889	West Africa	***Xylobanus***
Cautires	*pentagonus*	Kleine, 1926	South & Tropical Africa	
Cautires	*philippinensis*	Kleine, 1930	Philippines	*Bulenides*
Cautires	*pilosus*	Kleine, 1935	Central Africa	***Procautires***
Cautires	*planatus*	Kleine, 1926	Borneo	***Cladophorus***
Cautires	*pluto*	Bourgeois, 1908	Madagascar	***Xylobanus***
Cautires	*politus*	Kleine, 1935	DR Congo	
Cautires	*postmaculatus*	Kleine, 1926	India	
Cautires	*pouilloni*	Pic, 1922	Madagascar	
Cautires	*prescutellaris*	Pic, 1928	Uganda	*Cladophorus*
Cautires	*prominulithorax*	Pic, 1931	Vietnam	***Cladophorus***
Cautires	*prophanus*	Kleine, 1943	East Africa	
Cautires	*pudicus*	Kleine, 1931	Java	*Bulenides*
Cautires	*pulcher*	Kleine, 1926	Java	
Cautires	*purpureus*	Pic, 1922	Burma, Taiwan, India	*Bulenides*
Cautires	*pusillus*	Kleine, 1926	Cameroon	
Cautires	*rarus*	Kleine, 1929	Assam	
Cautires	*ratus*	Kleine, 1929	Assam	
Cautires	*reductus*	Pic, 1928	Uganda	*Cladophorus*
Cautires	*reductus*	Pic, 1922	Madagascar	
Cautires	*reflexicollis*	fairm. 1887	Madagascar	
Cautires	*regalis*	Kleine, 1929	Indien	*Bulenides*
Cautires	*renatae*	Jiruskova *et al*., 2016	Malaya	
Cautires	*reticulatus*	Kleine, 1930	Philippines	*Bulenides*
Cautires	*reticulatus*	Kleine, 1930	DR Congo	
Cautires	*reverandi*	Pic, 1925	Malaya	***Cladophorus***
Cautires	*rianganus*	Pic, 1925	Sumatra	*Bulenides*
Cautires	*ribottii*	Pic, 1926	Congo	*Cladophorus*
Cautires	*rivalis*	Kleine, 1935	Centr. Africa	***Procautires***
Cautires	*robustithorax*	Kleine, 1926	Uganda	
Cautires	*robustus*	Pic, 1931	Cameroon	
Cautires	*roepkei*	Kleine, 1931	Java	
Cautires	*rouyeri*	Pic, 1921	Sumatra	***Cladophorus***
Cautires	*ruandanus*	Pic, 1955	Rwanda	
Cautires	*rubricollis*	Pic, 1953	Madagascar	
Cautires	*rubromarginatus*	Kleine, 1926	Hainan	
Cautires	*rudeplicatus*	Pic, 1925	Sikkim	***Cladophorus***
Cautires	*rufus*	Fairmaire, 1896	Mayotte	
Cautires	*ruwenzorensis*	Kleine, 1935	DR Congo	
Cautires	*salatiganus*	Kleine, 1931	Java	
Cautires	*salubris*	Kleine, 1940	DR Congo	
Cautires	*salvazai*	Pic, 1929	Laos	***Cladophorus***
Cautires	*satanas*	Bourgeois, 1906	Borneo	***Cladophorus***
Cautires	*satrapa*	Bourgeois, 1905	Bangladesh	***Cladophorus***
Cautires	*schoutedeni*	Kleine, 1930	DR Congo	

Cautires	*scutellaris*	Pic, 1922	Madagascar	
Cautires	*selangorensis*	Kleine, 1930	Malaya	
Cautires	*semiflabellatus*	Thoms, 1858	Tropical West Africa	***Xylobanus***
Cautires	*semifumosus*	Pic, 1939	Indochina	
Cautires	*semiustus*	Kleine, 1939	Borneo	
Cautires	*seydeli*	Kleine, 1930	DR Congo	
Cautires	*sibutensis*	Pic, 1922	Central Africa	***Xylobanus***
Cautires	*sibutensis*	Pic, 1922	Central Africa	
Cautires	*sijthoffi*	Kleine, 1926	Java, Andamans	*Bulenides*
Cautires	*sikorai*	Pic, 1922	Madagascar	
Cautires	*silvestri*	Pic, 1926	Guinea	*Cladophorus*
Cautires	*similis*	Kleine, 1926	Cameroon	
Cautires	*simillimus*	Kleine, 1926	Malaya	
Cautires	*simulans*	Kleine, 1926	Tanzania	
Cautires	*sinensis*	Pic, 1925	China	***Cladophorus***
Cautires	*singularicollis*	Pic, 1925	Taiwan	***Cladophorus***
Cautires	*singularithorax*	Pic, 1925	Java	*Bulenides*
Cautires	*slamatensis*	Kleine, 1931	Java	
Cautires	*socius*	Kleine, 1926	Taiwan	***Procautires***
Cautires	*solutus*	Kleine, 1939	Borneo	***Cladophorus***
Cautires	*sublineatus*	Pic, 1922	Borneo	
Cautires	*subnitidus*	Pic, 1922	Madagascar	
Cautires	*subparallelus*	Pic, 1932	DR Congo	***Procautires***
Cautires	*subrecticollis*	Pic, 1922	Madagascar	
Cautires	*sulcicollis*	Thomson 1858	Tropical Africa	
Cautires	*sulcicollis miokoens*	Pic, 1953	Fernando Poo	
Cautires	*sumatrensis*	Pic, 1922	Sumatra	
Cautires	*taeniatus*	Bourgeois, 1902	Madagascar	*Cladophorus*
Cautires	*takakurai*	Nakane, 1980	Japan	
Cautires	*tanahratensis*	Jiruskova & Bocak, 2015	Malaya	
Cautires	*tananarivanus*	Pic, 1922	Madagascar	***Xylobanus***
Cautires	*tananarivanus*	Pic, 1922	Madagascar	
Cautires	*tanganensis*	Pic, 1922	East Africa	
Cautires	*tapahensis*	Jiruskova & Bocak, 2015	Malaya	
Cautires	*tenebricus*	Kleine, 1930	Malaya	
Cautires	*testaceicolor*	Pic, 1926	Fernando Poo	*Cladophorus*
Cautires	*testaceopunctatus*	Pic, 1921	Java	***Cladophorus***
Cautires	*testaceus*	Pic, 1921	Laos, Malaya, Burma, India	*Bulenides*
Cautires	*theresae*	Pic, 1928	Uganda	*Cladophorus*
Cautires	*thoracicus*	Kleine, 1932	Borneo	
Cautires	*togoensis*	Pic, 1952	Togo	
Cautires	*torquatus*	Klug 1832-33	Madagascar	
Cautires	*triangularis*	Kleine, 1930	Borneo	*Bulenides*
Cautires	*tricarinatus*	Pic, 1950	Madagascar	
Cautires	*turbidus*	Waterhouse, 1879	Sumatra	*Bulenides*
Cautires	*ugandanus*	Kleine, 1930	Uganda, Ruwenzori	***Xylobanus***
Cautires	*uniareolatus*	Pic, 1931	Congo	***Xylobanus***
Cautires	*vicinus*	Pic, 1928	Uganda	***Xylobanus***
Cautires	*vitalisi*	Pic, 1923	Vietnam	***Cladophorus***
Cautires	*voeltzkowi*	Bourgeois, 1908	Comoren, Madagascar	***Xylobanus***
Cautires	*wittmeri*	Pic, 1950	Madagascar	
Cautires	*xanthomerus*	Bourgeois, 1889	Ethiopia	***Xylobanus***
Cautires	*yuasai*	Nakane, 1969	Japan	

Cautires	*yunnanus*	Dudkova & Bocak, 2010	China	
Cautires	*zahradniki*	Winkler, 1953	Japan	***Cladophorus***

Xylobanus Waterhouse, 1878

Xylobanus	*alveolus*	Bourgeois, 1885	Burma
Xylobanus	*amandus*	Kleine, 1927	Java
Xylobanus	*angusticollis*	Motschoulsky, 1860	Siberia
Xylobanus	*angustior*	Pic, 1922	Sulawesi
Xylobanus	*approximans*	Bourgeois, 1885	Burma, India
Xylobanus	*assimilis*	Kleine, 1927	Borneo
Xylobanus	*aterrimus*	Kleine, 1926	Malaya
Xylobanus	*atricollis*	Gorham, 1895	India
Xylobanus	*atripennis*	Pic, 1935	Sumatra
Xylobanus	*atritarsis*	Pic, 1922	Lombok
Xylobanus	*attenuaticollis*	Pic, 1922	Java
Xylobanus	*bakeri*	Kleine, 1927	Philippines
Xylobanus	*barbarus*	Kleine, 1926	Philippines
Xylobanus	*basilensis*	Kleine, 1926	Philippines
Xylobanus	*basivittatus*	Nakane, 1969	Japan
Xylobanus	*beesoni*	Kleine, 1929	Burma
Xylobanus	*bellus*	Kleine, 1926	Philippines
Xylobanus	*beneficus*	Kleine, 1929	Vietnam
Xylobanus	*benignus*	Kleine, 1926	Philippines
Xylobanus	*biandus*	Kleine, 1926	Philippines
Xylobanus	*bicoloratus*	Kleine, 1926	Philippines
Xylobanus	*binhanus*	Pic, 1925	Vietnam
Xylobanus	*bogorensis*	Pic, 1922	Java
Xylobanus	*brevenotatus*	Pic, 1922	Sumatra
Xylobanus	*brevis*	Kleine, 1926	Philippines
Xylobanus	*bulenoides*	Kleine, 1926	Borneo
Xylobanus	*caelestis*	Kleine, 1926	Philippines
Xylobanus	*callosus*	Kleine 1939	Malaya
Xylobanus	*callosus*	Kleine, 1943	Malaya
Xylobanus	*canaliculatus*	Kleine, 1926	Philippines
Xylobanus	*candidus*	Kleine, 1926	Philippines
Xylobanus	*cantus*	Kleine, 1926	Borneo
Xylobanus	*captiosus*	Kleine, 1927	Java
Xylobanus	*cardoni*	Bourgeois, 1905	Bangladesh
Xylobanus	*castigatus*	Kleine, 1926	Sumatra
Xylobanus	*causarius*	Kleine, 1929	Malaya
Xylobanus	*celebicus*	Kleine, 1927	Sulawesi
Xylobanus	*celebratus*	Kleine, 1926	Sumatra
Xylobanus	*chinensis*	Kleine, 1927	Hainan
Xylobanus	*cinnabarinus*	Kleine, 1926	Sumatra
Xylobanus	*coenosus*	Lea, 1898	Bomeo
Xylobanus	*cognatus*	Kleine, 1928	Borneo
Xylobanus	*congoanus*	Pic, 1933	Sumatra
Xylobanus	*conjunctus*	Kleine, 1926	Borneo
Xylobanus	*consentaneus*	Kleine, 1926	Philippines
Xylobanus	*consimilis*	Kleine, 1926	Philippines
Xylobanus	*consobrinus*	Kleine, 1926	Philippines
Xylobanus	*consociatus*	Kleine, 1926	Philippines

Xylobanus	*contrarius*	Kleine, 1932	Borneo
Xylobanus	*coomani*	Pic, 1926	Vietnam
Xylobanus	*corporaali*	Pic, 1922	Sumatra, Java
Xylobanus	*costifer*	Walker, 1858	Sri Lanka
Xylobanus	*differens*	Pic, 1922	Sumatra
Xylobanus	*dimidiatus*	Gorham, 1882	Sumatra, Java
Xylobanus	*diversepunctatus*	Pic, 1923	Laos
Xylobanus	*diversicollis*	Pic, 1922	Sumatra
Xylobanus	*dohertyi*	Pic, 1922	Sulawesi
Xylobanus	*drescheri*	Kleine, 1927	Bali
Xylobanus	*electus*	Kleine, 1939	Burma
Xylobanus	*elongatus*	Bourgeois, 1883	Java
Xylobanus	*elusus*	Waterhouse, 1879	Borneo
Xylobanus	*fastidiosus*	Waterhouse, 1879	Himalayas, Thailand, Laos
Xylobanus	*fenestratus*	Pic, 1922	Sumatra, Borneo
Xylobanus	*ferreus*	Kleine, 1939	Sulawesi
Xylobanus	*flabellicornis*	Pic, 1922	Sumatra
Xylobanus	*foveatus*	Waterhouse, 1879	India
Xylobanus	*fractus*	Kleine, 1926	Borneo
Xylobanus	*fragilis*	Kleine, 1926	Philippines
Xylobanus	*fumigatus*	Waterhouse, 1879	Sumatra, Java, Borneo
Xylobanus	*goentoerensis*	Kleine, 1926	Java
Xylobanus	*grandicornis*	Pic, 1942	Vietnam
Xylobanus	*gratiosus*	Waterhouse, 1879	Java, Andamanes
Xylobanus	*hirtus*	Kleine, 1929	Sri Lanka
Xylobanus	*honestus*	Kleine, 1927	Sumbawa
Xylobanus	*horrendus*	Kleine, 1926	Java
Xylobanus	*humerifer*	F. Walker, 1858	Sri Lanka
Xylobanus	*humilis*	Waterhouse, 1879	Malaya, Borneo
Xylobanus	*ignitus*	Kleine, 1924	Sumatra
Xylobanus	*incertus*	Kleine, 1929	Burma, Assam
Xylobanus	*indicus*	Pic, 1922	India
Xylobanus	*indutus*	Waterhouse, 1879	Sumatra
Xylobanus	*intricatus*	Waterhouse, 1879	Java
Xylobanus	*longereticulatus*	Kleine, 1932	Borneo
Xylobanus	*irregularis*	Pic, 1923	Vietnam
Xylobanus	*luzonicus*	Pic, 1926	Luzon
Xylobanus	*japonicus*	Bourgeois, 1902	Japan
Xylobanus	*javanus*	Pic, 1922	Java
Xylobanus	*kunashirensis*	Medvedev, 1966	Kuriles, Japan
Xylobanus	*lanatus*	Kleine, 1926	Philippines
Xylobanus	*laosensis*	Pic, 1926	Laos
Xylobanus	*latefenestratus*	Pic, 1922	Sumatra
Xylobanus	*latefoveolatus*	Pic, 1925	Sumatra
Xylobanus	*leechi*	Nakane, 1971	Taiwan
Xylobanus	*longissimus*	Pic, 1922	Sulawesi
Xylobanus	*longus*	Pic, 1922	Java
Xylobanus	*mancus*	Kleine, 1933	Philippines
Xylobanus	*marginecinctus*	Kleine, 1931	Java
Xylobanus	*martapuranus*	Pic, 1922	Borneo
Xylobanus	*martopuranus*	Pic, 1935	Sumatra
Xylobanus	*mjobergi*	Kleine, 1928	Borneo
Xylobanus	*montanus*	Kleine, 1929	Burma

Xylobanus	*multiareolatus*	Pic, 1927	Indochina
Xylobanus	*niger*	Ohbayashi, 1954	Japan
Xylobanus	*nigricolor*	Pic, 1922	Sulawesi
Xylobanus	*nigrimeinbris*	Pic, 1922	Taiwan
Xylobanus	*nigripennis*	Pic, 1927	Vietnam
Xylobanus	*nigrofenestratus*	Pic, 1926	Vietnam
Xylobanus	*nigrolineatus*	Pic, 1939	Indochina
Xylobanus	*nigropunctatus*	Pic, 1923	Vietnam
Xylobanus	*nitidus*	Kleine, 1926	Philippines
Xylobanus	*noacki*	Kleine, 1950	China
Xylobanus	*notaticollis*	Pic, 1925	Philippines
Xylobanus	*notatipes*	Pic, 1922	Lombok
Xylobanus	*nothus*	Kleine, 1926	Malaya
Xylobanus	*novellus*	Kleine, 1926	Malaya
Xylobanus	*oculatus*	Kleine, 1927	Philippines
Xylobanus	*palawanus*	Pic, 1922	Palawan
Xylobanus	*pallidior*	Pic, 1922	Java
Xylobanus	*paradoxus*	Kleine, 1933	Borneo
Xylobanus	*parviareolatus*	Kleine, 1927	Java
Xylobanus	*paululus*	Kleine, 1926	Philippines
Xylobanus	*pendleburyi*	Kleine, 1932	Borneo
Xylobanus	*philippinensis*	Kleine, 1927	Basilan
Xylobanus	*phungi*	Pic, 1926	Vietnam
Xylobanus	*piceicollis*	Pic, 1922	Java
Xylobanus	*piceithorax*	Pic, 1922	Sumatra, Malaya, Java
Xylobanus	*piceofenestratus*	Pic, 1939	Indochina
Xylobanus	*piceonotatus*	Pic, 1926	Vietnam
Xylobanus	*popularis*	Kleine, 1936	Java
Xylobanus	*privatus*	Waterhouse, 1879	Borneo
Xylobanus	*pubens*	Kleine, 1926	Philippines
Xylobanus	*pudicus*	Kleine, 1926	Philippines
Xylobanus	*pullatus*	Kleine, 1926	Philippines
Xylobanus	*putris*	Kleine, 1926	India
Xylobanus	*quadratus*	Kleine, 1926	Philippines
Xylobanus	*quinqueareolatus*	Pic, 1926	Sumatra
Xylobanus	*recens*	Kleine, 1929	Tenasserim
Xylobanus	*recurvus*	Kleine, 1929	Assam
Xylobanus	*regularis*	Waterhouse, 1879	New Guinea
Xylobanus	*reticulatus*	Gorham, 1882	Borneo, Sumatra, Java
Xylobanus	*reverens*	Kleine, 1939	Sulawesi
Xylobanus	*rianganus*	Pic, 1922	Sumatra
Xylobanus	*rigidus*	Waterhouse, 1879	Sumatra, Java
Xylobanus	*ritsemae*	Bourgeois, 1892	Borneo
Xylobanus	*rubens*	Waterhouse, 1879	Thailand
Xylobanus	*rusticus*	Schaufuss, 1887	Sulawesi
Xylobanus	*saranganus*	Kleine, 1931	Java
Xylobanus	*semiluteus*	Pic, 1922	Java
Xylobanus	*senescens*	Bourgeois, 1906	Borneo
Xylobanus	*senex*	Waterhouse, 1879	Borneo
Xylobanus	*sericeus*	Pic, 1922	Sumatra, Borneo
Xylobanus	*sinuaticollis*	Pic, 1922	Palawan
Xylobanus	*subcinnaberinus*	Schaufuss, 1887	Great Sundas
Xylobanus	*sublineatus*	Pic, 1922	Java

Xylobanus	*sumatrensis*	Pic, 1922	Sumatra
Xylobanus	*sutschaensis*	Kleine, 1933	Russian Far East
Xylobanus	*tenggerensis*	Pic, 1925	Java
Xylobanus	*tenuis*	Kleine, 1936	Java
Xylobanus	*testaceipes*	Pic, 1922	Sulawesi
Xylobanus	*testaceus*	Pic, 1922	Sumatra, Java, Surabawa
Xylobanus	*tinctus*	Gorham, 1882	Sumatra
Xylobanus	*torridus*	Kleine, 1931	Java
Xylobanus	*tríangulifer*	Kleine, 1932	Malaya
Xylobanus	*vetulus*	Bourgeois, 1883	Borneo
Xylobanus	*Vitalisi*	Oic, 1923	Vietnam
Xylobanus	*vitiosus*	Kleine, 1928	Borneo
Xylobanus	*wittmeri*	Kleine, 1939	Bali
Xylobanus	*frater*	Bourgeois, 1883	Java

Metriorrhynchina Kleine, 1928
Procautires Kleine, 1926

Procautires	*bryanti*	New South Wales	New South Wales
Procautires	*divisus*	New Guinea	New Guinea
Procautires	*efferatus*	New Guinea	New Guinea
Procautires	*excitatus*	New Guinea	New Guinea
Procautires	*flavicolor*	New Guinea	New Guinea
Procautires	*honestus*	New Guinea	New Guinea
Procautires	*maculosus*	New Guinea	New Guinea
Procautires	*miniatus*	New Guinea	New Guinea
Procautires	*mixtus*	New Guinea	New Guinea
Procautires	*parallelus*	New Guinea	New Guinea
Procautires	*saturalis*	New Guinea	New Guinea
Procautires	*toxopei*	Buru	Buru

The species excluded from *Cautires* and *Xylobanus*
Metriorrhynchina Kleine, 1928
Metriorrhynchus Gemminger et Harold, 1869

Metriorrhynchus	*ampliatus*	Macleay, 1887	Queensland	***Xylobanus***
Metriorrhynchus	*australianus*	Kleine, 1927	New South Wales	***Xylobanus***
Metriorrhynchus	*basiflavus*	Lea, 1909	Queensland	***Xylobanus***
Metriorrhynchus	*cancellatus*	Lea, 1909	Queensland, N. S. Wales	***Xylobanus***
Metriorrhynchus	*canus*	Kleine, 1927	Australia	***Xylobanus***
Metriorrhynchus	*confluens*	Bourgeois, 1900	New Guinea	***Xylobanus***
Metriorrhynchus	*conquisitus*	Kleine, 1927	Tasmania	***Xylobanus***
Metriorrhynchus	*constricticollis*	Lea, 1909	Australia	***Xylobanus***
Metriorrhynchus	*corvus*	Kleine, 1935	New Guinea	***Xylobanus***
Metriorrhynchus	*densereticulatus*	Kleine, 1927	New Guinea	***Xylobanus***
Metriorrhynchus	*diminutivus*	Lea, 1909	Queensland	***Xylobanus***
Metriorrhynchus	*flavomarginatus*	Kleine, 1933	Australia	***Xylobanus***
Metriorrhynchus	*fumosus*	Macleay, 1887	Queensland	***Xylobanus***
Metriorrhynchus	*hackeri*	Kleine, 1933	Australia	***Xylobanus***
Metriorrhynchus	*heterodoxus*	Lea, 1909	New South Wales	***Xylobanus***
Metriorrhynchus	*insignipennis*	Blackburne, 1900	Tasmania	***Xylobanus***
Metriorrhynchus	*longicornis*	Macleay, 1887	Queensland	***Xylobanus***
Metriorrhynchus	*meyricki*	Blackburne, 1886	Australia	***Xylobanus***

Metriorrhynchus milnei	Pic, 1923	New Guinea	***Xylobanus***
Metriorrhynchus miniaticollis	Macleay, 1887	Australia	***Xylobanus***
Metriorrhynchus mirabiliis	Kleine, 1926	New Guinea	***Xylobanus***
Metriorrhynchus mobilis	Kleine, 1926	New Guinea	***Xylobanus***
Metriorrhynchus modestus	Kleine, 1926	New Guinea	***Xylobanus***
Metriorrhynchus neglectus	Kleine, 1926	New Guinea	***Xylobanus***
Metriorrhynchus nigronotatus	Pic, 1923	New Guinea	***Xylobanus***
Metriorrhynchus obscurus	Macleay, 1886	New Guinea	***Xylobanus***
Metriorrhynchus parallelus	Pic, 1922	New Guinea	***Xylobanus***
Metriorrhynchus parvulus	Pic, 1922	New Guinea	***Xylobanus***
Metriorrhynchus piceoscutus	Pic, 1922	New Guinea	***Xylobanus***
Metriorrhynchus ramosus	Lea, 1909	New South Wales	***Xylobanus***
Metriorrhynchus robustithorax	Kleine, 1927	Halmaheira	***Xylobanus***
Metriorrhynchus simplicicornis	Lea, 1909	Queensland	***Xylobanus***
Metriorrhynchus sodalis	Kleine, 1935	New Guinea	***Xylobanus***
Metriorrhynchus testaceicollis	Macleay, 1887	Queensland	***Xylobanus***
Metriorrhynchus testaceoapicalis	Pic, 1923	Australia	***Xylobanus***
Metriorrhynchus testaceohumeralis	Pic, 1923	Australia	***Xylobanus***
Metriorrhynchus testaceoscutus	Pic, 1922	New Guinea	***Xylobanus***
Metriorrhynchus uniseriatus	Lea, 1909	New South Wales	***Xylobanus***
Metriorrhynchus venustus	Kleine, 1935	New Guinea	***Xylobanus***
Metriorrhynchus versicolor	Kleine, 1927	South Australien	***Xylobanus***

Cautiromimus Kleine, 1926

Cautiromimus	*amabilis*	Waterhouse, 1884	Aru	***Cautires***
Cautiromimus	*atroscutus*	Pic, 1922	New Guinea	***Cautires***
Cautiromimus	*elegans*	Kleine, 1926	New Guinea	***Cautires***
Cautiromimus	*facetus*	Kleine, 1926	New Guinea	***Cautires***
Cautiromimus	*factus*	Kleine, 1926	New Guinea	***Cautires***
Cautiromimus	*fuliginosus*	Kleine, 1926	New Guinea	***Cautires***
Cautiromimus	*insulanus*	Kleine, 1926	New Britain	***Cautires***
Cautiromimus	*maculosus*	Kleine, 1926	New Guinea	***Cautires***
Cautiromimus	*maturus*	Kleine, 1926	Neu Guinea	***Cautires***
Cautiromimus	*mediocris*	Kleine, 1926	Neu Guinea	***Cautires***
Cautiromimus	*mendicus*	Kleine, 1926	New Guinea	***Cautires***
Cautiromimus	*mendosus*	Kleine, 1926	New Guinea	***Cautires***
Cautiromimus	*mimicus*	Kleine, 1926	New Guinea	***Cautires***
Cautiromimus	*papuanus*	Kleine, 1935	New Guinea	*Bulenides*
Cautiromimus	*socius*	Kleine, 1935	New Guinea	*Bulenides*