

UNIVERZITA PALACKÉHO V OLMOUCI
PŘÍRODOVĚDECKÁ FAKULTA
KATEDRA ZOOLOGIE



**DEFINICE DRUHŮ U POLYMORFNÍHO RODU *ENICLASES* (COLEOPTERA:
LYCIDAE)**

Diplomová práce

Vypracoval: Matěj Boček

Studijní program: Biologie

Studijní obor: Zoologie

Forma studia: prezenční

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Olomouc 2015

PROHLÁŠENÍ

Prohlašuji, že jsem diplomovou práci vypracoval samostatně pod vedením vedoucího Prof. Ing. Ladislava Bocáka, Ph.D. a použil jsem pouze uvedené bibliografické zdroje.

V Olomouci, 9. 5. 2015

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PODĚKOVÁNÍ

Rád bych poděkoval Prof. Ing. Ladislavu Bocákovi, Ph.D. za materiál a konzultace k tématu této práce. Zároveň nesmím opomenout poděkovat Mgr. Renatě Bílkové za vedení při práci v molekulární laboratoři. Dr. Timothy C. Bray komentoval anglickou verzi této studie. Samozřejmě jsem vděčný mé rodině a kamarádům za pomoc a podporu při psaní této diplomové práce.

BIBLIOGRAFICKÁ IDENTIFIKACE

Jméno a příjmení autora: Matěj Boček

Název práce: Definice druhů u polymorfního rodu *Eniclases*

Typ práce: Diplomová práce

Pracoviště: Katedra zoologie

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

Rok obhajoby práce: 2015

ABSTRAKT

Tématem diplomové práce je porovnání různých metod delimitace druhů ve skupině blízce příbuzných linií aposematicky zbarvených druhů rodu *Eniclases* (Coleoptera: Lycidae). K vymezení hranic druhů zde bylo použito široké spektrum delimitačních metod, konkrétně: morfologie, nekorigovaná párová genetická vzdálenost, Bayesiánská implementace Poisson Tree Processes modelu a definice molekulárních znaků.

V dosud neprozkoumaných oblastech Nové Guiney byla zjištěna mimořádná diverzita brouků ze skupiny rodu *Eniclases* (Lycidae: Metriorrhynchini), což vedlo k popsání 10 nových druhů z rodu *Eniclases*. V této práci byly identifikovány morfologické i genetické rozdíly mezi páry sesterských druhů s významnou heterogenitou rychlosti morfologické a molekulární evoluce. Proto bylo nutné použít více metod pro vymezení hranic druhu, ne pouze vymezení druhu pomocí morfologie nebo molekulárních dat, a taktéž bylo nutné kriticky zhodnotit rozdíly v delimitaci. Páry sesterských druhů s nízkou genetickou variabilitou bylo možné v některých případech odlišit podle velikosti očí, a je možné předpokládat, že ke speciaci těchto druhů došlo na základě změny denní aktivity.

Druhy v tomto rodu nebylo možno odlišit podle zbarvení těla, jelikož jedinci s velmi podobnými aposematickými vzory na krovkách vykazovaly velké genetické rozdíly, a naopak jedinci s odlišnými fenotypy byly geneticky neodlišitelní. Taxonomické zpracování skupiny je zde značně komplikováno genetickým polymorfismem. Genetická variabilita i mezi druhy, kteří nevykazovali žádné morfologické rozdíly, nízká disperzní schopnost a polymorfismus, vedou k velmi nejisté druhové klasifikaci v rodu *Eniclases*.

Klíčová slova. Aposematismus, bPTP model, Coleoptera, *cox1* mtDNA, genetická vzdálenost, morfologie, nové druhy, delimitace druhu.

BIBLIOGRAPHIC IDENTIFICATION

First name and surname of the author: Matěj Boček

Name of the thesis: Where are species limits in polymorphic mimetic beetles from New Guinean mountains: a case of *Eniclases* net-winged beetles (Coleoptera: Lycidae)

Type of thesis: Diploma thesis

Workplace: Department of Zoology

Thesis supervisor: Prof. Ing. Ladislav Bocák, Ph.D.

Year of defence: 2015

ABSTRACT

I compared species delimitation in a group of closely related lineages of aposematically coloured *Eniclases* (Coleoptera: Lycidae) using morphology, genetic distances, Bayesian implementation of the Poisson Tree Processes model, and DNA diagnostic characters. I found high diversity of net-winged beetles in the previously omitted regions of New Guinea and describe ten new species: *Eniclases bicolor* **sp. nov.**, *E. bokondinensis* **sp. nov.**, *E. brancuccii* **sp. nov.**, *E. elelimensis* **sp. nov.**, *E. infuscatus* **sp. nov.**, *E. niger* **sp. nov.**, *E. pseudoapertus* **sp. nov.**, *E. pseudoluteolus* **sp. nov.**, *E. tikapurensis* **sp. nov.**, and *E. variabilis* **sp. nov.**

Different levels of genetic and morphological diversification were identified in various sister-species pairs and these differences exclude species delimitation using just a single approach, either morphological or molecular. Sister-species with uncorrected pairwise genetic divergence as low as 0.45% can be morphologically distinct not only in colour pattern, but also in the relative size of eyes.

Conversely, the differences in colour patterns regardless of their magnitude do not necessarily indicate genetic distance and reproductive isolation as intraspecific mimicry polymorphism is common in *Eniclases*. Additionally, the genetic divergence without any morphological differentiation was detected in a sister-species pair. The low dispersal propensity, highly diverse mimicry patterns, and mimetic polymorphism result in complicated diversification of *Eniclases* and highly uncertain species delimitation in the recently diversified lineages.

Key words. Aposematism, bPTP model, Coleoptera, *coxI* mtDNA, genetic distance, morphology, new species, species delimitation.

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1. INTRODUCTION

Tropical biodiversity is poorly documented and especially the Papuan beetle fauna remains one of the most under-investigated despite high species richness and endemism in the Oceanian region (Holt et al., 2013). The taxonomical research on Papuan beetles has quite a long history (e.g. Kleine, 1926), but only recent studies have shown exceptional diversity (Riedel et al., 2013; Ballantyne & Lambkin, 2013; Toussaint et al., 2014). The morphology-based taxonomy of beetles is affected by the labour-intensive character of morphological methods, the shortage of taxonomists, and the burden of chaotic classification and poor species delimitation resulting from bad practice in the past (e.g. anecdotic uninformative descriptions or formal morphological descriptions using a semaphoront without diagnostic characters). The DNA data provide a tool, which can accelerate the much needed biodiversity research, but these data must be viewed as an integral part of a process of cross-validation of hypotheses on species limits based on morphology and genetic information and cannot provide answers alone under all circumstances (e.g. Meyer & Paulay, 2005; Meier, Shiyang, Vaidya, & Ng 2006; Baselga, Gomez-Rodriguez, Novoa, & Vogler, 2013; Jörger & Schrödl, 2013). Here, I present a taxonomical study dealing with high diversity of *Eniclases* Waterhouse, 1879 (Lycidae: Metriorrhynchini: Metriorrhynchina), a genus in which most species are aposematically coloured and living in an environment inhabited by multiple distant mimetic complexes. Additionally, the net-winged beetles are characteristically of limited dispersal ability and consequently prone to rapid differentiation of local populations (Li, Gunter, Pang, & Bocak, 2015).

The Papuan net-winged beetles share the most diverse genera with the Australian continental fauna (Kleine, 1933; Calder, 1998; Sklenarova, Kubecek, & Bocak, 2014), but besides these, several genera are endemic to the Moluccas, New Guinea, and other islands lying north of the Australian continent. These endemic lineages, including *Eniclases*, diversified very probably in New Guinea and adjacent islands (Sklenarova, Chesters, & Bocak, 2013) and in contrast with a supposedly short existence of New Guinea in its present form, they contain a high number of species. New Guinea is a newly assembled land and originated due to the uplift of the northern margin of the Australian tectonic plate and accretion of the oceanic islands about 5 mya (Hill & Hall, 2002; Lindley, 2006;

Baldwin, Fitzgerald, & Webb, 2012). The role of the uplift of the Central Mountains in beetle speciation was recently discussed by Toussaint et al. (2014).

Eniclases was revised by Bocak & Bocakova (1991) and 27 species have been reported from the New Guinea, Japan, Mysol, and Halmahera islands (Maps S1–S4). The morphology-based revision was primarily investigating material from the eastern part of New Guinea and the fauna of Western New Guinea remained poorly studied when only a limited number of species was reported from the lowlands at the northern coast (4 spp.), the Eastern highlands around the Panai Lake (Enarotali, 3 spp.), the Fak Fak Peninsula (2 spp.), and the border region of the Central Mts. (Oksibil area, 2 spp.; Figs S1–S4). The faunas of the Jayawijaya region of the Central Mts. region and the Bird's Head Peninsula have not yet been studied.

I present a taxonomical study based on material representing a dense sampling of closely related species of *Eniclases* from the western part of the island, mainly from the Central Mts. (Fig. 3). The aim is to compare species delimitations inferred from genetic distances (barcoding approach; Hebert, Ratnasingham, & deWaard, 2003; Meier et al., 2006), the tree shape (the Bayesian Poisson Tree Processes method, bPTP; Zhang, Kapli, Pavlidis, & Stamatakis, 2013), and the presence of diagnostic DNA characters (DeSalle, Egan, & Sidall, 2005; Sarkar, Planet, & DeSalle, 2008). I test the status of these putative species inferred from a single mtDNA fragment by the presence of morphological characters. Specifically, I investigate the presence of the intraspecific colour polymorphism and morphological diagnostic characters for all species of *Eniclases*. Descriptions and diagnoses of new species are presented using available evidence and possible scenarios for diversification of *Eniclases* are discussed.

2. MATERIAL AND METHODS

2.1. Material and laboratory procedures

In total, 81 specimens of *Eniclases* (Tab. S1) originate from the eastern part of New Guinea: in the Central, Cyclops and Arfak Mts. (Fig 3, Maps S1–S4); they were dried in silica gel and kept in -20°C until DNA isolation. All specimens were collected in private land outside protected areas and they are deposited in the voucher collection of the Laboratory of Molecular Systematics, Faculty of Science, Palacky University. The *cox1* +

tRNA-Leu + *cox2* mtDNA fragment (further referred as *cox1* only) was amplified using JerryM (CAACAYYTATTTTGRTTYTTTGG) and Marcy (TARTTCRTATGWRCAATAYCAYTGRTG) or JerryN (CAACAYYTATTTYTGATTYTTYGG) and MarcyN (TTCRTAWGTTTCARTATCATTGRTG). The isolation method, PCR settings and cycle sequencing conditions were used as reported by Bocak & Bocakova (2008). The PCR products were purified using PCR μ 96™ Plates (Millipore Inc.) and sequenced by an ABI 3130 automated sequencer using the BigDye® Terminator Cycle Sequencing Kit 1.1.

2.2. *Phylogenetic analyses and species delimitation*

Sequences were edited using the Sequencher 4.8 software package (Gene Codes Corp.) and combined with homologous sequences of 25 outgroup taxa representing Cautirina and Metriorrhynchina. The length invariable mtDNA fragment was aligned using ClustalX 2.1 (Thompson, Gibson, Plewniak, Jeanmougin, & Higgins, 1997) under default parameters and the phylogenetic analysis was carried out under the maximum likelihood criterion using the RAxML 7.3.1 (Stamatakis, 2006) and the GTR + I + G model for all partitions. All genes and codon positions in the protein coding fragments were partitioned and parameters unlinked for each partition. Bootstrap values (BS) were assessed by analysing 1000 pseudoreplicates using the rapid bootstrap algorithm under the GTRCAT model (Stamatakis, Hoover, & Rougemont, 2008). The trees were edited and visualized in Dendroscope 3.1 (Huson et al., 2007). In order to estimate the origin of closely related lineages with different mimetic patterns, I normalized the tree using Beast 1.8.1 (Drummond, Suchard, Xie, & Rambaut, 2012) with the same model as in the maximum likelihood analysis. As there is no fossil record of metriorrhynchine Lycidae, I relied on the molecular evolution rates used earlier. I tested two rates, 0.0115 substitutions per lineage and million year (s/l/my; Brower, 1994), which gave results in agreement with tectonics in earlier study on *Metriorrhynchus* (Bocak & Yagi, 2010) and the rate 0.0177 s/l/my calculated by Papadopoulou, Anastasiou, & Vogler (2010) for Tenebrionidae. I set the tree model to a Speciation: Birth Death Process and the MCMC parameters to 10 million generations with sampling every 1,000 generations. The first 4 million generations were discarded as burn-in after evaluation of likelihood values and the effective sample size in Tracer 1.6 (Rambaut, Suchard, & Drummond, 2013).

I estimated the genetic intra- and interspecific differentiation among whole fragment sequences (i.e., *cox1*, tRNA-Leu, and *cox2* mtDNA) using Kimura 2-parameter genetic distances in MEGA6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013) and I identified the clusters of similar sequences in Species Identifier 1.7.7 using 3% barcoding threshold (Meier et al., 2006). The densities for intra- and interspecific differences were visualized in R (<http://r-project.org>).

Further, I defined species level entities using the maximum likelihood and Bayesian implementation of the Poisson Tree Processes (bPTP) model for species delimitation (the bPTP server at species.h-its.org). The algorithm delimits putative species from the tree with branch lengths representing the number of substitutions (Zhang et al., 2013a) and provides posterior probabilities of all descendants under that node representing a single species.

When putative species were delimited, diagnostic mutations were identified for selected sister species pairs using Characteristic Attribute Organization System (CAOS; Sarkar et al., 2008). I considered only single homologous pure diagnostic characters (sPu) *sensu* Sarkar et al. (2008).

The morphological characters were identified for all sequenced specimens: the measurements of the body size, maximum diameter of eyes in the lateral view, the minimum interocular distance in the frontal part of cranium, colour patterns of the pronotum and elytra, shape of pronotum and antennae, and structure of the elytral costae. All measurements and photographs were taken using a binocular microscope with an eyepiece scale or an attached digital camera, respectively. The photographs were assembled from layers in Helicon Focus 6 (www.heliconsoft.com). Due to previously reported uniformity of the genitalia of both sexes (Bocak & Bocakova, 1991), only a part of individuals was dissected.

Abbreviations

DEIM – Deutsches Entomologisches Institute, Müncheberg, Germany

MHNP – Muséum national d'Histoire naturelle, Paris, France

3. RESULTS

The 1101 bp fragment of mtDNA was sequenced for 81 individuals of *Eniclases* from the western part of New Guinea. The sequenced fragment consisted of 782 base pairs (bp) *cox1* mtDNA, 59 bp tRNA-Leu, and 260 bp *cox2* mtDNA. I identified 38 unique haplotypes in the ingroup and the Kimura 2-parameter genetic distances among *Eniclases* sequences reached 0.09–14.31%. The maximum likelihood analysis produced the tree in Fig. 1. *Eniclases* formed a monophylum with 100% bootstrap support and the fauna of the Central Mts. was represented by four deeply rooted clades of closely related species. Two of these clades have sister-species occurring in the Bird's Head Peninsula. The normalized tree inferred with 0.0115 s/l/my rate is shown in Fig. 2 and suggest the origins of closely related species pairs in the last million years. The higher rate 1.77% produced even shallower splits for the terminal lineages (results not shown).

I evaluated the genetic divergence between all haplotypes and found the highest densities between 0.0–2.0% and 9.0–14% (Fig. 4). Further, I considered morphological divergence within genetically close terminals and identified three morphologically distinguishable species pairs: *E. elelimensis* and *E. bokondinensis* (mean interspecific K-2-P distance 0.79%, maximum intraspecific distance 0.17%); *E. infuscatus* and *E. bicolor* (1.07% and 0.12%); *E. niger* and *E. similis* (0.59% and 0.16%). Relatively low divergence was found between *E. variabilis* and *E. elelimensis* (<1.59%), *E. variabilis* and *E. bokondinensis* (<1.72%) and between *E. brancuccii* and three species in its sister clade (3.90–4.59%). The clade of *E. tikapurensis* and *Eniclases* sp. A consisted of two sister-subclades with inter-clade genetic difference 1.12–1.28% (Fig. 1) and these candidate species were morphologically indistinguishable.

Further, I identified putative species using genetic distance and the phylogenetic tree. The pairwise differences among *cox1* mtDNA sequences merged haplotypes in 9 clusters when the threshold 3% was applied. The inferred clusters merged *E. infuscatus* and *E. bicolor*, *E. tikapurensis* + *Eniclases* sp. A, the clade *E. elelimensis* + *E. bokondinensis* + *E. variabilis* and the pair *E. niger* + *E. similis* (Fig. 1, the clades labelled with triangles and intra-clade genetic distances). Most of these species differ at least in coloration or additionally in the size of eyes and geographic origin (see taxonomy section for detailed morphological descriptions). The maximum likelihood PTP method proposed identical species limits as the distance approach (results not shown). Unlike these, the

Bayesian implementation of the PTP model suggested 9–19 putative species, mean 11.97 species. The most supported partitions are displayed in Figure 1A (12 putative species designated by squares and labels designating posterior probabilities). The posterior delimitation probabilities (PP) were high only for *E. apertus* and *E. brancuccii* partitions ($\geq 90\%$); other clades obtained moderate to very low PPs. On the other hand, the alternative species delimitations corresponding to those from distance analyses and delimitations based on morphological traits showed even lower PPs (Fig. 1).

I identified 14 species in the sequenced material, ten of them new to science and described in the Taxonomy section. The delimitation of species was based on simultaneous consideration of morphological characters (the size of eyes, shape of male antennae and colouration) and the relationships inferred from the phylogenetic analysis, genetic distance and bPTP model (Tab. S1, Figs 1–2).

4. SYSTEMATICS

Eniclases Waterhouse, 1879

Type species. *Lycus luteolus* Waterhouse, 1878 – by monotypy.

Diagnosis. *Eniclases* is similar in general appearance with *Trichalus* and they share the small to medium sized, dorso-ventrally flattened body; the characteristic shape of the pronotum with acutely projecting posterior angles and a boulder in the posterior third of the pronotal margin; nine elytral costae in the humeral part of elytra (four robust primary costae and five weak secondary costae) and the shortened primary costa 1. Unlike *Trichalus*, the median pronotal areola is absent in *Eniclases* and only two divergent longitudinal keels are present in the pronotum (Figs 6–29). Additionally, all *Eniclases* have the characteristic cap-shaped apex of the phallus (Figs 43–46) similar to those of *Schizotrichalus* Kleine, 1926 (Bocak, 2002). The detailed redescription of *Eniclases* was published by Bocak & Bocakova (1991).

Phylogenetic relationships. The shape of the pronotum, shortened elytral costa 1, and shape of male genitalia (Figs 6–46) support relationships of *Eniclases* and other trichaline genera. At present, the trichaline lineages form a subordinate clade within Metriorrhynchina and consist of *Eniclases*, *Flabellotrichalus* Pic, 1921, *Microtrichalus*

Pic, 1921, *Schizotrichalus* Kleine, 1926, and *Trichalus* Waterhouse, 1877 (Bocak, 2002; Sklenarova et al., 2014).

4.1. A review of species included in the phylogenetic and species delimitation analyses

***Eniclases pseudoapertus* sp. nov.**

Figs 7, 42

HOLOTYPE: Male (BM0080), Indonesia, Irian Jaya, Arfak Mts., Maibri village, 1570 m, Nov.–Dec. 1991.

TYPE LOCALITY: Indonesia, Arfak Mts.

ETYMOLOGY: The specific name refers to similarity with *E. apertus*.

DIAGNOSIS: *E. pseudoapertus* sp. nov. resembles *E. apertus* Pic, 1923 in the small body and black coloration. These species differ in the relative size of male eyes. The *E. apertus* eye diameter equals interocular distance.

DESCRIPTION: Male. Body medium sized, uniformly dark coloured, only trochanters and bases of femora light brown. Head with large hemispherically prominent eyes, their maximum diameter 1.40 times minimal interocular distance, antennae slender, serrate, almost parallel-sided, with very short apical process of antennomere 3. Pronotum transverse, with almost straight lateral margins, elytra with very weak secondary costae and irregular cells.

***Eniclases divaricatus* (Pic, 1921)**

Figs 6, 34

Trichalus (Trichalolus) divaricatus Pic, 1921: 10.

LECTOTYPE: Female, New Guinea, Humboldt Bay, Doherty lgt., coll. Pic (MHNP).

OTHER MATERIAL EXAMINED: 4 males, 2 females (BM0001–2, 9, 15–17), Indonesia, Irian Jaya, Sentani, Cyclops Mts., 300 m, Nov.–Dec. 1991; female (BM0057), Indonesia, Irian Jaya, Elelim, path to Apalapsili, 600 m, Nov.–Dec. 1991.

TYPE LOCALITY: New Guinea, Humboldt Bay.

DIAGNOSIS: *E. divaricatus* is the only Papuan species with bicoloured elytra and flabellate male antennae (Figs 6, 34). Additionally, this species has a characteristic pattern

of bright humeri and dark coloured suture, which is shared only with some specimens of *E. similis* from the same locality (Figs 6, 13). Females of the similarly coloured forms can be hardly distinguished as their relative size of eyes is close (Tab. 1).

REDESCRIPTION: Male. Body medium sized, head, thorax, legs, and humeri yellow to orange, antennae except basal part, abdomen, and most of elytra dark coloured. Head with moderately large, hemispherically prominent eyes, their diameter 0.92–0.96 times minimum interocular distance, antennae flabellate, lamella of antennomeres 3 slightly longer than antennomere body, other lamellae of similar length (Fig. 34). Pronotum transverse, with almost straight, slightly elevated lateral margins, elytra with quite strong straight secondary costae and regular dense cells (Fig. 6)

DISTRIBUTION: Central North New Guinea.

Eniclases infuscatus sp. nov.

Figs 11, 35

HOLOTYPE: Female (BM0050), Indonesia, Irian Jaya, Bokondini, 1300 m, Nov.–Dec. 1991. PARATYPE: Female (BM0062), Indonesia, Irian Jaya, Elelim, path to Apalapsili, 600 m, Nov.–Dec. 1991.

TYPE LOCALITY: New Guinea, Bokondini region.

ETYMOLOGY: The specific name refers to blackened edge of the basal part of elytra.

DIAGNOSIS: *E. infuscatus* sp. nov. has a unique colour pattern among western Papuan *Eniclases*. The upper part of the body is yellow to orange and only tips of elytra and a posterior part of the lateral margins are infuscate. It partly resembles in coloration *E. tikapurensis*, which has a slender body and is pale coloured (Fig. 9).

DESCRIPTION: Female. Body large, robust, head brown, abdomen, meso- and metathorax dark coloured, most of legs similarly coloured, only trochanters and basal half of femora light brown; pronotum and elytra yellow to orange, only tips and posterior margins of elytra infuscate, transition between dark and bright parts of elytra gradual. Head with small hemispherically prominent eyes, their diameter 0.79–0.84 times minimum interocular distance, antennae flat, slender, serrate, antennomeres 3–4 triangular, further antennomeres almost parallel-sided (Fig. 35). Pronotum transverse, with almost straight lateral margins, elytra with weak, but regular secondary costae and regular, often transverse, small cells.

Homogenous sPu characters versus *E. bicolor*: 11:A, 107:T, 194:A, 272:T, 326:T, 656:A, 865:A, 956:A, 968:A, 1042:C, 1058:T.

Eniclases bicolor sp. nov.

Figs 10, 31

HOLOTYPE: Female (BM0046), Indonesia, Irian Jaya, Elelim, path to Apalapsili, 600 m, Nov.–Dec. 1991. PARATYPES: 2 females (BM0045, 47), same locality data as the holotype.

TYPE LOCALITY: New Guinea, Elelim region.

ETYMOLOGY: The specific name refers to coloration of elytra.

DIAGNOSIS: *E. bicolor* sp. nov. resembles in general appearance some forms of *E. similis* from the Cyclops Mts. and differs in a higher contrast between light coloured costae and dark cells in a transitional area between the dark and light parts of elytra. Additionally, the females of *E. bicolor* have very small eyes (Tab. 1).

DESCRIPTION: Female. Body medium sized, robust, head, basal part of antennae, pro- and mesothorax, basal half of elytra and legs yellow to light orange, apical half of antennae, metathorax, half of elytra and abdomen dark coloured, transition between dark and bright parts contrasting. Head with very small, hemispherically prominent eyes, their diameter 0.71–0.74 times minimum interocular distance, antennae flat, slender, serrate in basal antennomeres, apical antennomeres almost parallel-sided. Pronotum transverse, with almost straight lateral margins and prominent posterior angles, elytra with weak, but straight secondary costae and regular, often transverse, small cells.

Homogenous sPu characters versus *E. infuscatus*: 11:T, 107:C, 194:G, 272:C, 326:C, 656:G, 865:G, 956:G, 968:G, 1042:T, 1058:C.

Eniclases tikapurensis sp. nov.

Figs 9, 41

HOLOTYPE: Male (BM0039), Indonesia, Irian Jaya, Yiwika, N of Wamena, 2000 m, Nov.–Dec. 1991. PARATYPES: 3 males, 2 females (BM0040–44), Indonesia, Irian Jaya, Tikapura village, 2200 m, Nov.–Dec. 1991.

TYPE LOCALITY: New Guinea, Yiwika.

ETYMOLOGY: The specific name refers to the type locality, the village Tikapura, north of Tagime.

DIAGNOSIS: *E. tikapurensis* sp. nov. resembles in general appearance *E. papuensis* Bocak et Bocakova, 1991 from the Panai Lake area about 250 km west of the visited localities. Both species are characteristic in pale hue of the yellow upper part of body (Fig. 9), but differ in the relative size of eyes when *E. tikapurensis* has eyes much larger.

DESCRIPTION: Male. Body medium sized to large, slender; head, antennae, thorax, legs except trochanters and bases of femora bark brown to black, pronotum and elytra except posterior edge pale yellow. Head with large, hemispherically prominent eyes, their diameter 1.11–1.40 times minimum interocular distance, antennae slender, serrate, antennomere 3 triangular, with pointed apical process, antennomere 4 parallel-sided in most of its length, its process shorter, shape of other antennomeres similar (Fig. 41). Pronotum transverse, lateral margins with weak bulge in basal third and prominent posterior angles, elytra with weak but well developed, straight secondary costae and regular, mostly quadrate, small elytral cells.

Homogenous sPu characters versus *Eniclases* sp. A: 86:C, 104:C, 122:C, 281:C, 332:T, 437:T, 602:G, 749:T, 89:C8, 905:C, 1007:C.

DISTRIBUTION: New Guinea, Upper Baliem Valley.

REMARK: A genetically distant population from Bokondini is a sister to *E. tikapurensis*, but does not differ in any morphological character. As delimitation would be based only on mtDNA sequence and at least further information on nuclear markers and geographical distribution is needed for these two putative cryptic species, I postpone formal description of the population from Bokondini as a species. The following sPu characters define the population from Bokondini versus *E. tikapurensis*: 86:T, 104:T, 122:G, 281:C, 332:C, 437:C, 602:A, 749:A, 898:T, 905:T, 1007:T.

Eniclases brancuccii sp. nov.

Figs 12, 33

HOLOTYPE: Male (BM0006), Indonesia, Irian Jaya, Sentani, Cyclops Mts., 300 m, Nov.–Dec. 1991. PARATYPES: 3 females (BM0005, 7, 10), the same data as the holotype .

TYPE LOCALITY: New Guinea, Cyclops Mountains.

ETYMOLOGY: The specific name ‘*brancuccii*’ is proposed in honour of the late Michel Brancucci, a specialist in Dytiscidae and Cantharidae.

DIAGNOSIS: *E. brancuccii* sp. nov. resembles in colour pattern three species: *E. elelimensis*, *E. niger*, and *E. variabilis*. The last two of them are polymorphic and only some individuals share the colour pattern with *E. brancuccii* (Figs 12, 16, 24–25, 28–29). *Eniclases niger* differs in the large eyes and almost parallel-sided antennomeres 3–10. *Eniclases elelimensis* and *E. variabilis* have similar antennae and slightly larger eyes, but reliable identification of these species can only be based on the DNA sequences. The similarly coloured forms of these species do not occur together in a single locality (Tab. 1). DESCRIPTION: Male. Body medium sized, robust, head, antennae, thorax, elytra, and abdomen dark brown to black, pronotum, scutellum, and basal parts of femora yellow to orange, apical parts of femora, tibiae, and tarsi dark brown. Head with rather small, hemispherically prominent eyes, their diameter equals minimum interocular distance, antennae flat, slender, acutely serrate, apical process of antennomere 3 about half length of its body, further antennomeres similar in shape. Pronotum transverse, with apparent bulge in basal third, almost parallel-sided between bulge and posterior angles, elytra with weak but regular secondary costae and mostly regular, quadrate, small cells.

Eniclases elelimensis sp. nov.

Figs 19, 39

HOLOTYPE: Female (BM0056), Indonesia, Irian Jaya, Elelim, path to Apalapsili, 600 m, Nov.–Dec. 1991. PARATYPES: 2 females, the same locality data (BM0051–52).

TYPE LOCALITY: New Guinea, Elelim region.

ETYMOLOGY: The specific name refers to the type locality.

DIAGNOSIS: *E. elelimensis* differs from *E. brancuccii* in slightly smaller eyes, but no morphological difference has been found to discriminate this species from some similarly coloured individuals of *E. variabilis* (Figs 24–25, 28–29) and morphology based identification can reliably assign similarly coloured specimens only to the clade of *E. variabilis* and related species.

DESCRIPTION: Male. Body medium sized, robust, head, antennae, thorax, elytra, and abdomen dark brown to black, pronotum and femora yellow to light orange, apical part of femora, tibiae, and tarsi dark brown. Head with small, hemispherically prominent eyes, their diameter equals minimum interocular distance, antennae flat, slender, acutely serrate, apical process of antennomere 3 about half length of its body, further antennomeres similar in shape. Pronotum transverse, with apparent bulge in basal third, almost parallel-sided

between bulge and posterior angles, elytra with weak but regular secondary costae and mostly regular, quadrate, small cells.

Homogenous sPu characters versus *E. bokondinensis*: 149:T, 266:A, 404:T, 479:C, 641:C, 737:T, 922:T.

REMARK: I studied *E. versicolor* Kleine, 1926 from an unspecified locality in New Guinea (Holotype, male, 'Neuguinea, Coll. Kraatz' deposited in DEIM). This species is very similar in general appearance, but differs in the large male eyes. The female specimen of *E. versicolor* from the Jayapura district cited by Bocak & Bocakova (1991) might be conspecific with *E. variabilis* or *E. elelimensis* and these species might have allopatric distribution.

Eniclases bokondinensis sp. nov.

Figs 17, 32

HOLOTYPE: Female (BM0095), Indonesia, Irian Jaya, Bokondini, 1900 m, Nov.–Dec. 1991. PARATYPES: 2 females (BM0092, 94), the same locality data as the holotype.

TYPE LOCALITY: New Guinea, Bokondini region.

ETYMOLOGY: The specific name refers to the type locality.

DIAGNOSIS: *E. bokondinensis* has a characteristic combination of the black pronotum and mostly light yellow elytra infusate at apex (Figs 17–18). The shape of antennae and the relative size of eyes are similar to those of *E. variabilis* and *E. elelimensis* (Figs 32, 38, 39). The co-mimics of *E. bokondinensis* are large-bodied and this species has a larger body than its closest relatives (Fig. 1, Tab. 1).

DESCRIPTION: Female. Body medium sized, head, antennae, thorax, and abdomen dark brown to black, elytra light yellow in humeral half, very gradually infusate to apex (Figs 17–18), trochanters and basal parts of femora brown, rest of legs black. Head with small, hemispherically prominent eyes, their diameter 0.72–0.82 interocular distance, antennae flat, slender, acutely serrate, apical process of antennomere 3 about half length of its body, further antennomeres similar in shape. Pronotum transverse, with weak bulge in basal third, elytra with weak but regular secondary costae and mostly regular, subquadrate cells (Figs 17–18).

Homogenous sPu characters versus *E. elelimensis*: 149:C, 266:G, 404:C, 479:T, 641:T, 737:C, 922:C.

Eniclases variabilis sp. nov.

Figs 20–29, 38, 43, 45

HOLOTYPE: Male (BM0054), Indonesia, Irian Jaya, Elelim, path to Apalapsili, 600 m, Nov.–Dec. 1991. PARATYPES: Male, 3 females (BM0048–49, 53, 55), same data as the holotype; 7 males, 8 females (BM0025–32, 34–36, 86, 88, 90–91), Indonesia, Irian Jaya, Bokondini, 1300 m, Nov.–Dec. 1991; 4 males, female (BM0063–67), Indonesia, Irian Jaya, Dombomi, Lower Pass valley, 1200 m; 2 males (BM0008, 12), Indonesia, Irian Jaya, Sentani, Cyclops Mts., 300 m, Nov.–Dec. 1991.

TYPE LOCALITY: New Guinea, Elelim.

ETYMOLOGY: The specific name refers to exceptional variability in coloration.

DIAGNOSIS: *E. variabilis* is a widespread and species highly polymorphic in coloration and resembles in general appearance several distinct, sympatrical mimetic types. The colour forms are illustrated in Figs 20–29. Similarly coloured individuals of *E. niger* differ in the relative size of eyes and shape of antennae (Figs 38, 40), but the similarly coloured individuals of *E. elelimensis* can be identified only using the DNA data.

DESCRIPTION: Male, holotype (Fig. 20). Body small to medium sized, head, antennae, thorax, and abdomen dark black, elytra orange yellow in humeral third, rest of elytra black, transitional zone between bright and dark part of elytra is narrow (Figs 20, 38), trochanters brown, rest of legs black. Head with small, hemispherically prominent eyes, their diameter 0.83–0.95 interocular distance, antennae flat, slender, acutely serrate, apical process of antennomere 3 about half length of its body, further antennomeres similar in shape. Pronotum transverse, with weak bulge in basal third, elytra with weak secondary costae and mostly regular, subquadrate cells (Fig. 20).

Homogenous sPu characters versus the clade *E. elelimensis* + *E. bokondinensis*: 32:G, 173:T, 380:A, 506:C, 528:C, 578:C, 662:T, 683:G, 686:T, 711:A, 872:A, 919:T.

DISTRIBUTION: Central North New Guinea.

REMARK: *E. variabilis* can be differently coloured in various localities. Generally, the dark coloured specimens were found in higher elevations in Bokondini (1300 m) and Dombomi (1200 m) and bright coloured individuals were collected in lower elevations in Elelim (600 m) and Cyclops Mts. (300 m) (Fig. 3).

Eniclases pseudoluteolus sp. nov.

Figs 36, 44, 46

HOLOTYPE: Male (BM0084), Indonesia, Irian Jaya, Maibri vill., Arfak Mts., 1600 m, Nov.–Dec. 1991.

TYPE LOCALITY: New Guinea, Arfak Mts.

ETYMOLOGY: The specific name refers to the similarity with *E. luteolus*.

DIAGNOSIS: *E. pseudoluteolus* is belongs to a group of uniformly yellow species which additionally includes *E. luteolus* Waterhouse, 1878, *E. nigriceps* Bocak et Bocakova, 1991, *E. fuscicornis* Bocak et Bocakova, 1991, and *E. pallidus* Bocak et Bocakova, 1991, all of them having large eyes and *E. robustus* Bocak et Bocakova, 1991 and *E. proximus* Bocak et Bocakova, 1991 both of them having similar small eyes (Bocak & Bocakova, 1991). The later two species differ in the slender antennomere 3 and light coloured thorax (antennomere of *E. pseudoluteolus* as in Fig. 36). The similar species occur only in Eastern New Guinea in vicinity of Wau and Mt. Hagen (Fig. S2).

DESCRIPTION: Male. Body medium sized, head, apical antennomeres, thorax, and abdomen dark brown to black, pronotum and elytra yellow, trochanters brown, rest of legs black. Head with small, hemispherically prominent eyes, their diameter 0.90 interocular distance, antennae flat, acutely serrate, antennomere 3 triangular, wide, its apical process short (Fig. 36), further antennomeres similar in shape, becoming slenderer to apex of antennae. Pronotum transverse, with weak bulge in basal third, elytra with weak secondary costae and mostly regular, subquadrate cells.

Eniclases niger sp. nov.

Figs 15, 16, 40

HOLOTYPE: Male (BM0059, Fig. 15), Indonesia, Irian Jaya, Elelim, path to Apalapsili, 600 m. PARATYPES: 3 males (BM0058, 60–61), same data as the holotype; 2 males, female (BM0033, 87, 89), Indonesia, Irian Jaya, Bokondini, 1300 m, Nov.–Dec. 1991.

TYPE LOCALITY: New Guinea, Elelim.

ETYMOLOGY: The specific name refers to body coloration.

DIAGNOSIS: *E. niger* sp. nov. is polymorphic in coloration and can be either uniformly black or having the brightly coloured pronotum and scutellum (Figs 15–16). The later

specimens resemble some individuals of *E. variabilis* sp. nov. when they occur in the same locality. These species differ in the relative size of eyes (Tab. 1).

DESCRIPTION: Male, holotype. Body medium sized to large, uniformly dark coloured, only trochanters and bases of femora brown. Head with large hemispherically prominent eyes, their diameter 1.17–1.28 times distance between eyes, antennae slender, serrate, with apical process about a third of antennomere stem. Pronotum transverse, with almost straight lateral margins, lateral bulge inconspicuous, elytra with weak secondary costae and in some parts with irregular cells.

Homogenous sPu characters versus *E. similis*: 455:T, 566:C, 605:T, 847:G, 862:C.

INTRASPECIFIC VARIATION: *E. niger* has two forms (Figs 15, 16). The specimens from Bokondini have more or less brightly coloured pronotum and scutellum (Fig. 16)

DISTRIBUTION: New Guinea, Central Mountains.

Eniclases similis Bocak et Bocakova, 1991

Figs 13, 14, 37

Eniclases similis Bocak et Bocakova, 1991: 210.

MATERIAL EXAMINED: 10 males, 2 females (BM0003–4, 11, 13–14, 19–24, 37), Indonesia, Irian Jaya, Sentani, Cyclops Mts., 300 m, Nov.–Dec. 1991.

TYPE LOCALITY: New Guinea, Karimui.

DIAGNOSIS: *E. similis* differs from similarly coloured individuals of *E. divaricatus* in the large eyes (Tab. 1) and from *E. bicolor* in the gradual transition between the dark and bright part of elytra (Figs 10, 13–14) and extremely small female eyes. Despite distant relationships between *E. similis* and *E. bicolor* (Fig. 1) there is no clearly defined morphological character available for their identification.

REDESCRIPTION: Male. Body medium sized, pronotum, humeral part of elytra, and legs yellow to orange, metathorax, abdomen, apical part of elytra, and sometimes antennae dark brown to black (Figs 12–13). Head with moderately large hemispherically prominent eyes, their diameter 1.17–1.28 times longer than interocular distance, antennae slender, acutely serrate, with apical process of antennomere 3 about third of antennomere stem. Pronotum transverse, with weak lateral bulge in posterior third, elytra with weak, but straight secondary costae and regular, subquadrate cells.

Homogenous sPu characters versus *E. niger*: 455:C, 566:T, 605:C, 847:A, 862:T.

INTRASPECIFIC VARIATION: *E. similis* has two extreme forms in the extent of the bright part of elytra (Figs 13, 14) and transitional forms between these (Tab. S1). The similar colour patterns are present in sympatrically occurring species of *Trichalus*.

DISTRIBUTION: New Guinea Highlands.

REMARK: The species is identified as *E. similis* due to absence of any morphological difference when compared to the holotype of *E. similis*. The type locality of *E. similis* is Karimui in Eastern New Guinea and identity of the species needs further investigation.

5. DISCUSSION

The taxonomy of *Eniclases* has been based solely on the morphological species concept, which depends on the presence of the identifiable diagnostic traits (Kleine, 1926; Bocak & Bocakova, 1991). Such species delimitation is difficult as these beetles are morphologically similar and their diagnostic characters are limited to the relative size of eyes, the shape of antennomeres and eventually body coloration (Figs 6–42). The net-winged beetles are unpalatable and the advergence to the similar body shape and coloration has been proved in other metriorrhynchines (Bocak & Yagi, 2010). Therefore, I suggest that *Eniclases* are similarly selected to resemble sympatrically occurring net-winged beetles. The high degree of resemblance can be demonstrated by similar colour patterns of sympatrically occurring and distantly related *E. similis* and *E. divaricatus* (Figs 1, 6, 13). Already the morphology based revision of *Eniclases* by Bocak & Bocakova (1991) pointed to a high degree of uncertainty in species delimitation and suggested that some species, such as size and colour variable *E. luteolus*, very probably represent a group of morphologically similar species whose status cannot be solved due to uniform morphology.

I investigated morphological and genetic diversification in a clade of 14 *Eniclases* net-winged beetles from the western part of New Guinea, which I delimited as separate species using mtDNA haplotypes, morphological characters and biogeography or any combination of these (DeSalle et al., 2005). I hypothesize that these clusters of individuals represent biological species and are reproductively isolated.

Several species are unique in coloration, the shape of antennae, and size of eyes and they were inferred consensually as separate species by all DNA-based analyses: *E. pseudoapertus* (the closest interspecific match at 10.62%), *E. divaricatus* (11.02%), *E.*

apertus (6.20%), and *E. pseudoluteolus* (9.26%). The genetic distances between these species and their closest relatives are higher than generally accepted intraspecific genetic variation (Hebert et al., 2003; Meier et al., 2006), the posterior delimitation probabilities for the branches leading to these species were all over 90% except the branch of *E. divaricatus* (0.69%).

A much higher degree of uncertainty was found in pairs of closely related terminals, which were refused as putative species by various methods (Fig. 1). I can delimit broadly defined species as suggested by the barcoding threshold (Fig. 1) and consider internal clades as forms without formal taxonomic delimitation or I can delimit each clade as a separate species. The first approach makes morphological definitions very difficult, as at least in some cases, I would have to merge in a single species some individuals with clearly different morphology. Additionally, there are indications that the narrowly defined species are independently selected for different mimetic patterns in various localities and the colour patterns supposedly support reproductive isolation (Bocak & Yagi, 2010). Therefore, I prefer to split the closely related clades in the separate species when they are supported by clear morphological difference (e.g. size of eyes as *E. similis* and *E. niger* or *E. infuscatus* and *E. bicolor*); they occur allopatrically, belong to different mimicry rings and simultaneously differ in the sequence of *cox1* mtDNA (e.g., *E. bokondinensis* and *E. elelimensis*). In one case, the sister clades are defined by divergent DNA sequence and distribution, but no morphological divergence was identified (*E. tikapurensis* + *Eniclases* sp. A, Fig. 1). Below, I discuss reasons for species delimitation in detail.

The pair of *E. infuscatus* and *E. bicolor* represents sister species which differ in coloration (Figs 10–11) and the relative size of female eyes (Tab. 1). They were marginally inferred as separate species using the bPTP model (PP 0.47 and 0.52 versus 0.48 for the branch merging these two entities), but clustered together as a putative single species using the distance method (0.99–1.08% distance). Both species were recorded in Elelim, they are differently coloured, but no transitional haplotypes have been found. Therefore, based on coloration, size of eyes, and genetic difference, I consider these subclades as separate species.

Similarly, *E. bokondinensis* and *E. elelimensis* represent genetically close species with different colour patterns (Figs 17, 19). The bPTP model merged them in a single putative species and the distance method merged both of them with *E. variabilis*. Both species are known from the Central Mts.; *E. bokondinensis* from the mountain region north

of Bokondini (~1900 m a. s. l.) and *E. elelimensis* from Elelim (600 m a. s. l., Fig. 2) about 80 km away. I suppose that in this case the memberships in different mimetic rings play a role in genetic differentiation between these two species (Bocak & Yagi, 2010). Species with *E. elelimensis* colour pattern occur in low elevations and have never been collected in high mountains in the Bokondini area (Tab. S1). This pattern was recorded as high as 1300 m a. s. l. in, but in a biotope very different from mountain forests where *E. bokondinensis* occurs. I suppose that these species occur allopatrically despite the proximity of localities and additionally the colonization of high elevations could support their reproductive isolation (Toussaint et al., 2014).

Eniclases variabilis is a sister to *E. bokondinensis* + *E. elelimensis* clade and was identified as a separate entity using the bPTP model and can be identified by twelve sPu *coxI* mtDNA characters. Other methods merged this species with its sister clade (genetic distance, Fig. 1) or a part of it (morphology, see taxonomy section). The reproductive isolation of *E. variabilis* is supported by the sympatric occurrence of genetically differentiated *E. variabilis* and *E. elelimensis* in Elelim. *E. variabilis* is extremely polymorphic (Figs 20–29) and resembles black coloured *E. niger*, brightly coloured *E. similis* and *E. elelimensis* types, and one colour pattern is unique in *Eniclases* and resembles other net-winged beetles (Figs 20–29). No genetic differentiation has been found in their mtDNA and I consider all colour forms as a single species.

The clade of *E. similis* + *E. niger* was merged in a single putative species by all DNA based analyses, but they can be identified by morphology, colour patterns, and five homologous sPu characters. *Eniclases niger* has large eyes (diameter/distance ratio 1.17–1.28) and *E. similis* has smaller eyes (1.02–1.15). I suppose that the daytime or evening, eventually night activity of respective species might be the reason for observed morphological differentiation. Additionally these species belong to different mimetic complexes. *E. niger* is black coloured (Fig. 15) or has pronotum bright and elytra completely black (Fig. 16) and *E. similis* is brightly coloured. The bright patterns are similar to those of *E. divaricatus* and *E. bicolor* (Figs 6, 10, 13–14) and were recorded also in several *Trichalus* spp. in the respective localities (unpublished data). The sister-species *E. similis* and *E. niger* have not been collected together: *E. niger* occurs in lower mountain localities in the Central Mts. and *E. similis* in low elevations of the Cyclops Mts.

The clade of *E. tikapurensis* and *Eniclases* sp. A split in two subclades, which do not differ in morphology, but they are genetically distant. The levels of DNA distances between *E. tikapurensis* and *Eniclases* sp. A do not agree with geographical distance of

respective localities, when higher differentiation was found between populations from Bokondini and Tikapura (13 km apart) than between localities lying at the rim of the Baliem valley (Yiwika and Tikapura, 35 km apart). The observed genetic differentiation surpasses some cases when separate morphologically divergent sister species are delimited. Due to limited information I postpone formal description of the putative species from Bokondini.

Eniclases are very variable in colouration (Figs 6–29), but the differences in colouration regardless of their depth do not necessarily mean that they can be used for delimitation of reproductively isolated lineages. I found intraspecific colour variability in three species: *E. similis*, *E. niger*, and *E. variabilis* (Figs 13–14, 15–16, 20–29). I ascribe the polymorphism to the advergence to the most common models of other net-winged beetles as described by Bocak & Yagi (2010). Conversely, the colour patterns can be used in several species for their delimitation, e.g. in *E. bicolor* and very characteristic *E. bokondinensis*. Molecular data or further morphological characters are generally needed to investigate colour polymorphism and to support species limits. Uncorrelated morphological and genetic diversity has been reported in lyponiine lycids (Li et al., 2015) and other beetle families (e.g. Goldberg et al., 2012) and points to necessary evaluation of all evidence when species are delimited (Jörger & Schrödl, 2013). The *cox1* mtDNA fragment alone cannot not provide sufficient information on the diversification process, but even these limited data suggest that closely related lineages can develop distant mimetic patterns and start further morphological differentiation, for example in the relative size of eyes. The dated phylogeny suggest that all closely related sister species differentiated in the last million years (Fig. 2).

6. CONCLUSION

The study provided further data on exceptional diversity and endemism of the beetle fauna of in the central mountain range in New Guinea and support separation of the New Guinean fauna in a distinct zoogeographical region (Holt et al., 2013). The present study focused on delimitation of species for taxonomic purposes. I found intraspecific variability in colour patterns and genetic diversity in a very limited geographic space and between populations belonging to different mimicry rings. As a result, different approaches of delimitation provide conflicting results. The high turn over between fauna of western and eastern regions of New Guinea suggests that many broadly defined and widely distributed species described by previous authors (Kleine, 1926; Bocak & Bocakova, 1991) may in fact represent assemblages of morphologically similar, but unrelated taxa. As the short mtDNA fragment limits conclusions, further data are needed to investigate diversification processes in the aposematically coloured net-winged beetles in New Guinea.

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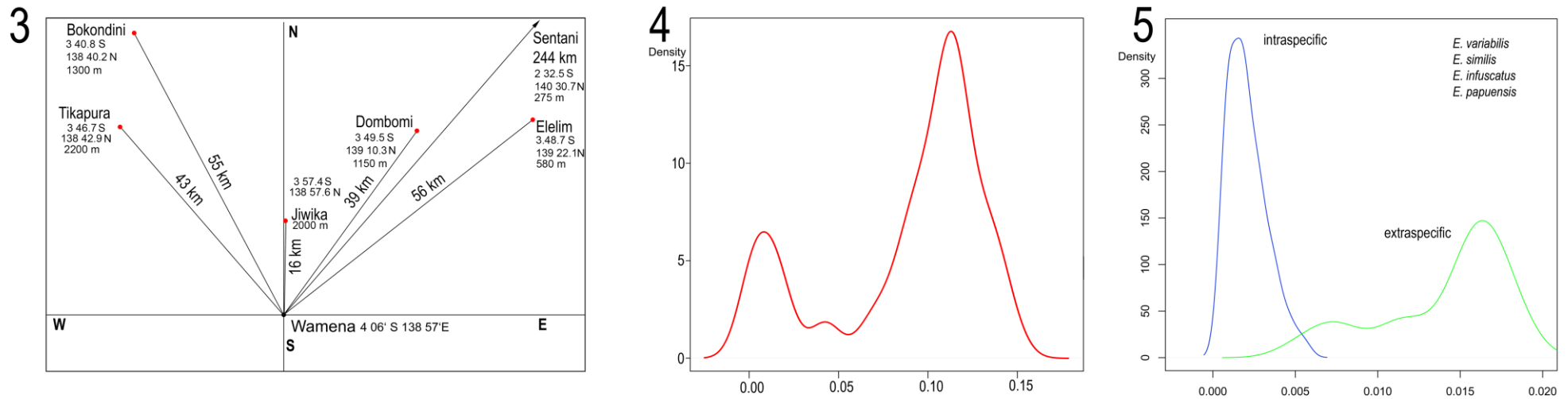
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8. SUPPLEMENTS

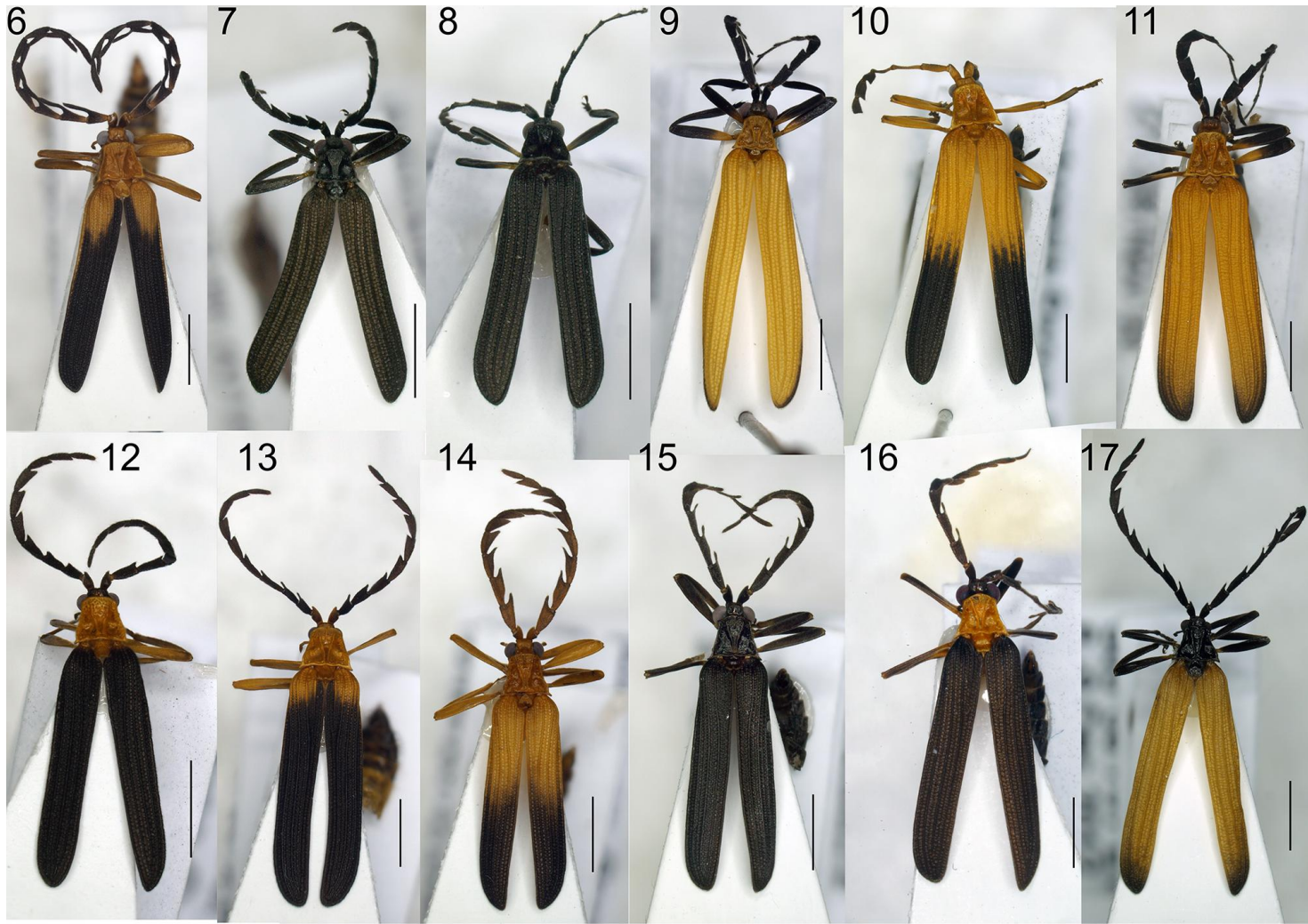
Table S1. Measurements of *Eniclases* spp. from Eastern New Guinea (EDiam = relative size of eye; Edist = distance between eyes)

	Body	Width	Pronotum		EDiam/Edist	
	length	humeri	length	width	male	female
<i>E. pseudoapertus</i>	6.3	1.6	0.75	1.2	1.4	n.a.
<i>E. divaricatus</i>	8.8–9.7	2.1–2.3	1.2–1.3	1.7–1.7	0.92–0.96	0.80–0.87
<i>E. pseudoluteolus</i>	9.3	2.3	1.15	1.6	0.9	n.a.
<i>E. apertus</i>	5.8–6.9	1.4–1.7	0.9	1.25	1.15–1.17	n.a.
<i>E. tagimensis</i>	9.5–11.1	2.0–2.5	1.1–1.3	1.4–1.7	1.11–1.40	0.92–1.06
<i>E. bicolor</i>	10.3	2.4	1.4	1.7	n.a.	0.71–0.74
<i>E. infuscatus</i>	12.1	2.5	1.25	1.6	n.a.	0.79–0.84
<i>E. brancuccii</i>	7.6–8.0	1.8–1.9	1.0–1.1	7.5–8.0	1.00	0.84–0.91
<i>E. bokondinensis</i>	9.2	2.05	1.0	1.35	n.a.	0.72–0.82
<i>E. elelimensis</i>	6.9–8.1	1.5–1.9	0.9–1.1	1.3–1.4	n.a.	0.78–0.89
<i>E. variabilis</i>	6.6–8.2	1.6–2.0	0.1–1.1	1.1–1.35	0.83–0.95	0.70–0.85
<i>E. niger</i>	9.2–11.6	2.2–2.8	1.3–1.6	9.0–11.5	1.17–1.28	0.89
<i>E. similis</i>	7.5–9.7	1.9–2.3	1.1–1.4	1.8–1.8	1.02–1.15	0.89

n.a. – not available



Figs 3–5. (3) The positions, coordinates and elevations of sampled localities in the Central Mountains of New Guinea as taken from Google Earth; (4) Density plots of genetic distances of all *Eniclases* samples; (5) Density plots of intra- and interspecific genetic distances between pairs of closely related species of *Eniclases* (*E. infuscatus* and *E. bicolor*; *E. tikapurensis* and *Eniclases* sp. A; *E. variabilis*, *E. elelimensis* and *E. bokondinensis*; *E. niger* and *E. similis*).

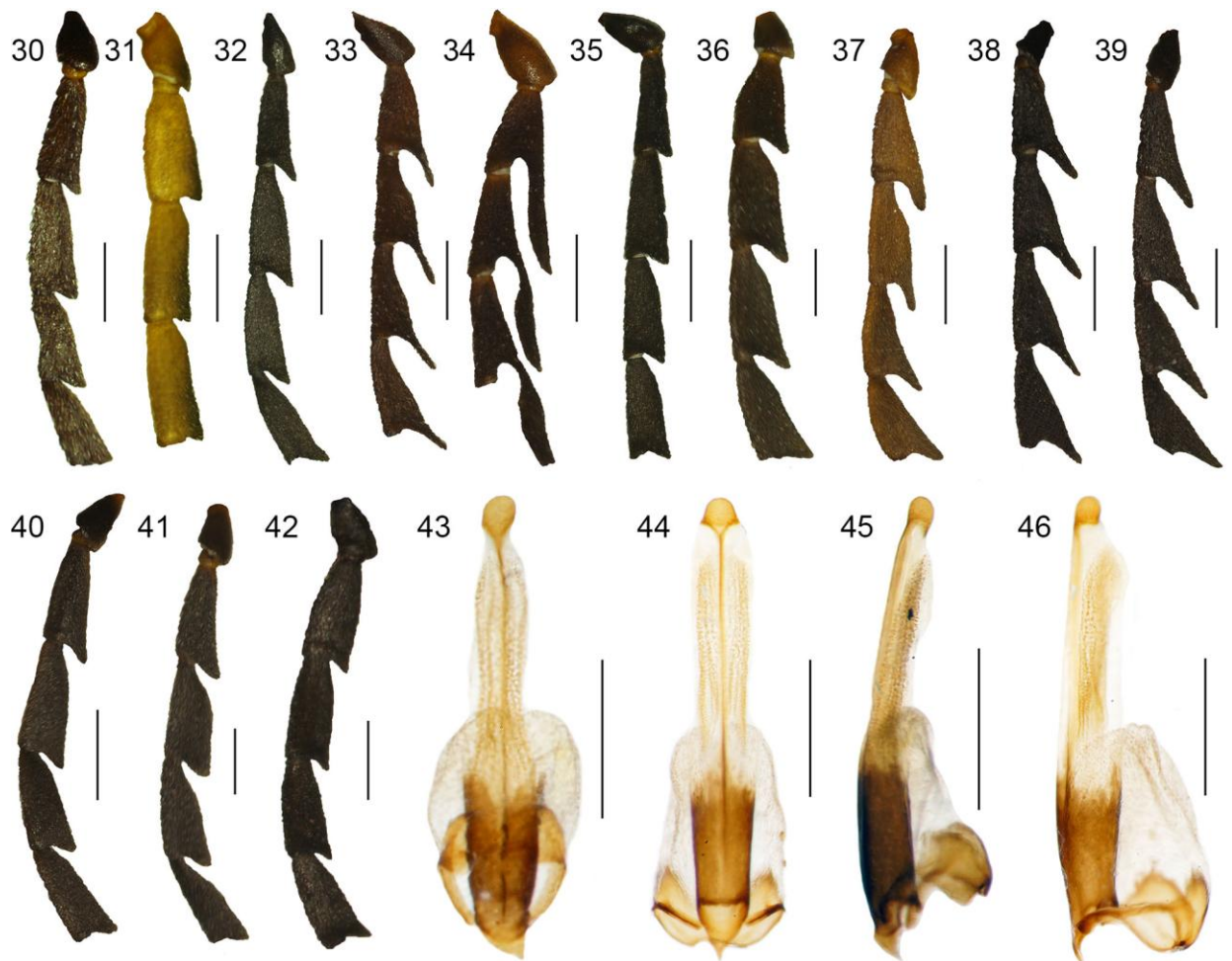


Figs 6–17. General appearance of *Eniclases*: (6) *E. divaricatus*, male; (7) *E. pseudoapertus* sp. nov., male; (8) *E. apertus*, male; (9) *E. tikapurensis* sp. nov., male; (10) *E. bicolor* sp. nov., female; (11) *E. infuscatus* sp. nov., female; (12) *E. similis*, female; (13) *E. similis*, male; (14, 15) *E. niger* sp. nov., male; (16) *E. brancuccii* sp. nov., female; (17) *E. bokondinensis* sp. nov., female. Scale bars: 2 mm.



Figs 18–29. General appearance of *Eniclases*: (18) *E. bokondinensis* sp. nov., female; (19) *E. elelimensis*, female; (20–29) *E. variabilis* sp. nov.

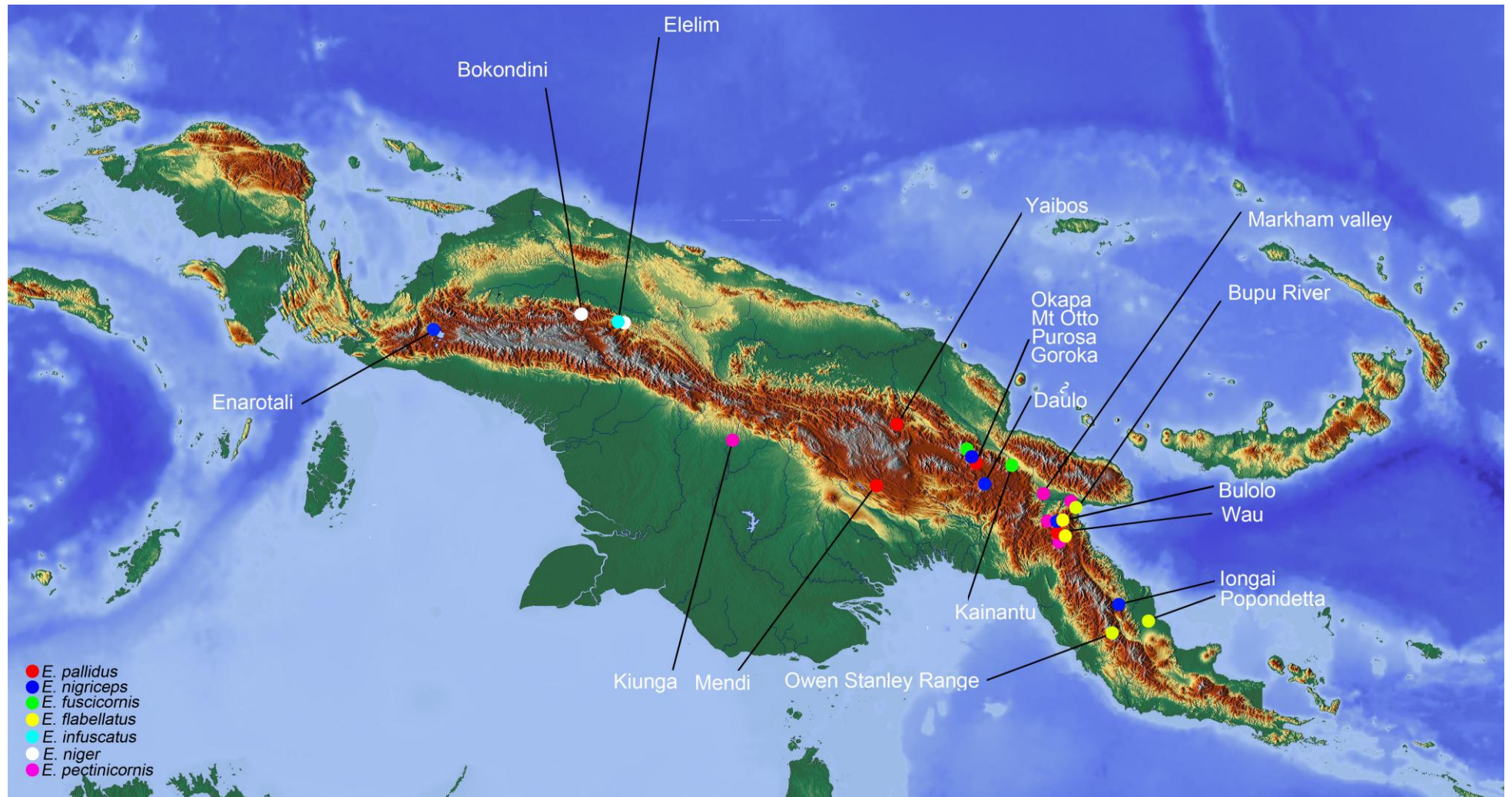
Scale bars: 2 mm.



Figs 30–46. Basal antennomeres (Figs 30–42): (30) *E. apertus*, male; (31) *E. bicolor* sp. nov., female; (32) *E. bokondinensis* sp. nov., female; (33) *E. brancuccii* sp. nov., male; (34) *E. divaricatus*, male; (35) *E. infuscatus* sp. nov., female; (36) *E. pseudoluteolus*, male; (37) *E. similis*, male; (38) *E. variabilis* sp. nov., male; (39) *E. elelimensis*, male; (40) *E. niger* sp. nov., female; (41) *E. papuensis*, male; (42) *E. pseudoapertus* sp. nov., male. Male genitalia (Figs 43–46): (43) *E. variabilis* sp. nov., ventral view; (44) *E. pseudoluteolus*, ventral view; (45) *E. variabilis* sp. nov., lateral view; (46) *E. pseudoluteolus*, lateral view.

Scale bars: 0.5 mm.

Maps S1–S4. Distribution of *Eniclases* in New Guinea.







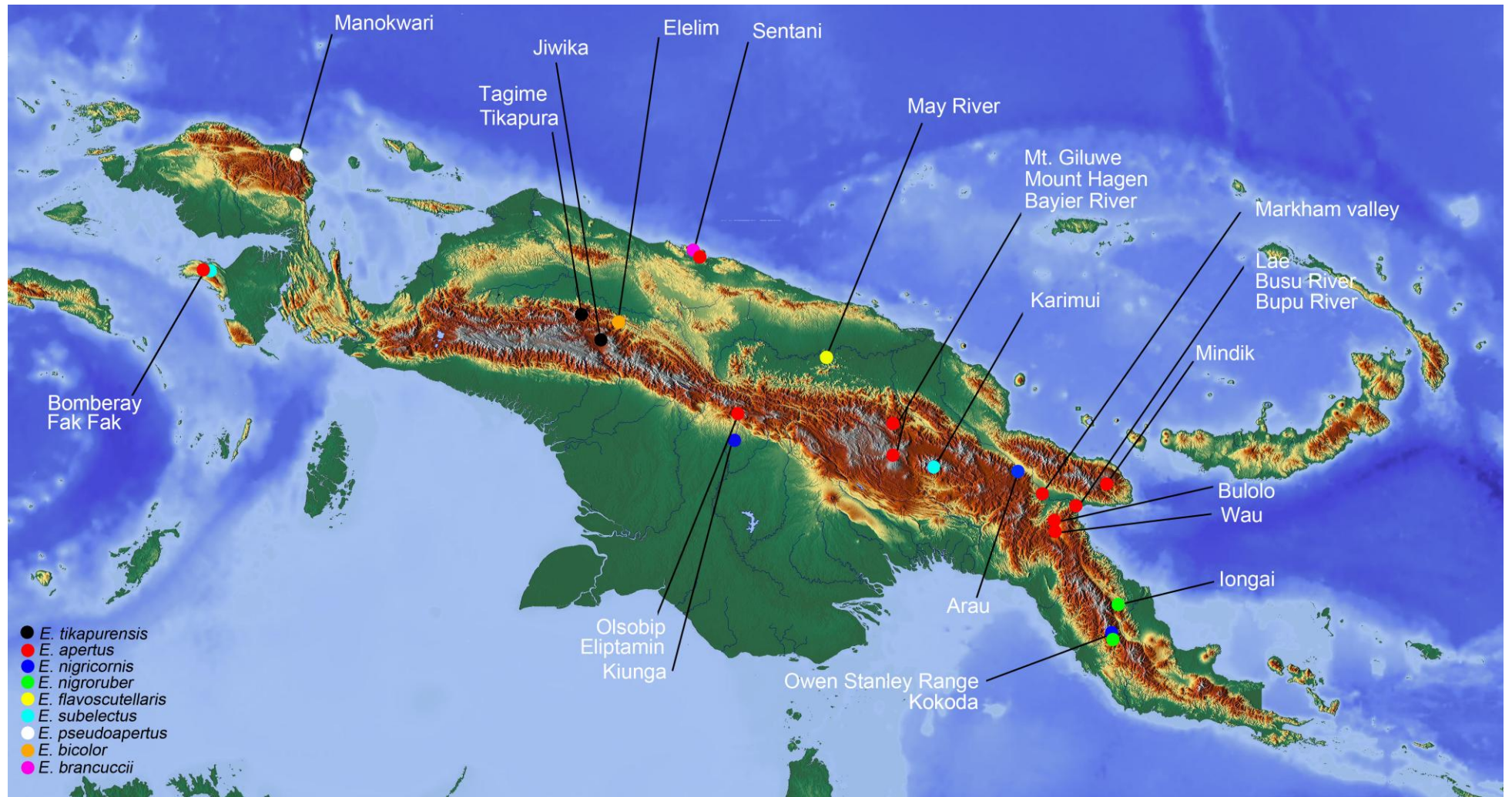


Table S2. The list of sequenced specimens, their voucher numbers, GenBank accession numbers, geographic origins, and the colour patterns.

<i>Eniclases</i> species	Voucher number	GenBank Access No.	Locality (all New Guinea)	Mimetic pattern
<i>E. pseudoapertus</i>	BM0080	XY111112	Irian Jaya, Arfak Mts., Maibri vill., 1600 m	Fig. 7
<i>E. pseudoluteolus</i>	BM0084	XY111113	Irian Jaya, Arfak Mts., Maibri vill., 1600 m	uniformly yellow
<i>E. niger</i>	BM0089	XY111114	Irian Jaya, Bokondini, 1300 m	Fig. 15
	BM0087	XY111115	Irian Jaya, Bokondini, 1300 m	intermediate, as Figs 14 and 15
	BM0060	XY111116	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 14
	BM0059	XY111117	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 14
	BM0061	XY111118	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 14
	BM0033	XY111119	Irian Jaya, Bokondini, 1300 m	similar to Fig. 14
	BM0058	XY111120	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 14
<i>E. similis</i>	BM0024	XY111121	Irian Jaya, Cyclops Mts., Sentani, 300 m	Fig. 13
	BM0037	XY111122	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 13
	BM0020	XY111123	Irian Jaya, Cyclops Mts., Sentani, 300 m	intermediate, as Figs 12 and 13
	BM0019	XY111124	Irian Jaya, Cyclops Mts., Sentani, 300 m	intermediate, as Figs 12 and 13
	BM0022	XY111125	Irian Jaya, Cyclops Mts., Sentani, 300 m	intermediate, as Figs 12 and 13
	BM0021	XY111126	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 12
	BM0023	XY111127	Irian Jaya, Cyclops Mts., Sentani, 300 m	intermediate, as Figs 12 and 13
	BM0003	XY111128	Irian Jaya, Cyclops Mts., Sentani, 300 m	Fig. 12
	BM0014	XY111129	Irian Jaya, Cyclops Mts., Sentani, 300 m	intermediate, as Figs 12 and 13
	BM0013	XY111130	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 12
	BM0011	XY111131	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 13
	BM0004	XY111132	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 12
<i>E. divaricatus</i>	BM0057	XY111133	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 6
	BM0001	XY111134	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 6
	BM0009	XY111135	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 6
	BM0015	XY111136	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 6
	BM0017	XY111137	Irian Jaya, Cyclops Mts., Sentani, 300 m	no photo
	BM0016	XY111138	Irian Jaya, Cyclops Mts., Sentani, 300 m	Fig. 6
<i>E. apertus</i>	BM0002	XY111139	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 6
	BM0038	XY111140	Irian Jaya, Cyclops Mts., Sentani, 300 m	Fig. 8
	BM0018	XY111141	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 8
<i>E. infuscatus</i>	BM0050	XY111142	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 11
	BM0062	XY111143	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 11
<i>E. bicolor</i>	BM0045	XY111144	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 10
	BM0046	XY111145	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 10
	BM0047	XY111146	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 10
<i>Eniclases</i> sp. A	BM0093	XY111147	Irian Jaya, Bokondini, 1800 m	similar to Fig. 9
	BM0097	XY111148	Irian Jaya, Bokondini, 2100 m	similar to Fig. 9
	BM0096	XY111149	Irian Jaya, Bokondini, 2100 m	similar to Fig. 9
<i>E. tikapurensis</i>	BM0043	XY111150	Irian Jaya, Tagime, Tikapura village, 2200 m	similar to Fig. 9
	BM0040	XY111151	Irian Jaya, Tagime, Tikapura village, 2200 m	similar to Fig. 9
	BM0044	XY111152	Irian Jaya, Tagime, Tikapura village, 2200 m	similar to Fig. 9
	BM0042	XY111153	Irian Jaya, Tagime, Tikapura village, 2200 m	similar to Fig. 9
	BM0039	XY111154	Irian Jaya, N of Wamena, Yiwika, 2100 m	Fig. 9
	BM0041	XY111155	Irian Jaya, Tagime, Tikapura village, 2200 m	similar to Fig. 9
<i>E. brancuccii</i>	BM0006	XY111156	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 16
	BM0005	XY111157	Irian Jaya, Cyclops Mts., Sentani, 300 m	Fig. 16
	BM0010	XY111158	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 16
	BM0007	XY111159	Irian Jaya, Cyclops Mts., Sentani, 300 m	similar to Fig. 16
<i>E. elelimensis</i>	BM0052	XY111160	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 19
	BM0051	XY111161	Irian Jaya, Elelim, path to Apalapsili, 600 m	similar to Fig. 19
	BM0056	XY111162	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 19
<i>E. bokondinensis</i>	BM0092	XY111163	Irian Jaya, Bokondini, 1800 m	Fig. 18
	BM0094	XY111164	Irian Jaya, Bokondini, 1800 m	similar to Fig. 18
	BM0095	XY111165	Irian Jaya, Bokondini, 1800 m	Fig. 17
<i>E. variabilis</i>	BM0035	XY111166	Irian Jaya, Bokondini, 1300 m	Fig. 27
	BM0029	XY111167	Irian Jaya, Bokondini, 1300 m	similar to Fig. 28
	BM0028	XY111168	Irian Jaya, Bokondini, 1300 m	similar to Fig. 28
	BM0027	XY111169	Irian Jaya, Bokondini, 1300 m	similar to Fig. 28
	BM0091	XY111170	Irian Jaya, Bokondini, 1300 m	similar to Fig. 25
	BM0090	XY111171	Irian Jaya, Bokondini, 1300 m	similar to Fig. 27
	BM0088	XY111172	Irian Jaya, Bokondini, 1300 m	similar to Fig. 27
	BM0086	XY111173	Irian Jaya, Bokondini, 1300 m	similar to Fig. 27
	BM0036	XY111174	Irian Jaya, Bokondini, 1300 m	similar to Fig. 27
	BM0063	XY111175	Irian Jaya, Lower Pass valley, Dombomi, 1200 m	similar to Fig. 29
	BM0053	XY111176	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 24
	BM0049	XY111177	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 22
	BM0054	XY111178	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 20

BM0055	XY111179	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 21
BM0048	XY111180	Irian Jaya, Elelim, path to Apalapsili, 600 m	Fig. 23
BM0012	XY111181	Irian Jaya, Cyclops Mts., Sentani, 300 m	Fig. 26
BM0008	XY111182	Irian Jaya, Cyclops Mts., Sentani, 300 m	Fig. 25
BM0065	XY111183	Irian Jaya, Lower Pass valley, Dombomi, 1200 m	similar to Fig. 29
BM0066	XY111184	Irian Jaya, Lower Pass valley, Dombomi, 1200 m	similar to Fig. 29
BM0067	XY111185	Irian Jaya, Lower Pass valley, Dombomi, 1200 m	similar to Fig. 29
BM0026	XY111186	Irian Jaya, Bokondini, 1300 m	similar to Fig. 28
BM0025	XY111187	Irian Jaya, Bokondini, 1300 m	Fig. 28
BM0030	XY111188	Irian Jaya, Bokondini, 1300 m	similar to Fig. 28
BM0031	XY111189	Irian Jaya, Bokondini, 1300 m	similar to Fig. 27
BM0064	XY111190	Irian Jaya, Lower Pass valley, Dombomi, 1200 m	Fig. 29
BM0034	XY111191	Irian Jaya, Bokondini, 1300 m	similar to Fig. 27
BM0032	XY111192	Irian Jaya, Bokondini, 1300 m	similar to Fig. 27

Table S3. The list of outgroup taxa, their voucher numbers, and geographic origins (sequences published by Sklenarova et al. 2013).

Specimen	Voucher number	Geographic origin
<i>Cautires</i> sp.	000088	Malaysia, Pahang, Cameron Highlands, Tanah Rata, 1600 m
<i>Cautires</i> sp.	000206	Indonesia, Sumatra, Mount Tujuh, 5 km E Kersik Dua, 1900 m
<i>Cautires</i> sp.	000262	Indonesia, Centr. Kalimantan, North Barito, 60 km SE Muara Teweh, 01°20.25'S, 115°20.16'E, 150 m
<i>Cautires</i> sp.	000342	Indonesia, South Kalimantan, 10 km E of Loksado, 02°43.57'S, 115°32.50'E, 600-1100 m
<i>Leptotrichalus</i> sp.	A00451	Indonesia, Java, Ijen NP, 12 km W of Sodong, 1000 m
<i>Metriorrhynchus</i> sp.	A00043	Australia, Queensland, Lamington NP
<i>Metriorrhynchus</i> sp.	A00217	Australia, Queensland, Lamington NP, Lahey Nem., 28°11.28'S, 153°07.156'E
<i>Metr. sericans</i>	A00381	Laos, Houa Phan. prov., 20°07' N, 103°35.4'E, Bam Saleuy-Phou Pane Mt., 1340-1870 m
<i>Porrostoma</i> sp.	A00035	Australia, Queensland, Lamington NP
<i>Trichalus</i> sp.	A00320	Australia, Queensland, Fletcher Creek, 19°48.552'S, 146°03.233'E, 310 m
<i>Diatrichalus</i> sp.	A00208	Australia, Chilverston
<i>Diatrichalus</i> sp.	A00118	Papua New Guinea, Haia, Crater Mt., 06°40.047'S, 145°03.464'E, 1350 m
<i>Diatrichalus</i> sp.	A00156	Papua New Guinea, Goroka, Mt.Gahavisuka, 06°00.864'S, 145°24.779'E, 2150-2280 m
<i>Diatrichalus</i> sp.	A00298	Australia, Queensland, Pascoe Riv. Xing, 12°53.599'S, 143°00.252'E
<i>Diatrichalus</i> sp.	A00423	Malaysia, W. Kelantan, 30 km NW of Gua Musang, Ulu Lalat Mt., Kampong Sungai Om, 800-1000 m
<i>Diatrichalus</i> sp.	BM0068	Indonesia, Maluku, E Buru isl., Ilath env., Remaja Mt., 200 m
<i>Microtrichalus</i> sp.	A00357	Australia, Queensland, East Claudie River, 12°42.504'S, 143°17.132'E, 15 m
<i>Microtrichalus</i> sp.	000375	Australia, Queensland, Molloy, Julatten
<i>Microtrichalus</i> sp.	000376	Australia, Queensland, Molloy, Julatten
<i>Microtrichalus</i> sp.	A00399	Cambodia, SW, 20 km SE, Koh Kong, Tatai riv., 11°34'N, 103°07'E, 200 m
<i>Microtrichalus</i> sp.	A00454	Indonesia, Sumatra Utara, Brastagi, Gn Sibayak, 1600-2200 m
<i>Flabellotrichalus</i> sp.	A00170	Papua New Guinea, Haia, Crater Mt., 06°41.553'S, 145°00.355'E, 800-960 m
<i>Villosotrichalus</i> sp.	A00172	Papua New Guinea, Haia, Crater Mt., 06°41.955'S, 145°00.147'E, 780 m
<i>Trichalus</i> sp.	A00363	Australia, Queensland, East Claudie River, 12°42.504'S, 143°17.132'E, 15 m
<i>Trichalus</i> sp.	A00370	Australia, Queensland, Bunya Mts. NP, 26°52.12'S, 151°35.24'E

Supplementary data. Alignment of the ingroup taxa in the fasta format.

>BM0060

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>BM0087

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>BM0020

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>BM0011

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