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The Phylogenetic Structure of Metriorrhynchini Fauna of Sulawesi (Coleoptera: Lycidae) with Descriptions of a New Genus, *Mangkutanus*, and Three New Species of *Xylobanus*

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Vaclav Kubecek, Milan Dvorak, and Ladislav Bocak (2011) The phylogenetic structure of Metriorrhynchini fauna of Sulawesi (Coleoptera: Lycidae) with descriptions of a new genus, *Mangkutanus*, and three new species of *Xylobanus*. *Zoological Studies* **50**(5): 645-656. The phylogenetic structure of the Metriorrhynchini fauna from Sulawesi was investigated. We obtained DNA sequences for 3 fragments of the mitochondrial genome: cytochrome oxidase I, tRNA-Leu, and cytochrome oxidase subunit 2; NADH dehydrogenase subunit 5, tRNA-Ser, tRNA-Glu, and tRNA-Phe; and *rrnl*, tRNA-Leu, and NADH dehydrogenase subunit 1 for a total of 3070 aligned nucleotide positions, and performed a phylogenetic analysis of 12 genera of the Metriorrhynchini from Sulawesi and adjacent regions. Metriorrhynchini formed a monophylum that was split into 2 clades: an Afro-Oriental clade consisting of *Cautires* Waterhouse, 1879 and *Xylobanus* Waterhouse, 1879, and an Austral-Oriental clade formed by 10 genera distributed either only in the Australian Region, or with hundreds of species in Australia and New Guinea and a few in the Oriental region. Altogether, 11 genera are known from Sulawesi, four of them endemic to the island, only 2 genera, *Xylobanus* and *Cautires*, with a presumed Oriental origin, and 9 belonging to the Australian clade. All 87 metriorrhynchine species except 1 are endemic to Sulawesi, and 79 (91%) of them belong to the Australian lineage. We propose *Mangkutanus* gen. nov. for 2 species, which were previously placed in *Sulabanus* Dvorak and Bocak, 2007. The genus is described, diagnostic characters are illustrated, and relationships are discussed. We further redescribe the genus *Xylobanus*, describe 3 new species, and provide a key to Sulawesi species. http://zoolstud.sinica.edu.tw/Journals/50.5/645.pdf

Key words: Phylogeny, mtDNA, Endemism, Dispersal, Taxonomy, Wallacea.

Wallace's line was proposed as a zoogeographic border between continental Asia and Australia 150 yr ago (Wallace 1860). Although permeability of the line is widely acknowledged (Mayr 1944), the dispersal history of various lineages depends on their biology, and consequently the phylogenetic structure of the Sulawesi fauna remains poorly studied. Several authors examined the phylogeny and distribution of animals found in the transitional zone between the Oriental and Australian regions including Sulawesi in the last 10 yr, but either focused on populations of a single species or the distributions of closely related species in the entire region including Sulawesi (Maekawa et al. 2001, Balke et al. 2004 2009, Campbell et al. 2004, Sikes et al. 2006). Herein, we analyzed relationships among genera of the Metriorrhynchini to investigate the phylogenetic structure of the Sulawesi net-winged beetle fauna.

The island of Sulawesi began to form about 23 × 10^6 yr ago (mya) as a result of collisions between several oceanic landmasses and an Asian continental fragment (Hall 2002), and has never been connected to the Asian continent, although the Makassar Strait was much narrower during cold periods (Voris 2000). The Buton-Tukang Besi

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Platform which forms the southwestern peninsula of Sulawesi is a microcontinent of Australian origin, which collided with Sulawesi about 15 mya. The Banggai Sula Block drifted to Sulawesi 6 mya (Hall 2002). As a consequence, the Sulawesi fauna may be a mixture of both Asian and Australian continental faunas, but little is known about the balance between them in Sulawesi or about relationships among the faunas of Sulawesi, the Philippines, and Sundaland. Similarities of Sulawesi and Philippine fauna led to the definition of Huxley's line, which excludes the Philippines from the Oriental Region, the significance of which was supported by numerous studies (Atkins et al. 2001, de Bruyn et al. 2004).

Although the 1st species of net-winged beetles from Sulawesi was described in the 19th century, study of the fauna was neglected for a long time, and only a few species were described by R. Kleine and M. Pic in 1920s and 1930s (Kleine 1933). Recently, 2 metriorrhynchine genera and several dozen species were described in a series of taxonomical studies (Bocak 2000a 2001, Bocak and Jass 2004, Bocak et al. 2006, Dvorak and Bocak 2007 2009). Herein, we conducted a phylogenetic analysis to address relationships and the zoogeography of the Metriorrhynchini from Sulawesi. The principal question we addressed was the proportions of Asian and Australian lineages based on the phylogenetic hypothesis. Additionally, we also addressed the question of the monophyly of morphologically defined genera of previous studies, described a new genus, and redescribed the genus *Xylobanus*, describing 3 new species and providing a key to Sulawesi species. The role of molecular data has increased in taxonomic research (Nalugwa 2010, Chullasorn 2011), and we used both sources of information to delimit the described genera and species. We consider the availability of DNA information for primary-type specimens as an integral part of delimitation of new taxa.

MATERIAL AND METHODS

Sampling and geographic origin

In total, 23 species representing 8 genera of the Metriorrhynchini were sequenced, with GenBank accession numbers given in table 1. All known genera from Sulawesi were included in the analysis, except for *Diatrichalus* Kleine, 1926 and *Lobatang* Bocak, 1998. The properly fixed tissues for DNA extraction were unavailable for these taxa. Sequences representing a further 31 species available from GenBank were added to the dataset (Bocak et al. 2006 2008).

DNA extraction, polymerase chain reaction (PCR) amplification, and DNA sequencing

Total DNA was extracted using the phenol-chloroform protocol, and the extraction yield was determined using a NanoDrop-1000 spectrophotometer (NanoDrop Technologies, Inc., Wilmington, USA). The PCR was performed using 0.5-0.6 U Taq polymerase, 1 mM $MgCl_2$, 50 mM of each dNTP, 0.2 mM primer, and typically 0.03 mg of a template in a 50-ml reaction volume. Cycle conditions were generally 35-40 cycles of 2 min at 94°C, 30-60 s at 94°C, 30-60 s at 45-52°C, and 1-2 min at 72°C, with a final 10 min at 72°C. Three fragments were included in the study: 1100 bp comprising *cox1*, *tRNA-Leu*, and *cox2*; a 1180-bp fragment comprising *nad5* and the adjacent *tRNA-Phe*, *tRNA-Glu*, and *tRNA-Ser*; and an 800-bp fragment comprising *rrnl*, *tRNA-Leu*, and *nad1* (respectively referred to as *cox1*, *nad5*, and *rrnl* hereafter). The primers used are listed by Bocak and Yagi (2010). Purified PCR products were sequenced on an ABI 3130 automated sequencer (Applied Biosystems, Foster City, USA) using the Big Dye Terminator Cycle Sequencing Kit vers. 1.1 (Applied Biosystems, Foster City, USA).

Sequence handling and phylogenetic analyses

Sequences were edited using the Sequencher 4.6 software package (Gene Codes, Ann Arbor, USA) and aligned with ClustalX 1.8 using the default settings (Thompson et al. 1997). The aligned sequences were inspected with the naked eye, and some minor adjustments were made.

A phylogenetic analysis was carried out under parsimony criteria using PAUP vers. 4.0.10 (Swofford 2003). All DNA fragments were combined for the final analysis. Equal weights were assigned to all positions, and gaps were treated as a 5th character state. For the bootstrap analysis, 1000 pseudoreplicates were generated and subsequently analyzed. The concatenated matrix was further analyzed under the likelihood criterion with RAxML vers. 7.2.3 (Stamatakis et al. 2008), and the support of the branches was assessed by analyzing 100 pseudoreplicates. All genes and codon positions in the protein coding fragments were partitioned. The model was

Table 1. Specimens included in the study

Species	Voucher number	Geographic origin	*rrnl*	*cox1*	*nad5*
Cantharis decipiens Baudi	00M14	Czech Republic	DQ198685	DQ198608	DQ181417
Lyropaeus sp.	000L11	Malaysia	DQ180968	DQ181190	DQ181344
Scarelus nigricornis Malohlava et Bocak	000L15	Malaysia	-	DQ181194	DQ181348
Lyponia nigrohumeralis Pic	000L17	China	DQ180974	DQ181196	DQ181350
Dihammatus sp.	000L12	Malaysia	DQ180969	DQ181191	DQ181345
Plateros sp.	000L13	Malaysia	DQ180970	DQ181192	DQ181346
Calochromus sp.	000L16	China	DQ180973	DQ181195	DQ181349
Macrolycus sp.	000L18	China	DQ180975	DQ181197	DQ181351
Broxylus pfeifferi Waterhouse	MD0099	Sulawesi	HQ456957	HQ456980	HQ457002
B. malinensis Bocak et Jass	MD0101	Sulawesi	HQ456958	HQ456981	HQ457003
Cautires sp. (A)	000L14	RSA	DQ180971	DQ181193	DQ181347
Cautires sp. (B)	000L06	Malaysia	DQ180967	DQ181189	DQ181343
Cautires sp. (C)	A00021	Taiwan	HQ456947	HQ456965	-
Cautires sp. (D)	A00048	Malaysia	HQ456948	HQ456967	HQ456990
Cautires sp. (E)	A00080	Cameroon	HQ456950	HQ456969	HQ456992
Cautires sp. (F)	A00022	Madagascar	-	HQ456966	HQ456989
Cautires sp. (G)	000132	SE Asia	-	HQ456987	HQ457009
Cautiromimus sp.	000459	New Guinea	-	DQ144680	DQ144704
Cladophorus sp.	000451	New Guinea	-	DQ144681	DQ144705
Leptotrichalus sp. (A)	000208	Sabah	-	DQ181212	DQ181366
Leptotrichalus sp. (B)	A00052	Philippines	HQ456949	HQ456968	HQ456991
Mangkutanus tenggahensis Dvorak et Bocak	MD0002	Sulawesi	HQ456951	HQ456970	-
Metriorrhynchus sp. (B)	000169	New Guinea	-	DQ144663	DQ144689
Metriorrhynchus sp. (A)	000170	New Guinea	-	DQ144664	DQ144690
Metriorrhynchus sp. (C)	000447	New Guinea	-	DQ144669	DQ144695
Metriorrhynchus sp. (D)	000010	Sulawesi	-	DQ144659	DQ144685
M. thoracicus (Fabr.)	000519	Sulawesi	-	DQ144672	DQ144698
M. lobatus Bocak et Matsuda	000017	Sulawesi	-	DQ144662	DQ144688
Metriorrhynchus sp. (E)	000011	Sulawesi	-	DQ144660	DQ144686
M. sericans Waterhouse	000526	Laos	-	DQ144673	DQ144699
M. sericeus Waterhouse	00517	Bali	-	DQ144670	DQ144696
Metriorrhynchus sp. (F)	000597	Philippines	-	DQ144676	DQ144701
M. philippinensis Waterhouse	000558	Philippines	-	DQ144675	DQ144691
M. palawanensis Bocak, Matsuda et Yagi	000366	Philippines	-	DQ144665	DQ144691
M. lineatus Kirsch	000L05	Sabah	DQ180966	DQ181188	DQ181342
Microtrichalus sp. (A)	000L23	Sabah	DQ180978	DQ181200	DQ181354
Microtrichalus sp. (B)	MD0097	Sulawesi	HQ456955	HQ456978	HQ457000
Microtrichalus sp. (C)	MD0098	Sulawesi	HQ456956	HQ456979	HQ457001
Porrostoma sp.	000378	Australia	-	DQ144679	DQ144703
P. rhipidium W. M'Leay	000372	Australia	-	DQ144678	DQ144702
Sulabanus major Dvorak et Bocak	000500	Sulawesi	-	DQ144683	DQ144707
S. mamasensis Dvorak et Bocak	000498	Sulawesi	-	DQ144682	DQ144706
S. pendolensis Dvorak et Bocak	000501	Sulawesi	-	DQ144684	DQ144708
S. lineatus Dvorak et Bocak	MD0060	Sulawesi	HQ456954	HQ456976	HQ456998
S. brancuccii Dvorak et Bocak	MD0082	Sulawesi	-	HQ456977	HQ456999
Wakarumbia petri Bocak	MD0118	Sulawesi	HQ456960	HQ456983	HQ457005
W. mamasensis Bocak	MD0122	Sulawesi	HQ456962	HQ456985	HQ457007
W. amporiwensis Bocak	MD0123	Sulawesi	HQ456963	HQ456986	HQ457008
W. monacha Bocak	MD0110	Sulawesi	HQ456959	HQ456982	HQ457004
W. montana Bocak	MD0119	Sulawesi	HQ456961	HQ456984	HQ457006
Xylobanus sp. (A)	A00018	Taiwan	HQ456946	HQ456964	HQ456988
Xylobanus taupensis sp. n.	MD0059	Sulawesi	HQ456953	HQ456975	HQ456997
Xylobanus sp. (B)	MD0026	Sulawesi	HQ456952	HQ456971	HQ456993
Xylobanus panensis sp. n.	MD0045	Sulawesi	-	HQ456974	HQ456996
Xylobanus kundratai sp. n.	MD0029	Sulawesi	-	HQ456972	HQ456994
Xylobanus kundratai sp.n.	MD0036	Sulawesi	-	HQ456973	HQ456995

proposed by jModelTest 0.1.1 (Posada 2008). The dataset was additionally analyzed using MrBayes vers. 3.1.2 (Huelsenbeck and Ronquist 2001). A Monte Carlo Markov chain (MCMC) was set for independent variability of parameters in individual coding and non-coding genes under the GTR+I+G model. Four chains were run simultaneously for 5 × 10^6 generations, with trees being sampled each 1000 generations; all fragments were partitioned and unlinked. The 1st 1000 trees were discarded as burn-in, and posterior probabilities at nodes were determined from the remaining trees.

Taxonomy

The morphological part of the study was based on adult males, as females do not have reliable diagnostic characters. Male genitalia were dissected after muscles and fat bodies had been removed by briefly boiling in 10% KOH. Illustrations were derived from photographs taken with a digital camera attached to a stereoscopic microscope. Measurements were taken under a dissecting microscope using an ocular micrometer.

The following measurements were taken: BL, body length; WH, width at the humeri; PL, pronotum length; PW, pronotum width; Edist, minimum interocular distance at the frontal part of the cranium; and Ediam, maximum eye diameter in lateral view.

Specimens are deposited in the following institutions: Natural History Museum, London (BMNH) and the Department of Zoology, Palacky Univ., Olomouc, Czech Republic (LMBC).

RESULTS

The *rrnl*, *cox1*, and *nad5* sequences for all taxa were aligned along 3070 homologous positions, of which 1239 characters were constant, 386 were variable and parsimoniously uninformative, and 1445 were parsimoniously informative. Uncorrected pairwise sequence divergence reached 25.73% among the 48 ingroup specimens. The *rrnl* fragment reached 17.75%, *cox1* reached 23.04%, and *nad5* reached 25.73% divergences.

The parsimony analysis (with all positions equally weighted and gaps considered to be the 5th character) returned 8 most-parsimonious trees (13,176 steps, consistency index = 0.249, retency index = 0.390; trees not shown). The strict consensus tree contained 2 basal clades: an Oriental clade formed by *Cautires* and *Xylobanus*, and an Australian clade represented by the remaining genera. The monophyly of the genera was consistently recovered. The basal topology of the Australian clade obtained generally low bootstrap values and slightly differed in subsequent analyses. Topologies produced by the maximum-likelihood (ML) and Bayesian analyses were similar to the parsimony tree in the basal split, and all genera were recovered as monophyletic lineages in both model-based analyses (Fig. 1A). The trees differed in the position of the *Cautiromimus* Pic, 1926 + *Broxylus* Waterhouse, 1879 and *Leptotrichalus* Kleine, 1925 + *Wakarumbia* Bocak, 1999 clades. These were the 2 most-basal branches of the Australian clade in both analyses, but their relative positions varied. Other relationships were recovered under the 2 optimization criteria.

All analyses suggested close relationships between the Sulawesi and New Guinean faunas. *Xylobanus* and *Cautires* predominantly occurred in the Afrotropical and Oriental Regions and were consistently placed as a sister group to the Australian clade. The Philippine fauna consisted of both lineages, *Xylobanus* and *Cautires*, from the Oriental clade, and several genera of the Australian clade. The Sulawesi taxa belonged to the Australian lineage, apart from 4 species of *Xylobanus* and 2 species of *Cautires* (Fig. 1A).

TAXONOMY

Mangkutanus gen. nov.

(Figs. 1A, 7-9, 11)

Type species: *Sulabanus tenggahensis* Dvorak and Bocak, 2007.

Etymology: The generic name *Mangkutanus* is derived from the local name, Mangkutana, a village in central Sulawesi on the road between Pendolo and Wotu. *Mangkutanus* is a masculine noun.

Description: Male. Body medium-sized, slender, dorsoventrally flattened, slightly wider to rear (Fig. 1B). Head small, hypognathous partly covered by pronotum, with large hemispherical eyes. Cranium covered with sparse pubescence. Frons with deep transverse depression. Mandibles slender and glossy, long, curved nearly to right angle apically, incisor simple, without teeth. Maxillary palpi 4-segmented, palpomere 1 slender, palpomeres 2-4 more robust, apical palpomere securiform. Antennae moderately long, reaching beyond middle of elytral length, slender, serrate, flattened (Fig. 9), covered with slightly decumbent pubescence. Scape pear-shaped, robust, slender basally, pedicel small, partly hidden in scape, 1.7-times wider then long. Antennomeres 3-10 similar in shape, triangular, about 1.7-times longer than wide at apex. Widest part of last antennomere 2.8-times narrower than apical part of 6th antennomere.

Pronotum slightly trapezoidal, with convex anterior margin, lateral margins slightly concave, basal margin bisinuate, pronotum 1.08-1.27-times wider at base than long at midline (Fig. 3), margins thickened. Pronotum with conspicuous keels forming 5 areolae; median areola slender, widest in anterior part, with short, slender longitudinal keel in frontal part, median areola connected to anterior margin by short keel (Fig. 3), pronotum covered with short decumbent pubescence. Scutellum small, flat, sparsely pubescent, deeply emarginate at apex.

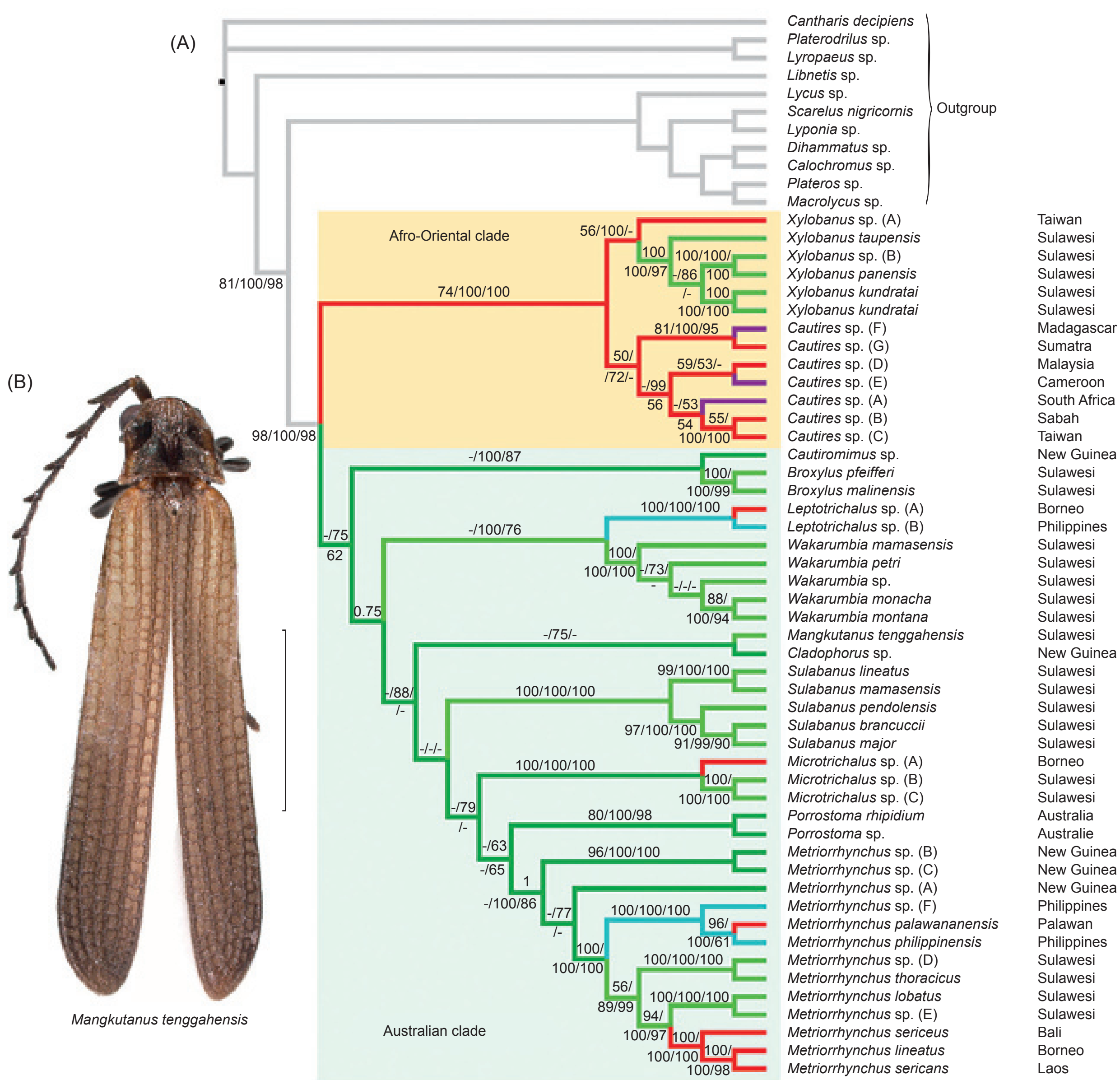

Fig. 1. (A) Phylogenetic hypothesis of the Metriorrhynchini inferred using a Bayesian analysis of the concatenated dataset. Numbers above the branches indicate bootstrap values produced by a parsimony analysis, posterior probability values (× 100), and ML bootstrap values, respectively. (B) *Mangkutanus tenggahensis* gen. nov., general appearance. Scale bar = 2.0 mm.

Elytra flat, slender, slightly widened posteriorly, widest at 5/6 of length, each with 4 longitudinal costae (Fig. 11). Elytra 4.07-times longer than wide at humeri. Primary costae connected by transverse keels forming elytral cells. Longitudinal costae and margins of elytra stout, covered with short, decumbent pubescence. Elytral cells square or slightly rectangular; bottom of cells finely structured, with very short, fine setae. Legs long, slender, shortly pubescent. Femora 4.55-times longer than wide, flat, robust. Tibiae similar to femora in length, slenderer. Tarsi slender, claws simple, without teeth.

Male genitalia with slender phallus, its apical part partly membranous and internal sac sclerotized, long, rod-shaped (Figs. 7, 8). Female unknown.

Relationships: Two *Mangkutanus* gen. nov. species, *M. tenggahensis* (Dvorak et Bocak, 2007) and *M. utarensis* (Dvorak et Bocak 2007), were considered to be a species group in *Sulabanus* (Dvorak and Bocak 2007). The external

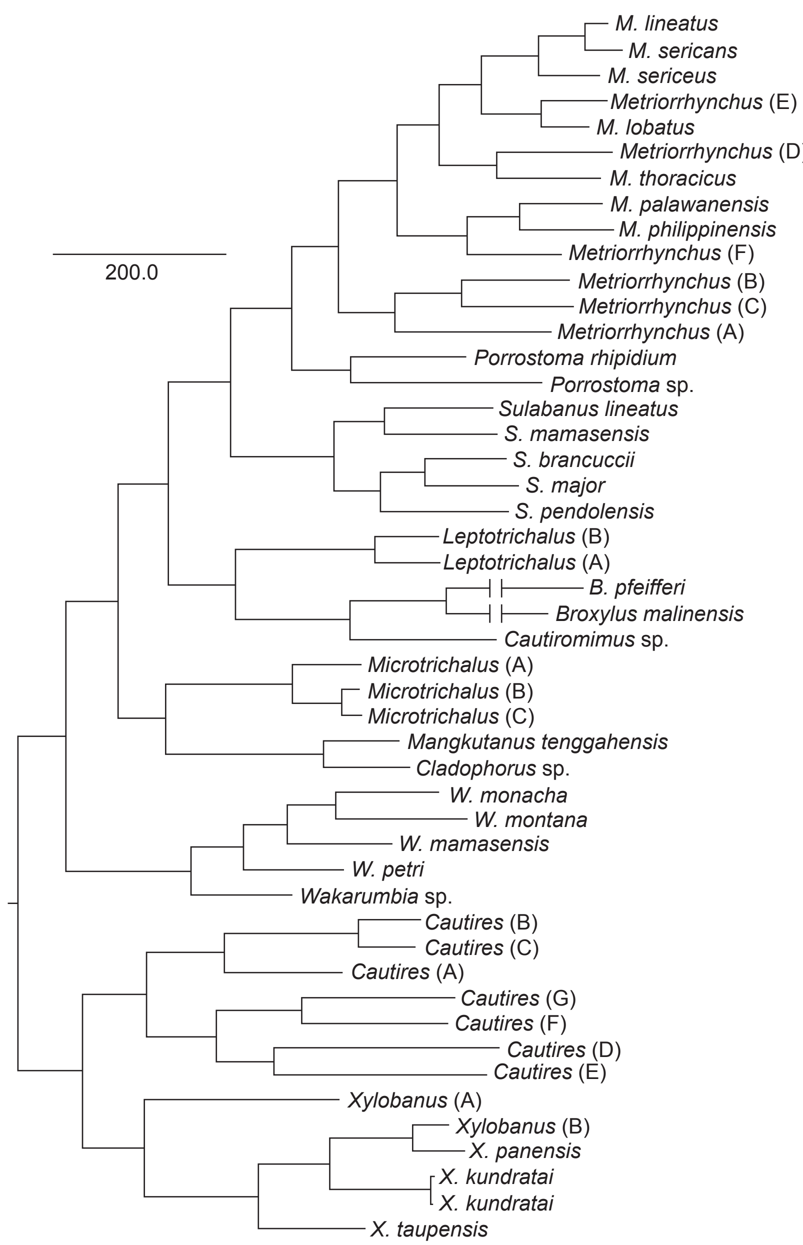

Fig. 2. Phylogenetic hypothesis of the Metriorrhynchini inferred from the parsimony analysis of the concatenated dataset with indels considered the 5th character.

morphology of *Sulabanus* and *Mangkutanus* gen. nov. is very similar, and the only difference was found in the structure of the male genitalia. The very distinct shape of the genitalia was not used previously to define the genus, and only molecular data showed the distant position of these genera. The above presented analyses suggest close relationships of *Mangkutanus* gen. nov. and *Cladophorus* (Figs. 1A, 2). The external similarity may be a result of coevolution of unpalatable metriorrhynchine lineages, *Sulabanus*, *Mangkutanus* gen. nov., *Wakarumbia*, and *Broxylus*, which share similar shapes, sizes, and colorations in Sulawesi.

Distribution: *Mangkutanus* gen. nov. is endemic to Sulawesi.

Material examined: Holotype. ♂. Indonesia, Sulawesi Utara, Danau Mooat, 1200 m, nr. Kotamobagu, 21 June 1985. R. Entomol. Soc. Lond. Project Wallace, B. M. 1985. 10 (BMNH). Holotype. ♂. C Sulawesi, 38 km SE Pendolo Village, 1200 m. 120.46.55°E, 2.14.03°S, 10-11 July 2001. Bolm lgt. (LMBC).

Genus *Xylobanus* Waterhouse, 1879
(Figs. 4-6, 10, 12-20)

Type species: *Lycus costifer* Walker, 1858.

Redescription of male: Body small to medium-sized, slender, dorsoventrally flattened. Body mostly brown, pronotum and elytra often brightly colored. Head without rostrum, partly hidden by pronotum, eyes medium-sized to large, hemispherically prominent. Mandibles slender, moderately curved, with simple incisor. Maxillary palpi 4-segmented, labial palpi 3-segmented, apical palpomeres parallel-sided to securiform in both palpi. Antennae reaching about middle of elytra, serrate or flabellate, usually shortly pubescent, scapus pear-shaped, pedicel small, short, antennomeres 3-10 parallel-sided, slightly serrate to flabellate, apical antennomere slender, parallel-sided, antennomeres 3-11 compressed.

Pronotum flat, variable in shape, with distinct carinae, median areola slender, attached to anterior margin by keel, lateral carinae forming 4 areolae at frontal margin and 2 carinae at posterior angles, lateral carinae sometimes less conspicuous; posterior margins with median notch, curved, posterior angles usually projected; anterior margin convex, lateral margins concave to straight. Scutellum small, flat, emarginate at apex.

Elytra parallel-sided, about 4-times longer than wide at humeri, each elytron with 4 robust longitudinal costae connected by weaker transverse costae forming elytral cells of variable shape. Male genitalia formed by phallus and phallobase only, parameres absent, phallus symmetrical, lanceolate, widened apically, internal sac with 2 spines, phallobase large, circular (Figs. 15-20).

Sexual dimorphism: Females usually larger, always with serrate antennae.

Differential diagnosis: The Sulawesi *Xylobanus* species resemble *Sulabanus*, *Mangkutanus* gen. nov., and 1 species of *Metriorrhynchus* in the 4 elytral costae. Although the body and pronotum shapes slightly differ, the genera cannot be reliably defined exclusively using external characters, and identification must be based on the male genitalia. *Xylobanus* is the only genus from Sulawesi with a slender lanceolate to parallel-sided phallus and an internal sac with a pair of slightly curved thorns. Most parts of the internal sac of *Metriorrhynchus* are sclerotized, often coiled, and sometimes accompanied by a group of minute spines; *Sulabanus* has a mostly short, robust phallus, and its internal sac never has any spines. *Mangkutanus* gen. nov. has a very different, slender, apically membranous phallus (Figs. 7, 8). *Mangkutanus* gen. nov. and *Sulabanus* have very similar, slender bodies; *Xylobanus* species are usually slightly more robust.

Due to general similarities of all species, the descriptions are limited to information useful for identification within *Xylobanus*, with shared characters only being described in the redescription of the genus.

List of the newly described *Xylobanus* species from Sulawesi

Xylobanus panensis sp. nov.
(Figs. 6, 13, 17-18)

Type material: Holotype. ♂, S Sulawesi, 25 km E Mamasa (Kalama), 1100 m, 119.28.39°E, 3.02.10°S, 1-3 July 2001, Bolm lgt. (GenBank voucher UPOL MD0045, LMBC).

Etymology: The specific epithet is derived from the name of the village Pana in the Mamasa Valley.

Differential diagnosis: *X. panensis* sp. nov. resembles *X. kundratai* in general appearance. Except for the antennae, the entire body of *X. panensis* sp. nov. is light brown compared to a dark-brown body in *X. kundratai*. Additionally, *X. panensis* sp. nov. differs in the parallel-sided frontal part of the pronotum (Fig. 6). The phallus of *X. panensis* sp. nov. has the characteristically backward curved apical part (Fig. 18). The different structure of the elytral costae and low uncorrected pairwise distance between the *cox1* and *nad5* sequences of the holotype of *X. panensis* sp. nov. and an unidentified female (GenBank voucher UPOL MD0026) suggest that another closely related species occurs in Sulawesi.

Description: Male. Body medium-sized, slender. Head, pronotum, elytra, antennae, and legs dark brown, margins of pronotum light brown, upper side of cranium and pronotum covered with short, yellowish pubescence. Head small with large, hemispherically prominent eyes, maximum eye diameter 1.13-times interocular distance. Antennae serrate, reaching slightly beyond 1/2 of elytral length, antennomeres triangular in shape, slightly pubescent, antennomere 3 length 1.48-times width, apical antennomere slender, parallel-sided. Pronotum flat with distinct carinae, 1.28-times wider than long at midline, disc with short pubescence (Fig. 6). Elytra slender, parallel-sided, 4.29-times longer than wide at humeri, reticulate cells well-developed, mostly transverse (Fig. 13). Phallus of male genitalia gradually widening apically, apex of phallus slightly curved, internal sac with 2 separate sclerotized spines (Figs. 17, 18).

Measurements: BL 6.80 mm, WH 1.36 mm, PL 0.96 mm, PW 1.23 mm, Ediam 0.45 mm, Edist 0.40 mm.

Distribution: Sulawesi, known only from the type locality.

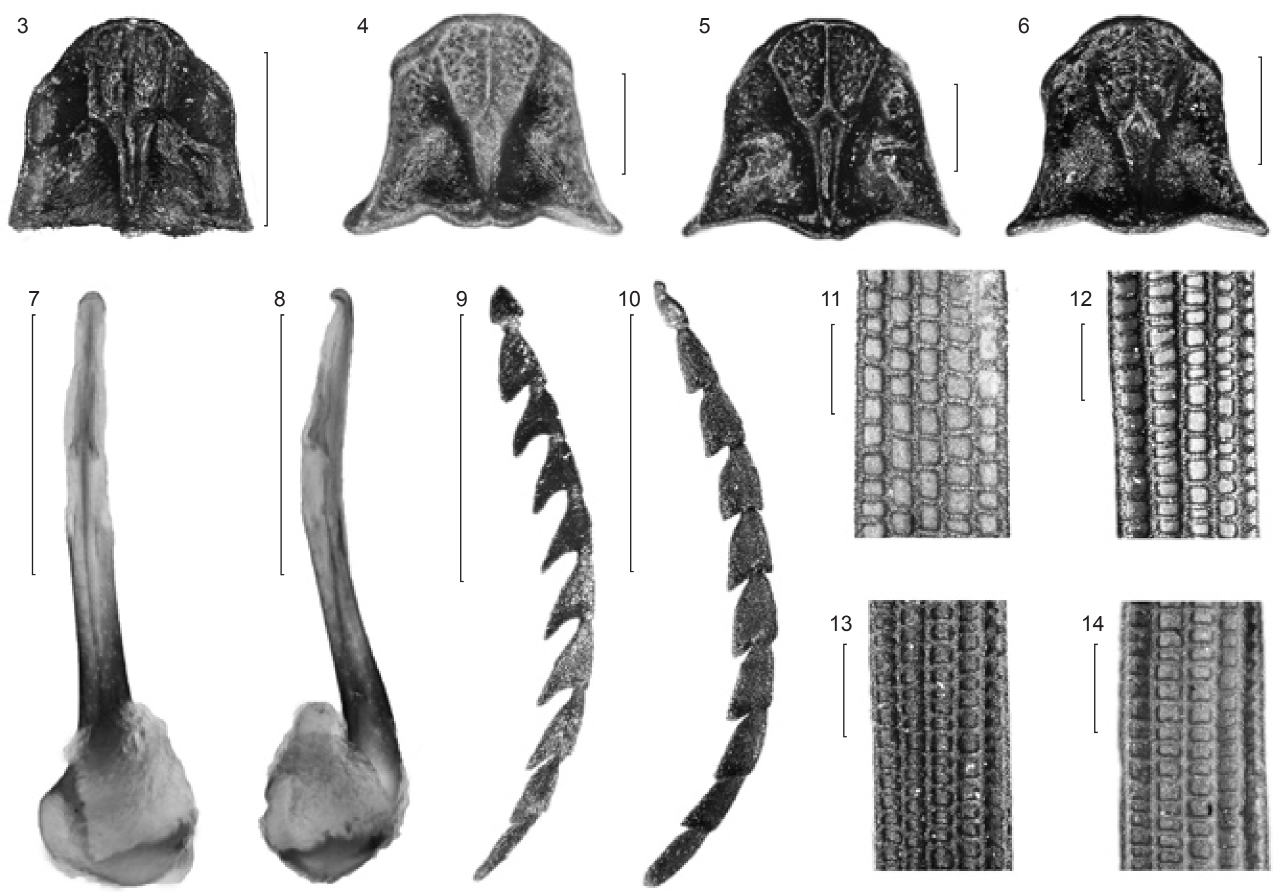

Fig. 3-14. 3. *Mangkutanus tenggahensis* gen. nov., pronotum. **4.** *Xylobanus taupensis* sp. nov., pronotum. **5.** *Xylobanus kundratai* sp. nov., pronotum. **6.** *Xylobanus panensis* sp. nov., pronotum. **7** and **8.** Male genitalia; *Mangkutanus tenggahensis* gen. nov. **7.** ventral view; **8.** lateral view. **9.** *Mangkutanus tenggahensis* gen. nov., antenna. **10.** *Xylobanus taupensis* sp. nov., antenna. **11.** *Mangkutanus tenggahensis* gen. nov., middle part of elytra. **12.** *Xylobanus kundratai* sp. nov., middle part of elytra. **13.** *Xylobanus panensis* sp. nov., middle part of elytra. **14.** *Xylobanus taupensis* sp. nov., middle part of elytra. Scale bars: 3 = 0.25 mm, 4-8 = 0.5 mm, 9, 10 = 2.0 mm, 11-14 = 0.5 mm.

Xylobanus kundratai sp. nov.
(Figs. 5, 12, 15-16)

Type material: Holotype. Male, S Sulawesi, Malino, Gn. Lompobatang, 1800 m, 119.53.31°E, 5.17.50°S, 13-14 July 2001, Bolm lgt. (GenBank voucher UPOL MD0029, LMBC). Paratypes. 2 ♂♂, data same as for holotype, 2 ♂♂, S Sulawesi, 25 km SSE Malino, Gn. Lompobatang, 119.53.31°E, 5.17.50°S, 26-28 July 1999, Bolm lgt., 1800 m (GenBank voucher UPOL MD0036, LMBC).

Etymology: The specific epithet is a patronym in honor of Robin Kundrata, Czech Republic.

Differential diagnosis: *X. kundratai* sp. nov. and *X. panensis* sp. nov. are the only *Xylobanus* species from Sulawesi with dark-colored elytra. These species differ in the shape of male genitalia. The phallus of *X. kundratai* sp. nov. is longer and slenderer in the middle part. Unlike *X. panensis* sp. nov., the apex of the phallus is not curved backwards.

Description: Male. Body medium-sized, slender. Elytra dark brown, other body parts darker, almost black, with very short, dense pubescence. Head with large, hemispherically prominent eyes, maximum eye diameter 1.12-1.18-times interocular distance. Antennae long, reaching 2/3 of elytral length, slightly pubescent, antennomeres 3-10 parallel-sided to slightly serrate, apical antennomere very slender, parallel-sided; antennomere 3 length 1.80-times maximum width. Pronotum flat, 1.24-1.28-times wider than long, with distinct carinae forming 5 areolae, lateral keels inconspicuous (Fig. 5). Elytra parallel-sided 3.95-4.17-times longer than wide at humeri, reticulate cells regular, mostly quadrate (Fig. 12). Male genitalia with slender symmetrical phallus; apex of phallus rounded and constricted, internal sac with 2 separate sclerotized spines (Figs. 15, 16).

Measurements: BL 8.95 mm, WH 1.78 mm, PL 1.26 mm, PW 1.61 mm, Ediam 0.60 mm, Edist 0.51 mm.

Distribution: Sulawesi, Mt. Lompobatang.

Xylobanus taupensis sp. nov.
(Figs. 4, 10, 14, 19-20)

Type material: Holotype. ♂, S Sulawesi, 8 km W Mamasa (Nepe), 950 m, 119.20.32°E, 2.56.13°S, 29-31 June 2001, Bolm lgt. (GenBank voucher UPOL MD0059, LMBC).

Etymology: The specific epithet is derived from the name of the village Taupe.

Differential diagnosis: *X. taupensis* sp. nov. resembles *X. testaceipes* Pic, 1922 and *X. celebicus* Kleine, 1927. These species have a similar yellow body coloration and similar body sizes. Unlike them however, the pronotum of *X. taupensis* sp. nov. has a deeply sinuate posterior margin, concave lateral margins of pronotum, and more-projecting posterior angles (Fig. 4). A quantifiable difference between these species is the number of cells between costae 1 and 2: there are 38 areoles in *X. testaceipes*, 52 in *X. celebicus*,

Fig. 15-20. Male genitalia. *Xylobanus kundratai* sp. nov. **15.** Ventral view; **16.** lateral view. *Xylobanus panensis* sp. nov. **17.** Ventral view; **18.** lateral view. *Xylobanus taupensis* sp. nov. **19.** Ventral view; **20.** lateral view. Scale bars = 0.5 mm.

and 60 in *X. taupensis* sp. nov. The types of *X. celebicus* and *X. testaceipes* are females, so other characters cannot be compared.

Description: Male. Body medium-sized. Head, pronotum and elytra yellow to light brown, antennae and legs dark brown, only bases of femora lighter; entire body covered with short, light pubescence. Head small, with large, hemispherically prominent eyes, eye diameter 1.70-times frontal interocular distance. Antennae long, serrate, reaching to 2/3 of elytral length, antennomeres 3-10 becoming gradually slenderer, apical antennomere parallel-sided, antennomere 3 length 1.59-times width (Fig. 10). Pronotum flat, 1.30-times wider than long at midline, with 7 areolae, 3 areolae in middle part of disc shallow, 2 lateral areolae deeper (Fig. 4). Elytra parallel-sided, 3.88-times longer than wide at humeri, with distinct, mostly quadrate, elytral cells, elytral cells tiny, around 60 cells between 1st and 2nd costae (Fig. 14). Male genitalia with wide phallus, internal sac with 2 separate sclerotized spines (Figs. 19, 20).

Measurements: BL 7.45 mm, WH 1.60 mm, PL 1.10 mm, PW 1.43 mm, Ediam 0.56 mm, Edist 0.33 mm.

Distribution: Sulawesi, the Mamasa Valley.

A key to *Xylobanus* species of Sulawesi

1. Entire elytra yellow to light brown 2
- Elytra dark brown to black 4
2. Lateral margins of pronotum straight, entire pronotum light-colored 3
- Lateral margins of pronotum concave, bottom of lateral areolae in pronotum brown, phallus as in figures 19 and 20, elytral areolae small, transverse, with 60 transverse costae between 1st and 2nd elytral costae .... *X. taupensis* sp. nov.
3. Pronotum 1.45-times wider at posterior margin than long at midline, anterior margin of the pronotum slightly projecting forward, elytral costae transverse, about 50 transverse costae between elytral costae 1 and 2 .... *X. celebicus* Kleine, 1927
- Pronotum 1.27-times wider at posterior margin than long at midline, anterior margin of pronotum strongly projecting forward, elytral costae rectangular, 39 transverse costae between elytral costae 1 and 2..... *X. testaceipes* Pic, 1922
4. Frontal angles of pronotum conspicuous, lateral margins almost parallel-sided frontally (Fig. 6); apical part of phallus curved to rear (Figs. 17, 18) .... *X. panensis* sp. nov.
- Frontal angles of pronotum obtuse, pronotum gradually widening to posterior angles (Fig. 5); apical part of phallus simple (Figs. 15, 16) .... *X. kundratai* sp. nov.

It should be noted that another species, closely related to *X. panensis* sp. nov., was collected in the Poso Valley. That species is available only in a unique female specimen and has not been formally described.

DISCUSSION

The phylogenetic analyses based on 3 molecular markers support the basal split in the Asia/African (i.e., *Cautires* + *Xylobanus*) and Australian clades, as suggested by Bocak et al. (2006). Although the basal split is unambiguously inferred from all analyses, the exact relationships among Australian genera remain weakly supported and need further data for more-robust resolution. Nevertheless, we repeatedly found the *Porrostoma* Castelnau, 1838 + *Metriorrhynchus* Gemminger and Harold, 1869 clade, the restricted concept of Trichalina as proposed by Bocak (2002), the close relationships of *Cautiromimus* + *Broxylus*, and an independent position of *Sulabanus tenggahensis* Dvorak and Bocak, 2007 with respect to the remaining species of *Sulabanus*. Some of these relationships were also inferred from the morphological analysis of the lineage (Bocak 2002), but the deep split between *Cautires* + *Xylobanus* and *Metriorrhynchus* + related genera, is supported by a more-extensive molecular dataset for the 1st time. Similarly, the distant position of *Xylobanus* and *Sulabanus* inferred from morphology (Dvorak and Bocak 2007) is confirmed here.

The permeability of Wallace’s line for many widespread insect groups is well documented (Balke et al. 2009, Müller et al. 2010). But the propensity for dispersal is generally limited in net-winged beetles (Bocak and Yagi 2010), and we found that the Afro-Oriental metriorrhynchine lineages clade rarely dispersed across Wallace’s line. Although 6 Sulawesi species were originally classified as *Xylobanus* (Kleine 1933), several of them are only superficially similar to the genus and do not belong to the Afro-Asian lineage of the Metriorrhynchini. After several studies, 2 *Xylobanus* species were transferred to *Wakarumbia* and *Sulabanus* (Bocak 2001, Dvorak and Bocak 2007), *Xylobanus rusticus* Schaufuss, 1887 may belong to *Sulabanus* according to Kleine’s concept of the species, but the type is not available for study, and another species was placed in *Metriorrhynchus* (Bocak et al. 2006). *Metanoeus* Waterhouse, 1879 is known from continental Asia and the Philippines, but does not cross Wallace’s line to Sulawesi. We found that most specimens identified as *Cautires* from the Australian region in collections belong to the superficially similar *Cautiromimus*, a genus distributed in New Guinea and the Philippines, and only 2 undescribed species of *Cautires* from Sulawesi were found in the BMNH collection. Therefore, *Xylobanus* and *Cautires* represent the only Afro-Oriental lineage of the Sulawesi fauna of the Metriorrhynchini. Similarly, few cases were inferred for dispersal in the opposite direction. The Australian origin of *Metriorrhynchus* (Fig. 1A) as proposed by Bocak (2002 2007) and Bocak and Yagi (2010) was consistently found in all analyses, and *Microtrichalus* Pic, 1921 may have a similar dispersal history in the region.

The dispersal history within the Australian region cannot be unanimously inferred from the topology due to limited sampling and a bias toward the Sulawesi taxa. Although the most parsimonious optimization would suggest the origin of Australian Metriorrhynchini in Sulawesi, considering the tectonic history (Hall 2002) and the number of known genera and species (Bocak 2002), we prefer to place their origin in the Australian region (Fig. 1A). The genera *Cautiromimus*, *Porrostoma*, *Cladophorus* Guérin-Méneville, 1830, *Microtrichalus*, and *Metriorrhynchus* are known for 100-300 species each from New Guinea and Australia. Either they do not cross Weber's line (*Porrostoma* and *Cladophorus*), or only a few species are known from Sulawesi and the Philippines (*Cautiromimus*).

Four genera, *Sulabanus*, *Broxylus*, *Wakarumbia*, and *Mangkutanus* gen. nov., are endemic to Sulawesi. Although species-level endemicity of the Sulawesi fauna was recognized a long time ago (Kleine 1933), the number of endemic genera is rather surprising. All these genera are known to have high species numbers despite all material being collected in restricted areas of west-central and northern Sulawesi (Bocak 2000a, Dvorak and Bocak 2007, 2009) during short expeditions, and therefore we might expect further species to be described in the future. *Leptotrichalus* does not belong to any of the above described groups of lineages, and its distribution is rather exceptional. *Leptotrichalus* occurs only in the Moluccas (1 sp., unpublished record), Sulawesi (4 spp.), the Philippines (28 spp.), Sundaland (15 spp.), and continental Asia (3 spp.) (Bocak 2000b, Kleine 1933). The origin of *Leptotrichalus* may be placed in either western Wallacea or the Philippines with supposed dispersal among these islands.

Summarizing the numbers of species in genera known from Sulawesi, the absolute prevalence of the species belonging to the Australian clade is apparent. There are 87 known species of the Metriorrhynchini in Sulawesi and only eight of them belong to the Afro-Oriental clade. All species are endemic to Sulawesi, except *Metriorrhynchus thoracicus* (Fabr., 1801) known from the Moluccas (Kleine 1933). The small ranges are characteristic of net-winged beetles. Nevertheless, almost complete endemicity of the Sulawesi fauna is exceptional when compared to other beetle families.

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