The phylogenetic position of Artematopodidae (Coleoptera: Elateroidea), with description of the first two *Eurypogon* species from China

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Abstract

The Artematopodidae is a species-poor beetle family with contentious relationships to byrrhoid and elateroid families. Recent molecular phylogenetic analyses brought ambiguous results based on a single sequenced species. We investigated the taxonomic placement of Artematopodidae within Elateriformia using ribosomal (18S, 28S) and mitochondrial (*rrnL*, *cox1*) molecular markers and three artematopodid species. Our analyses placed Artematopodidae close to Omethidae+Telegeusidae in a basal position of broadly defined Elateroidea. Additionally, we described the first artematopodid species from China – *Eurypogon jaechi* sp. nov. and *E. heishuiensis* sp. nov. These species are reported from mountains of Yunnan and can be easily distinguished from their Palaearctic congeners by their large bodies and metallic green elytra. They differ from each other by the shape of the pronotum, puncturation of the head and pronotum, the relative lengths of the antennomeres 3-5, and the morphology of the female genitalia. With respect to our findings, we discussed the phylogeny, diversity and distribution of the family Artematopodidae.

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Introduction

The Artematopodidae is a species-poor beetle lineage currently classified in Elateroidea (Bouchard *et al.*,

2011). Altogether 66 extant species are placed in eight genera; six species were described from amber fossils (Hörschemeyer, 1998; Lawrence, 2010). Artematopodids are characterized by the presence of paired carinae on the prosternum, connate abdominal ventrites, and an interlocking tongue-like process on the internal part of the elytral apex (Lawrence, 1995). Three subfamilies are recognized: Artematopodinae, which consist of Artematopodini, Ctesibiini and Macropogonini, monogeneric Allopogoniinae, and Electribiinae (Lawrence, 2005; Table S3).

The relationships of the Artematopodidae were contentious since their description by Lacordaire (1857) and even recent studies did not provide a robust phylogenetic hypothesis (Lawrence, 1995). The Artematopodidae were originally treated as a subgroup of the Dascillidae (*e.g.* Horn, 1880; Pic, 1914), mainly because of the similar general appearance and the presence of membranous lamellae on the ventral parts of the tarsomeres. Forbes (1926) placed them with Cerophytidae and Brachypsectridae among the basal Elateriformia. Using larval characters, Böving and Craighead (1931) classified them under the name Eurypogonidae into the Dryopoidea. Crowson (1955) formally followed their concept, but discussed the conflicting signal from adult morphology which suggests relationships to elateroid lineages. Later, he erected the superfamily Artematopoidea for the Artematopodidae, Brachypsectridae and Callirhipidae and discussed the relationships of the Artematopoidea with the Elateroidea and Cantharoidea (Crowson, 1973). Lawrence and Newton (1982) separated the Callirhipidae from the Artematopodidae. Lawrence (1988) merged the Artematopoidea, Elateroidea and Cantharoidea into a single broadly defined Elateroidea and inferred the Artematopodidae in variable positions: as sister to the Elateroidea *sensu stricto* (Crowson, 1955) + Brachypsectridae, sister to the Elateroidea *sensu stricto* + Brachypsectridae + some dryopoid lineages,

Table 1. The list of newly sequenced taxa with GenBank accession and voucher numbers.

Family	Genus/Species	Geographical origin	Markers 18S rDNA	28S rDNA	16S mtDNA	COI mtDNA	Specimen voucher
Artematopodidae	<i>Eurypogon japonicus</i>	Japan, Nara Pref.	KF294761	KF294767	KF294755	KF294774	UPOL RK0091
Artematopodidae	<i>Eurypogon hisamatsui</i>	Japan, Tokushima Pref.	KF294762	KF294768	KF294756	KF294775	UPOL RK0128
Artematopodidae	<i>Eurypogon brevipennis</i>	Japan, Nagano Pref.	KF294763	KF294769	KF294757	KF294776	UPOL 001335
Omethidae	<i>Drilonius</i> sp. b	India, Kunchappanai	KF294764	KF294770	KF294758	KF294777	UPOL 001273
Omethidae	<i>Drilonius</i> sp. c	Philippines, Mindanao	KF294765	KF294771	KF294759	KF294778	UPOL RK0134
Throscidae	<i>Trixagus meybohmii</i>	Czech Republic, Moravia	KF294766	KF294772	KF294760	KF294779	UPOL RK0139

or as a basal lineage of the Elateroidea. Beutel (1995) analyzed larval characters and found artematopodids regularly in monophyletic Elateroidea *sensu* Lawrence (1988) either close to the Elateridae, Cebrionidae and Cantharidae, or sister to the remaining Elateroidea. Lawrence *et al.* (1995) combined larval and adult characters and artematopodids either occupied a basal position in Elateroidea, were sister to the Elateroidea *sensu stricto*, formed a basal lineage in a clade containing the Elateroidea and several unrelated lineages, or were in an unresolved position within Elateriformia. The latest morphology-based phylogeny of Coleoptera (Lawrence *et al.*, 2011) found Artematopodidae to be the basalmost lineage of Elateroidea.

No artematopodids were included in most molecular phylogenetic studies (Bocakova *et al.*, 2007; Hunt *et al.*, 2007; McKenna and Farrell, 2009; Kundrata and Bocak, 2011). Only Sagegami-Oba *et al.* (2007) used the artematopodid genus *Eurypogon* in their dataset of 18S rDNA sequences and placed *Eurypogon japonicus* as a sister to the Heteroceridae in a wider clade of several byrrhoid families and Buprestidae. In the latest molecular phylogeny of the Coleoptera, Bocak *et al.* (2013) analyzed over 8000 terminals and Artematopodidae formed one of the basal lineages in Elateroidea, however, only two ribosomal loci (18S and 28S rDNA) represented *Eurypogon japonicus* in the five-marker dataset. Although the placement of the Artematopodidae in the Elateroidea is widely accepted (Cooper, 1991; Lawrence and Newton, 1995; Young, 2002; Lawrence, 2010; Bouchard *et al.*, 2011), an underlying phylogenetic hypothesis is absent.

In this study, we expand available complete four-marker data by newly sequenced representatives of basal elateroid lineages and three *Eurypogon* species to investigate the position of Artematopodidae within the elateriform series, and we describe two *Eurypogon* species, which represent the first record of the family in China.

Material and methods

Molecular dataset and laboratory procedures

The dataset contained 158 terminals. The newly sequenced 18S rDNA (~1900 bp), 28S rDNA (~700 bp), *rrnL* mtDNA (~600 bp), and *cox1* mtDNA (723 bp) fragments were produced for three *Eurypogon* species (Artematopodidae), two species of *Drilonius* Kiesenwetter (Omethidae) and *Trixagus meybohmii* Leseigneur, 2005 (Throscidae; Table 1). Total DNA was extracted using the Wizard SV96 Purification System (Promega Corp., Madison, WI, USA). Further laboratory procedures, sequencing and primers were reported by Kundrata and Bocak (2011). The newly obtained data were merged with the dascilloid, byrrhoid and elateroid sequences used in recent molecular phylogenetic studies of Elateroidea (Kundrata and Bocak, 2011; Table S1). *Dascillus cervinus* Linnaeus, 1758 (Dascillidae) as a member of basal Elateroidea (Bocak *et al.*, 2013) was used as an outgroup. Only taxa with a complete set of four DNA markers were included in the dataset. GenBank accession numbers of sequences are listed in Tables 1 and S1. The classification follows Bouchard *et al.* (2011), with modifications made by Kundrata and Bocak (2011; for Elateridae and Omalidae) and Janisova and Bocakova (2013; for Lampyridae: Ototretinae).

Sequence handling, alignment and phylogenetic analyses

Sequences were edited using Sequencher 4.7 (Gene Codes Corp., Ann Arbor, MI, USA). Protein-coding *cox1* sequences containing no indels were aligned by ClustalX 1.81 under default settings (Thompson *et al.*, 1997). Additionally, for the alignment of rDNA and *rrnL* mtDNA sequences we used either ClustalX or BlastAlign, which omits parts of the length varia-

ble loops when reliable alignment cannot be inferred (Belshaw and Katzourakis, 2005). The concatenated datasets were analyzed under parsimony (MP), maximum likelihood (ML) and Bayesian algorithms. The MP analyses were carried out using TNT 1.0 (Goloboff *et al.* 2003, 2008) with gaps treated as missing characters. The most parsimonious trees were found 50 times and the bootstrap values were calculated from 1000 pseudoreplicates. Consensus trees were inferred from PAUP* 4.03b10 (Swofford, 2002). For ML and Bayesian analyses, the datasets were partitioned by genes and codon positions, yielding a total of six partitions. The Bayesian analyses were performed with Mr. Bayes 3.1.2 (Huelsenbeck and Ronquist, 2001). Four chains were run for 40.10^6 generations, with trees sampled every 1,000 generations. The stationarity was detected in Tracer 1.5 (Rambaut and Drummond, 2007). For each analysis, the first 15% of trees were discarded as burn-in. The posterior probabilities were determined from the remaining trees. The ML analyses were conducted using RAxML 7.3.1 (Stamatakis, 2006) via the CIPRES web server (www.phylo.org; Miller *et al.*, 2010). Branch supports were calculated using the rapid bootstrap algorithm (Stamatakis *et al.*, 2008) with 1000 bootstrap iterations under the GTRCAT model.

Morphological taxonomy

The morphological study was based on adult semaphoronts. Genitalia were dissected, cleared in 10% aqueous solution of potassium hydroxide, dyed by chlorazol black and photographed using a digital camera mounted on a stereoscopic microscope. The following measurements were taken: BL-body length, measured from the fore margin of the head to the elytral apex; EL-elytral length; WHe-width of head including eyes; WH-width at humeri; PL-pronotal length at midline; PWA-pronotum width at anterior angles; PWP-pronotum width at posterior angles; Edist-minimum interocular distance in the frontal part of the cranium; Ediam-maximum eye diameter in lateral view; LV-length of valvifer; LC-length of coxite. A forward slash (/) separates different lines on a label. The species descriptions follow in general the recommendations of Ratcliffe (2013) and the morphological terminology follows those of Sakai (1982) and Lawrence (2010). The type material is deposited in the Naturhistorisches Museum Wien in Austria (NHMW).

Results

The 158-taxa concatenated BlastAlign and ClustalX datasets contained 4675 and 4330 homologous positions with 31.1 and 39.6% parsimony-informative characters, respectively. The numbers of homologous positions and constant, variable parsimony-informative and parsimony-uninformative characters for total matrices and individual markers shows the Table S2. The *rrnL* and *coxI* mtDNA fragments contained considerably higher percentage of parsimony-informative characters than 18S and 28S rDNA. Base frequencies showed high AT levels in mitochondrial DNA (Table S2). The maximum uncorrected pairwise distances among investigated taxa varied between 8.9% for 18S rDNA and 35.0% for *coxI* mtDNA (Table S2).

The phylogenetic analyses of data in the present constellation recovered Elateroidea *sensu* Lawrence and Newton (1995; *i.e.*, including Armatopodidae) as a monophylum (Fig. 1). The concept of Elateroidea was supported by bootstrap values (BS) of 58–68% in ML analyses, less than 50% in MP analyses, and 74–88% posterior probabilities (PP) in Bayesian analyses (Fig. 1). The Byrrhoidea was strongly supported in ML and Bayesian analyses of ClustalX alignment and weakly supported or paraphyletic in the remaining analyses. Armatopodidae were recovered in a basal position of the broadly defined Elateroidea; they formed an independent lineage in ML analysis of BlastAlign alignment (Fig. 1B; less than 50% BS) or they were sister to Omethidae + Telegeusidae in all remaining analyses (Fig. 1A; 58 and 100% PP in Bayesian analyses of BlastAlign and ClustalX alignments, respectively, 97% BS in ML analysis of ClustalX alignment, and less than 50% BS in MP analyses). Elateroidea *minus* Armatopodidae + (Omethidae + Telegeusidae) obtained strong support in analyses of BlastAlign alignment (84% BS, 100% PP) and low to moderate support in analyses of ClustalW alignment (Fig. 1). Throscidae and Eucnemidae formed either independent lineages (4 analyses, Fig. 1B) or a single clade (2 analyses, Fig. 1A). The strongly supported clade consisting of two subclades Lycidae + Lampyridae + Cantharidae and Omalisidae + Phengodidae + Rhagophthalmidae + Elateridae was found in all analyses. All analyses recovered elateroid families monophyletic, only Bayesian analysis of BlastAlign alignment showed paraphyletic Elateridae including a clade Omalisidae + Phengodidae + Rhagophthalmidae (less than 50% BS). All families but Omalisidae (<50–92% BS, 99–100% PP) and Elateridae (<50–75% BS, 94%

Fig. 1. Maximum likelihood (ML) phylogenetic trees based on analyses of 158-taxon concatenated datasets aligned by ClustalX (A) and BlastAlign (B). Numbers at branches represent ML bootstrap values and Bayesian posterior probabilities, respectively. Selected long branches in Lycidae, Lampyridae and Cantharidae were manually shortened as indicated by two vertical lines.

PP) obtained strong support in all analyses (92–100% BS, 100% PP). Among Artematopodidae, the sister-group relationship between *Eurypogon hisamatsui* Sakai, 1982 and *E. brevipennis* Sakai, 1982 obtained strong support in 4 analyses. In ML and Bayesian analyses of BlastAlign alignment, *E. hisamatsui* was found sister to *E. japonicus* Sakai, 1982 (65% BS and 99% PP, respectively).

Discussion

The phylogenetic position of Artematopodidae

In this study, we combined ribosomal and mitochondrial DNA data to investigate the position of Artematopodidae. According to our analyses, Artematopodidae were never recovered near byrrhoid lineages as suggested by Sagegami-Oba *et al.* (2007; Fig. 1). The position of the Callirhipidae as a part of the Byrrhoidea and distant from Artematopodidae rejects Crowson's Artematopoidea (Crowson, 1973). The results placed artematopodids as a part of deep radiation of elateroid lineages in concordance with some recently published morphological and molecular analyses (*e.g.* Lawrence *et al.*, 2011; Bocak *et al.*, 2013; Fig. 1). Lawrence *et al.* (2011) recovered Artematopodidae as the basalmost elateroid lineage and Bocak *et al.* (2013) inferred artematopodids as a sister to Elateroidea minus Telegeusidae and Omethidae. The basal position of Artematopodidae is also indicated by the fact that several species of Macropogonini feed on mosses (Lawrence, 2010). In our study, five out of six analyses revealed heretofore unknown sistergroup relationships of Artematopodidae and Omethidae + Telegeusidae (Fig. 1A). Only one analysis showed Artematopodidae sister to the remaining Elateroidea, but this topology was weakly supported (Fig. 1B). The Elateroidea except the three above mentioned basal lineages showed consistent support across the recent molecular analyses (Bocakova *et al.*, 2007; Kundera & Bocak, 2011; this study; Fig. 1). On the other hand, although we can consider the placement of Artematopodidae in the basal radiation of the Elateroidea as well supported, their relationships to Omethidae and Telegeusidae remain unresolved (Bocak *et al.*, 2013; this study; Fig. 1). The Brachypsectridae (supposed as the close relatives of Artematopodidae by *e.g.*, Crowson, 1973) fixed for the DNA isolation and more data for Omethidae and Telegeusidae are needed for better understanding of the relationships among the basal elateroid lineages.

The zoogeography and diversity of the Asian Artematopodidae

Currently, eight extant artematopodid genera are defined (Lawrence, 2010; Table S3). *Artematopus* Perty is the most diverse genus (44 species), three genera contain 2–11 species, and four genera are monotypic. The artematopodids have the highest diversity in the New World (all genera and most species; Table S3), with *Macropogon* Motschulsky and *Eurypogon* distributed additionally in the Palaearctic Region. Three species of *Macropogon* occur in the Russian Far East, one *Eurypogon* species is known from southern Europe and seven *Eurypogon* species are distributed in East Asia (Sakai, 1982; Hörnschemeyer, 1998; this study). *Eurypogon* had contained only Nearctic species until Sakai (1982) described four species from Japan and one from Taiwan (Table S4), but no species was recorded from continental Asia. Here, we described two *Eurypogon* species from the geographically very distant area in Yunnan (Fig. 3; for the species descriptions see the Appendix). Hörnschemeyer (1998) considered the pattern of Artematopodidae distribution as relict. The distant isolated ranges of Chinese and Japanese species of *Eurypogon* suggest much more extensive distribution of this genus in the past. Of course, we cannot exclude further records of these rare beetles from further localities in China, but all *Eurypogon* occur in a low number of species in small isolated ranges across the World and they have not been reported from large regions between the known ranges (Tables S3 and S4).

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On-line Supplementary Information

Table S1. The list of previously published sequences used in the dataset (Bocakova *et al.*, 2007; Kunderata and Bocak 2011).

Table S2. Numbers of characters, base frequencies and maximum uncorrected pairwise distances.

Table S3. List of artematopodid genera, with geographical distributions.

Table S4. List of described species of the genus *Eurypogon* Motschulsky, with geographical distributions.

Fig. 2. Habitus of *Eurypogon* spp.: (A) *E. jaechi* sp. nov., dorsal habitus, (B) ventral habitus, (C) *E. heishuiensis* sp. nov., dorsal habitus; antenna: (D) *E. jaechi* sp. nov., (E) *E. heishuiensis* sp. nov.; pronotum: (F) *E. jaechi* sp. nov., (G) *E. heishuiensis* sp. nov.; *E. jaechi* sp. nov.: (H) prosternum, (I) elytron, dorsolaterally, (J) tarsomeres, dorsally, (K) ventrally; abdominal ventrites: (L) *E. jaechi* sp. nov., (M) *E. heishuiensis* sp. nov.; spiculum ventrale and valvifer with coxites: (N) *E. jaechi* sp. nov., (O) *E. heishuiensis* sp. nov. Scale bars: 2 mm (Figs 2-4, 10, 13-14), 1 mm (Figs 5-8, 15-16), 0.5 mm (Figs 9, 11-12).

Appendix

Systematics

Eurypogon Motschulsky, 1859

Diagnosis. Within Macropogonini, *Eurypogon* can be easily distinguished from *Macropogon* by subequal antennomeres 4 and 5 which are each considerably longer than antennomere 3 (in *Macropogon* antennomere 5 is 2.5 times longer than antennomere 4 which is subequal to antennomere 3), basal pro- and mesotarsomeres without ctenidium and larva without distinct paired urogomphi on the 9th abdominal tergite (Crowson, 1973; Lawrence, 2005). The East Palaearctic *Eurypogon* species were described in detail by Sakai (1982).

Eurypogon jaechi sp. nov.

Fig. 2A-B, D, F, H-L, N

Type material. Holotype, 1 female, “China Yunnan, 1-19.VII. / HEISHUI, 35 km N Lijiang / 27° 13'N 100° 19'E / E. Jendek leg. 1992” (NHMW).

Diagnosis. *Eurypogon jaechi* sp. nov. and *E. heishuiensis* sp. nov. are the only known artematopodids from continental Asia and can be easily distinguished from their Japanese and Taiwanese congeners by larger body and metallic green coloration of elytra (species from Japan and Taiwan are uniformly black). *E. jaechi* sp. nov. differs from similar *E. heishuiensis* sp. nov. by the following characters: dull metallic elytral coloration, slightly wider body (Fig. 2A, C), pronotum with less concave sides and less prominent hind angles, larger and denser punctures on head and pronotum (Fig. 2F-G), different relative lengths of antennomeres 3-5 (Fig. 2D-E), less prominent elevations near lateral sides of abdomen (Fig. 2L-M), and higher valvifer/coxite length ratio (Fig. 2N-O).

Description. Female. Body 6.1 mm long, 2.7 times as long as wide at humeri (Fig. 2A-B). Body coloration grey to black; elytra metallic dark green, moderately shiny; legs dark brown, tarsal lamellae yellow. Entire body densely covered by suberect or erect pubescence. Head deflexed (i.e., there is a deflexion point between frons and clypeus; anterior part of cranium is declined), cranium irregularly covered with large punctures; punctures circular to oval, sparser and variable in size on clypeus, interstices smooth, narrow, up to width of puncture diameter on clypeus; anterior clypeal margin slightly convex (Fig. 2F). Eyes protuberant; interocular distance 2.0 times eye diameter in dorsal view. Maxil-

lary palpi almost 2 times longer than labial palpi, apical palpomere slender, widest at apex (Fig. 2F). Antennae 11-segmented, reaching second third of elytral length, covered by suberect hairs; antennomere 1 pear-shaped, antennomeres 2-3 simple, their combined lengths slightly longer than length of antennomere 4; antennomeres 4-10 slightly serrate, subequal in length, apical antennomere simple (Fig. 2D). Pronotum pentagonal, moderately convex, anterior edge simple, almost straight, lateral margins moderately straight, posterior margin evenly rounded, slightly sinuate in middle part. Anterior angles almost rectangular; posterior angles acute (Fig. 2F); surface with large, ovoid, moderately deep punctures, with smooth, very narrow interstices; shiny, covered by erected, long setae, mainly at margins. Prosternum transverse, with paired longitudinal ridges in front of coxae, continuing as sides of prosternal process; prosternal process overlapping mesoventrite (Fig. 2B, H). Scutellum flat, triangle-shaped. Elytra moderately shiny, sinuate behind humeri, widest at third fourth, finely and deeply punctate with distinct puncture rows (Fig. 2A, I); covered by suberect pubescence; elytral margins strengthened, particularly apically. Legs slender, femora widest mesally, tibiae elongate, bearing spurs apically. Tarsomeres 2-4 ventrally with deeply bifid lamellae; lamella of tarsomere 3 largest; penultimate tarsomere shortest, ultimate tarsomere slender, longest; claws slightly curved (Fig. 2J, K). Abdomen short, well-sclerotized, finely and moderately deeply punctate, with suberect pubescence. All ventrites connate, each ventrite with a circular smooth elevation near lateral edges (Fig. 2L). Spiculum ventrale long, slender (Fig. 2N). Female genitalia with long and slender valvifer; valvifer 2.5 times longer than coxite (Fig. 2N).

Measurements. BL 6.1 mm, EL 4.7 mm, WHe 1.1 mm, WHum 2.2 mm, PL 1.1 mm, PWA 1.2 mm, PWP 1.9 mm, Edist 0.8 mm, Ediam 0.4 mm, LV 1.4 mm, LC 0.6 mm.

Distribution. This species is known only from the type locality in Yunnan, China (Fig. 3).

Etymology. The species is dedicated to Manfred Jäch (NHMW) who provided us with the type material.

Eurypogon heishuiensis sp. nov.

Fig. 2C, E, G, M, O

Type material. Holotype, 1 female, “China Yunnan, 1-19.VII. / HEISHUI, 35 km N Lijiang / 27° 13'N 100° 19'E / E. Jendek leg. 1992” (NHMW).

Fig. 3. The distribution of the genus *Eurypogon* in East Palearctic Region.

Diagnosis. *E. heishuiensis* sp. nov. differs from *E. jaechi* sp. nov. by more metallic elytral coloration, narrower body (Fig. 2A, C), more concave pronotal sides and more prominent pronotal hind angles, smaller and sparser punctures on head and pronotum (Fig. 2F-G), different relative lengths of antennomeres 3-5 (Fig. 2D-E), more prominent elevations near lateral sides of abdomen (Fig. 2L-M), and lower valvifer/coxite length ratio (Fig. 2N-O).

Description. Body 6.1 mm long, 2.9 times as long as wide at humeri (Fig. 2C). Body coloration grey to black; elytra strongly metallic green, shiny; legs dark brown, tarsal lamellae yellow. Head irregularly and sparsely covered with moderately large punctures. Eyes protuberant; interocular distance 1.9 times eye diameter. Antennae with antennomere 1 pear-shaped, antennomeres 2-3 simple, minute, their combined lengths subequal to length of antennomere 4; antennomeres 4-10 slightly serrate; antennomere 5 slightly longer than antennomere 4; antennomeres 6-10 slightly short-

er than antennomere 5, subequal in length; apical antennomere simple (Fig. 2E). Pronotum with anterior edge almost straight, lateral margins slightly concave, posterior margin evenly rounded, slightly sinuate in middle part. Anterior angles deflexed, almost rectangular; posterior angles acute (Fig. 2G); surface of disc shiny, with moderately large, ovoid punctures. Elytra shiny, finely and deeply punctate with distinct puncture rows (Fig. 2C). Abdominal ventrites with apparent circular smooth elevation near lateral edges (Fig. 2M). Spiculum ventrale moderately long, slender (Fig. 2O; valvifer 2.0 times longer than coxite (Fig. 2O).

Measurements. BL 6.1 mm, EL 4.7 mm, WHe 1.2 mm, WHum 2.1 mm, PL 1.0 mm, PWA 1.2 mm, PWP 1.8 mm, Edist 0.8 mm, Ediam 0.4 mm, LV 1.2 mm, LC 0.6 mm.

Distribution. This species is known only from the type locality in Yunnan, China (Fig. 3).

Etymology. The species name *heishuiensis* refers to the type locality of the species.

Table S1. The list of previously published sequences used in the dataset (Bocakova *et al.*, 2007; Kundrata and Bocak 2011).

superfamily/family	subfamily	genus/species	geographic origin	markers			
				18S rDNA	28S rDNA	16S mtDNA	COI mtDNA
DASCILLOIDEA							
Dascillidae	Dascillinae	<i>Dascillus cervinus</i>	United Kingdom	AY745558	DQ198700	DQ198621	DQ198543
BYRRHOIDEA							
Byrrhidae	Byrrhinae	<i>Byrrhus pilula</i>	United Kingdom	AF427604	DQ198705	DQ198625	DQ198548
Limnichidae	Limnichinae	<i>Limnichus pygmaeus</i>	United Kingdom	AF451923	DQ198719	DQ198631	DQ198554
Chelonariidae		<i>Chelonarium</i> sp.	Indonesia	DQ100488	DQ198724	DQ198635	DQ198558
Heteroceridae		<i>Heterocerus</i> sp.	Slovakia	AF451928	DQ198718	DQ198630	DQ198553
Dryopidae		<i>Pomatinus substriatus</i>	United Kingdom	AF451924	DQ198708	DQ198626	DQ198549
Psephenidae	Eubrianacinae	<i>Eubrianax</i> sp.	Indonesia	DQ100485	DQ198721	DQ198632	DQ198555
Elmidae	Elminae	<i>Limnius volckmari</i>	Spain	AF451914	DQ198712	DQ198627	DQ198550
Elmidae	Elminae	<i>Oulimnius rivularis</i>	Portugal	AF451913	DQ198714	DQ198628	DQ198551
Elmidae	Larainae	<i>Potamodytes</i> sp.	South Africa	AF451912	DQ198715	DQ198629	DQ198552
Callirhipidae		gen. sp.	Malaysia	DQ100490	DQ198726	DQ198637	DQ198560
Ptilodactylidae	Ptilodactylinae	<i>Ptilodactyla serricornis</i>	Japan	AF451932	DQ198723	DQ198634	DQ198557
Ptilodactylidae	Cladotominae	<i>Paralichas pectinatus</i>	Japan	DQ100486	DQ198722	DQ198633	DQ198556
Eulichadidae		<i>Eulichas</i> sp.	Malaysia	DQ100489	DQ198725	DQ198636	DQ198559
ELATEROIDEA							
Telegeusidae		<i>Telegeusis nubifer</i>	USA	DQ100503	DQ198751	DQ198660	DQ198582
Omethidae	Driloniinae	<i>Drilonius</i> sp. a	Indonesia	DQ100502	DQ198750	DQ198659	DQ198581
Throscidae		<i>Trixaqus dermestoides</i>	United Kingdom	AF451950	DQ198747	DQ198656	DQ198578
Eucnemidae		gen. sp. a	Indonesia	HQ333807	HQ333902	HQ333716	HQ333988
Eucnemidae		gen. sp. b	Indonesia	HQ333829	HQ333923	HQ333736	HQ334009

Eucnemidae		gen. sp. c	Indonesia	HQ333830	HQ333924	HQ333737	HQ334010
Eucnemidae	Macraulacinae	<i>Formax</i> sp.	Bolivia	DQ100492	DQ198729	DQ198640	DQ198562
Eucnemidae	Macraulacinae	<i>Nematodes</i> sp.	Bolivia	DQ100495	DQ198731	DQ198642	DQ198564
Eucnemidae	Eucneminae	<i>Idiotarsus</i> sp.	Bolivia	DQ100493	DQ198730	DQ198641	DQ198563
Lycidae	Libnetinae	<i>Libnetis granicollis</i>	Japan	DQ181107	DQ181181	DQ181033	DQ181255
Lycidae	Dictyopterinae	<i>Lycoprogenthes</i> sp.	Indonesia	DQ181070	DQ181144	DQ180996	DQ181218
Lycidae	Dictyopterinae	<i>Taphes brevicollis</i>	Laos	DQ181098	DQ181172	DQ181024	DQ181246
Lycidae	Dictyopterinae	<i>Dictyoptera elegans</i>	Japan	DQ181073	DQ181147	DQ180999	DQ181221
Lycidae	Dictyopterinae	<i>Benibotarus nigripennis</i>	Japan	DQ181075	DQ181149	DQ181001	DQ181223
Lycidae	Dictyopterinae	<i>Pyropterus nigroruber</i>	Japan	DQ181077	DQ181151	DQ181003	DQ181225
Lycidae	Lyropaeinae	<i>Ahyculus kurbatovi</i>	Indonesia	DQ181072	DQ181146	DQ180998	DQ181220
Lycidae	Lyropaeinae	<i>Lyropaeus</i> sp.	Malaysia	DQ181042	DQ181116	DQ180968	DQ181190
Lycidae	Lyropaeinae	<i>Antennolycus constrictus</i>	Malaysia	DQ181051	DQ181125	DQ180977	DQ181199
Lycidae	Lyropaeinae	<i>Microlyrop. dembickyi</i>	Indonesia	DQ181071	DQ181145	DQ180997	DQ181219
Lycidae	Lyropaeinae	<i>Platerodrilus</i> sp.	Malaysia	DQ181037	DQ181111	DQ180963	DQ181185
Lycidae	Lyropaeinae	<i>Macrolibnetis</i> sp.	Malaysia	DQ181050	DQ181124	DQ180976	DQ181198
Lycidae	Lyropaeinae	<i>Pendola</i> sp.	Indonesia	DQ181058	DQ181132	DQ180984	DQ181206
Lycidae	Lyropaeinae	<i>Horakiella emasensis</i>	Malaysia	DQ181110	DQ181184	DQ181036	DQ181258
Lycidae	Ateliinae	<i>Dilophotes</i> sp.	Malaysia	DQ181066	DQ181140	DQ180992	DQ181214
Lycidae	Ateliinae	<i>Scarelus</i> sp.	Malaysia	DQ181085	DQ181159	DQ181011	DQ181233
Lycidae	Lycinae	<i>Dihammatus</i> sp.	Malaysia	DQ181043	DQ181117	DQ180969	DQ181191
Lycidae	Lycinae	<i>Eurrhacus</i> sp.	Ecuador	DQ181056	DQ181130	DQ180982	DQ181204
Lycidae	Lycinae	<i>Macrolycus</i> sp.	China	DQ181049	DQ181123	DQ180975	DQ181197
Lycidae	Lycinae	<i>Thonalmus hubbardi</i>	Montserrat	DQ181094	DQ181168	DQ181020	DQ181242
Lycidae	Lycinae	<i>Lyponia quadricollis</i>	Korea	DQ181101	DQ181175	DQ181027	DQ181249
Lycidae	Lycinae	<i>Lycus</i> sp.	South Africa	DQ181039	DQ181113	DQ180965	DQ181187

Lycidae	Lycinae	<i>Idiopteron biplagiatum</i>	Ecuador	DQ181057	DQ181131	DQ180983	DQ181205
Lycidae	Lycinae	<i>Metriorrhynchus lineatus</i>	Malaysia	DQ181040	DQ181114	DQ180966	DQ181188
Lycidae	Lycinae	<i>Platycis minutus</i>	Czech Republic	DQ181069	DQ181143	DQ180995	DQ181217
Lampyridae	Lampyrinae	<i>Vesta</i> sp.	Indonesia	DQ100511	DQ198760	DQ198669	DQ198592
Lampyridae	Lampyrinae	gen. sp.	Indonesia	DQ100509	DQ198759	DQ198667	DQ198590
Lampyridae	Luciolinae	<i>Curtos</i> sp.	Indonesia	DQ100513	DQ198761	DQ198671	DQ198594
Lampyridae	Luciolinae	gen. sp.	Indonesia	DQ100514	DQ198762	DQ198672	DQ198595
Lampyridae	Ototretinae	<i>Mimophaeopterus</i> sp.	Indonesia	DQ100521	DQ198764	DQ198679	DQ198602
Lampyridae	Ototretinae	<i>Flabellotreta</i> sp.	Indonesia	DQ100520	DQ198763	DQ198678	DQ198601
Lampyridae	Ototretinae	<i>Ototretadrilus</i> sp. a	India	DQ100524	DQ198765	DQ198682	DQ198605
Lampyridae	Ototretinae	<i>Ototretadrilus</i> sp. b	India	DQ100525	DQ198766	DQ198683	DQ198606
Cantharidae	Malthininae	<i>Malthinus flaveolus</i>	United Kingdom	AF451938	DQ198775	DQ198692	DQ198615
Cantharidae	Malthininae	<i>Malthodes</i> sp.	France	DQ100532	DQ198776	DQ198693	DQ198616
Cantharidae	Malthininae	<i>Maltypus</i> sp.	Indonesia	DQ100533	DQ198777	DQ198694	DQ198617
Cantharidae	Malthininae	<i>Imalthodes</i> sp.	Indonesia	DQ100534	DQ198778	DQ198695	DQ198618
Cantharidae	Chaulionathinae	<i>Ichthyurus</i> sp.	Indonesia	DQ100531	DQ198774	DQ198691	DQ198614
Cantharidae	Cantharinae	<i>Cantharis decipiens</i>	Czech Republic	DQ100526	DQ198768	DQ198685	DQ198608
Cantharidae	Cantharinae	<i>Rhagonycha lignosa</i>	United Kingdom	AF451939	DQ198770	DQ198687	DQ198610
Cantharidae	Cantharinae	<i>Rhagonycha nigriceps</i>	France	DQ100527	DQ198769	DQ198686	DQ198609
Cantharidae	Silinae	<i>Astosilis</i> sp.	Indonesia	DQ100530	DQ198773	DQ198690	DQ198613
Cantharidae	Silinae	<i>Laemoglyptus</i> sp.	Indonesia	DQ100528	DQ198771	DQ198688	DQ198611
Cantharidae		gen. sp.	Indonesia	DQ100529	DQ198772	DQ198689	DQ198612
Omaliidae		<i>Omalius fontisbellaquei</i>	Czech Republic	AF451948	DQ198749	DQ198658	DQ198580
Omaliidae		<i>Pseudeuanoma</i> sp.	Greece	HQ333832	KF294773	HQ333738	HQ334011
Phengodidae	Phengodinae	<i>Phengodes</i> sp.	USA	DQ100504	DQ198752	DQ198661	DQ198583
Rhagophthalmidae		<i>Bicladodrilus</i> sp.	China	DQ100507	DQ198755	DQ198664	DQ198586

Rhagophthalmidae					Malaysia	DQ100505	DQ198753	DQ198662	DQ198584
Rhagophthalmidae					India	DQ100508	DQ198756	DQ198665	DQ198587
Rhagophthalmidae					Indonesia	DQ100506	DQ198754	DQ198663	DQ198585
Elateridae	Agrypninae				Japan	HQ333757	HQ333852	HQ333676	HQ333941
Elateridae	Agrypninae				Indonesia	HQ333783	HQ333878	HQ333697	HQ333965
Elateridae	Agrypninae				Japan	HQ333810	HQ333905	HQ333719	HQ333991
Elateridae	Agrypninae				Indonesia	HQ333820	HQ333915	HQ333727	HQ334000
Elateridae	Agrypninae				Japan	HQ333772	HQ333867	HQ333689	HQ333955
Elateridae	Agrypninae				Japan	HQ333778	HQ333873	HQ333694	HQ333961
Elateridae	Agrypninae				Japan	HQ333817	HQ333912	HQ333724	HQ333997
Elateridae	Agrypninae				Indonesia	HQ333806	HQ333901	HQ333715	HQ333987
Elateridae	Agrypninae				Malaysia	HQ333818	HQ333913	HQ333725	HQ333998
Elateridae	Agrypninae				Panama	HQ333746	HQ333841	HQ333665	HQ333931
Elateridae	Agrypninae				Panama	HQ333747	HQ333842	HQ333666	HQ333932
Elateridae	Agrypninae				Slovakia	HQ333793	HQ333888	HQ333704	HQ333975
Elateridae	Agrypninae				Morocco	HQ333816	HQ333911	HQ333723	HQ333996
Elateridae	Agrypninae				Malaysia	HQ333798	HQ333893	HQ333708	HQ333980
Elateridae	Agrypninae				Panama	HQ333748	HQ333843	HQ333667	HQ333933
Elateridae	Agrypninae				Panama	HQ333751	HQ333846	HQ333670	HQ333936
Elateridae	Agrypninae				Panama	HQ333752	HQ333847	HQ333671	HQ333937
Elateridae	Agrypninae				Japan	HQ333768	HQ333863	HQ333685	HQ333951
Elateridae	Agrypninae				Malaysia	HQ333834	HQ333926	HQ333740	HQ334014
Elateridae	Agrypninae				South Africa	HQ333824	HQ333919	HQ333731	HQ334004
Elateridae	Agrypninae				South Africa	HQ333825	HQ333920	HQ333732	HQ334005
Elateridae	Agrypninae				Greece	HQ333826	HQ333921	HQ333733	HQ334006
Elateridae	Agrypninae				Spain	HQ333836	HQ333927	HQ333742	HQ334015

Elateridae	Agrypninae	<i>Drilus mauritanicus</i>	Spain	HQ333837	HQ333928	HQ333743	HQ334016
Elateridae	Agrypninae	<i>Agrypnus murinus</i>	Slovakia	AF451943	DQ198735	DQ198645	DQ198567
Elateridae	Agrypninae	<i>Drilus flavescens</i>	Malta	DQ100501	DQ198748	DQ198657	DQ198579
Elateridae	Cardiophorinae	gen. sp.	Namibia	AF451942	DQ198739	DQ198649	DQ198571
Elateridae	Cardiophorinae	<i>Cardiophorus erichsoni</i>	Slovakia	HQ333790	HQ333885	HQ333701	HQ333972
Elateridae	Denticollinae	<i>Athous vittatus</i>	Czech Republic	HQ333755	HQ333850	HQ333674	HQ333939
Elateridae	Denticollinae	<i>Limoniinus quercus</i>	Czech Republic	HQ333775	HQ333870	HQ333692	HQ333958
Elateridae	Denticollinae	<i>Cidnopus pilosus</i>	Slovakia	HQ333792	HQ333887	HQ333703	HQ333974
Elateridae	Denticollinae	<i>Anostirus purpureus</i>	Slovakia	HQ333761	HQ333856	HQ333679	HQ333945
Elateridae	Denticollinae	<i>Neopristilophus serrifer</i>	Japan	HQ333765	HQ333860	HQ333682	HQ333948
Elateridae	Denticollinae	<i>Selatosomus gravidus</i>	Czech Republic	HQ333774	HQ333869	HQ333691	HQ333957
Elateridae	Denticollinae	gen. sp.	Japan	HQ333787	HQ333882	HQ333700	HQ333969
Elateridae	Denticollinae	<i>Platiana</i> sp.	Indonesia	HQ333782	HQ333877	HQ333696	HQ333964
Elateridae	Denticollinae	<i>Hypolithus</i> sp.	Japan	HQ333795	HQ333890	HQ333705	HQ333977
Elateridae	Denticollinae	<i>Semiotus</i> sp.	Chile	HQ333799	HQ333894	HQ333709	HQ333981
Elateridae	Denticollinae	<i>Oxyntopterus</i> sp.	Philippines	HQ333800	HQ333895	HQ333710	HQ333982
Elateridae	Denticollinae	<i>Panspaeus guttatus</i>	United Kingdom	DQ100499	DQ198742	DQ198652	DQ198574
Elateridae	Denticollinae	<i>Stenagostus rhombeus</i>	United Kingdom	AF451945	DQ198744	DQ198653	DQ198576
Elateridae	Denticollinae	<i>Denticollis linearis</i>	Czech Republic	DQ100498	DQ198741	DQ198651	DQ198573
Elateridae	Denticollinae	<i>Athous haemorrhoidalis</i>	United Kingdom	AF451944	DQ198738	DQ198648	DQ198570
Elateridae	Elaterinae	<i>Octinodes</i> sp.	Panama	HQ333749	HQ333844	HQ333668	HQ333934
Elateridae	Elaterinae	<i>Elater</i> sp.	Japan	HQ333766	HQ333861	HQ333683	HQ333949
Elateridae	Elaterinae	<i>Tomicephalus</i> sp.	Panama	HQ333750	HQ333845	HQ333669	HQ333935
Elateridae	Elaterinae	Elaterini gen. sp. a	Indonesia	HQ333773	HQ333868	HQ333690	HQ333956
Elateridae	Elaterinae	Elaterini gen. sp. b	Indonesia	HQ333819	HQ333914	HQ333726	HQ333999
Elateridae	Elaterinae	<i>Ludioschema</i> sp.	Japan	HQ333777	HQ333872	HQ333693	HQ333960

Elateridae	Elaterinae	<i>Anoploschius</i> sp.	Panama	HQ333745	HQ333840	HQ333664	HQ333930
Elateridae	Elaterinae	<i>Ampedus</i> sp. a	Japan	HQ333758	HQ333853	HQ333677	HQ333942
Elateridae	Elaterinae	<i>Ampedus sanguinolentus</i>	Slovakia	HQ333760	HQ333855	HQ333678	HQ333944
Elateridae	Elaterinae	<i>Ampedus rufipennis</i>	Slovakia	HQ333762	HQ333857	HQ333680	HQ333946
Elateridae	Elaterinae	<i>Ampedus</i> sp. b	Japan	HQ333771	HQ333866	HQ333688	HQ333954
Elateridae	Elaterinae	<i>Ampedus sinuatus</i>	Slovakia	HQ333791	HQ333886	HQ333702	HQ333973
Elateridae	Elaterinae	<i>Ampedus sinuatus</i>	Czech Republic	HQ333822	HQ333917	HQ333729	HQ334002
Elateridae	Elaterinae	<i>Agriotes acuminatus</i>	Czech Republic	HQ333756	HQ333851	HQ333675	HQ333940
Elateridae	Elaterinae	<i>Agriotes ustulatus</i>	Czech Republic	HQ333786	HQ333881	HQ333699	HQ333968
Elateridae	Elaterinae	Megapenthini gen. sp.	Japan	HQ333767	HQ333862	HQ333684	HQ333950
Elateridae	Elaterinae	Adrastini gen. sp. a	Japan	HQ333769	HQ333864	HQ333686	HQ333952
Elateridae	Elaterinae	Adrastini gen. sp. a	Japan	HQ333770	HQ333865	HQ333687	HQ333953
Elateridae	Elaterinae	Adrastini gen. sp. b	Japan	HQ333779	HQ333874	HQ333695	HQ333962
Elateridae	Elaterinae	Adrastini gen. sp. c	Malaysia	HQ333801	HQ333896	HQ333711	HQ333983
Elateridae	Elaterinae	Adrastini gen. sp. d	Malaysia	HQ333812	HQ333907	HQ333720	HQ333993
Elateridae	Elaterinae	<i>Melanotus villosus</i>	Czech Republic	HQ333754	HQ333849	HQ333673	HQ333938
Elateridae	Elaterinae	<i>Priopus ornatus</i>	Laos	HQ333785	HQ333880	HQ333698	HQ333967
Elateridae	Elaterinae	<i>Priopus humeralis</i>	Indonesia	HQ333821	HQ333916	HQ333728	HQ334001
Elateridae	Elaterinae	<i>Anchastus</i> sp. a	Indonesia	HQ333804	HQ333899	HQ333714	HQ333986
Elateridae	Elaterinae	<i>Anchastus</i> sp. b	Indonesia	HQ333809	HQ333904	HQ333718	HQ333990
Elateridae	Elaterinae	<i>Anchastus</i> sp. c	Indonesia	HQ333813	HQ333908	HQ333721	HQ333994
Elateridae	Elaterinae	<i>Anchastus</i> sp. d	Indonesia	HQ333814	HQ333909	HQ333722	HQ333995
Elateridae	Elaterinae	<i>Cebrio</i> sp.	Spain	DQ100497	DQ198740	DQ198650	DQ198572
Elateridae	Elaterinae	<i>Ampedus balteatus</i>	United Kingdom	AF427605	DQ198736	DQ198646	DQ198568
Elateridae	Lissominae	<i>Drapetes</i> sp.	Czech Republic	HQ333828	HQ333922	HQ333735	HQ334008
Elateridae	Negastriinae	<i>Zorochros</i> sp.	Malaysia	HQ333796	HQ333891	HQ333706	HQ333978

Elateridae	Negastriinae	<i>Zorochores</i> sp.	Malaysia	HQ333797	HQ333892	HQ333707	HQ333979
Elateridae	Negastriinae	<i>Quasimus</i> sp. a	Malaysia	HQ333802	HQ333897	HQ333712	HQ333984
Elateridae	Negastriinae	<i>Quasimus</i> sp. b	Malaysia	HQ333803	HQ333898	HQ333713	HQ333985

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Table S2. Numbers of characters, base frequencies and maximum uncorrected pairwise distances. * *coxI* mtDNA aligned only by ClustalX..

alignment/ partition	number of characters	constant variable		parsimony		base frequencies (%)			max. uncorrec.		
		characters	uninformative	informative	uninformative	informative	A	C	G	T	pairw. dist. (%)
BlastAlign											
Total dataset	4675	2781	441	1453			27.17	21.08	24.38	27.38	15.41
18S rDNA	2186	1587	163	436			24.03	24.44	27.94	23.59	08.90
28S rDNA	1001	635	128	238			25.49	23.46	30.93	20.12	16.74
<i>rrnL</i> mtDNA	765	334	104	327			32.28	09.73	17.13	40.87	26.58
<i>cox I</i> mtDNA*	723	225	046	452			33.25	17.86	14.51	34.39	35.00
ClustalX											
Total dataset	4330	2245	372	1713			27.12	20.99	24.37	27.53	19.07
18S rDNA	2130	1449	160	521			23.94	24.52	27.97	23.57	12.40
28S rDNA	910	396	123	391			25.33	23.57	30.97	20.13	30.47
<i>rrnL</i> mtDNA	567	175	43	349			32.18	09.47	17.01	41.33	32.28
<i>cox I</i> mtDNA*	723	225	046	452			33.25	17.86	14.51	34.39	35.00

Table S3. The list of the artematopodid genera, with geographical distributions.

subfamily	tribe	genus	nr. of species	recent species	fossil species	geographical distribution
Artematopodinae Lacordaire, 1857						
Artematopodini Lacordaire, 1857						
		<i>Artematopus</i> Perty, 1830	44	44	0	South and Central America (from Bolivia to Nicaragua)
		<i>Carcinognathus</i> Kirsch, 1873	1	1	0	Peru
		<i>Protartematopus</i> Crowson, 1973	1	0	1	–
Ctesibiini Crowson, 1973						
		<i>Brevipogon</i> Lawrence, 2005	1	1	0	USA
		<i>Ctesibius</i> Champion, 1897	1	1	0	Mexico
Macropogonini LeConte, 1861						
		<i>Eurypogon</i> Motschulsky, 1859	11	11	0	USA, Canada, Italy, China, Taiwan, Japan
		<i>Macropogon</i> Motschulsky, 1845	7	7	0	USA, Canada, Eastern Siberia, Far East
Allopogoniinae Crowson, 1973						
		<i>Allopogonia</i> Cockerell, 1906	1	1	0	USA
Electribiinae Crowson, 1975						
		<i>Electribius</i> Crowson, 1973	6	2	4	Salvador, Mexico
<i>Incertae sedis*</i>						
Electrapatini Cobos, 1963						
		<i>Electrapate</i> Iablukoff-Khnzorian, 1962	1	0	1	–

* – The genus *Electrapate* Iablokoff-Khnzorian was placed in Armatopodidae by Lawrence (2010) without mentioning a reason, although previous authors classified this taxon in Buprestoidea (e.g., Bellamy, 1995; Bouchard *et al.*, 2011).

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Table S4. The list of described species of the genus *Eurypogon* Motschulsky, with geographical distributions.

spp. of <i>Eurypogon</i> Motschulsky, 1859	geographical distribution
Nearctic Region	
<i>E. californicus</i> Horn, 1880	USA, Canada
<i>E. harrisi</i> (Westwood, 1862)	USA
<i>E. niger</i> (Melsheimer, 1846)	USA, Canada
Palearctic Region	
<i>E. cribratus</i> (Hampe, 1866)	Italy
<i>E. brevipennis</i> Sakai, 1982	Japan (Honshu, Shikoku)
<i>E. hisamatsui</i> Sakai, 1982	Japan (Honshu, Shikoku)
<i>E. japonicus</i> Sakai, 1982	Japan (Honshu, Shikoku, Kyushu)
<i>E. ocellaris</i> Sakai, 1982	Japan (Honshu)
<i>E. granulatus</i> Sakai, 1982	Taiwan
<i>E. jaechi</i> sp. nov.	China (Yunnan)
<i>E. heishuiensis</i> sp. nov.	China (Yunnan)

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