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Phylogenetically problematic *Aater cangshanensis* gen. et sp. nov. from Southwest China suggests multiple origins of prosternal canal in Molytinae weevils (Coleoptera: Curculionidae)

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Abstract

A new weevil taxon, *Aater cangshanensis* **gen. et sp. nov.** is established for a single female specimen sifted from the forest litter on the Cang Shan Mountain Range in Yunnan, China. This small flightless beetle (the combined length of pronotum and elytra is 3.4 mm) has relatively long and straight rostrum, contiguous procoxae and tuberculate elytra with effaced shoulders. Remarkably, the new genus has a prosternal canal on the ventral side of the prothorax. This feature is characteristic to the weevils of the Old World nominal tribe Aminyopini (=Euderini of some authors) and to the China-Nepal genus *Niphadomimus* (Typoderini). A phylogenetic molecular analysis using an alignment of 2,956 bp from one mitochondrial and two nuclear fragments outputted a mainly inconclusive topology with low backbone resolution. Terminals with prosternal canal were grouped into four clades not most closely related to each other: *Aater cangshanensis* **gen. et sp. nov.**, *Niphadomimus*, African Aminyopini and Asian Aminyopini; the latter three clades each with bootstrap support of 100%. The prosternal canal has either evolved more than once, or reversed once or more, or both. The sister group of *Aater* **gen. nov.** cannot be reliably identified and, therefore, the new genus is assigned to Molytinae *incertae sedis*.

Key words: Hengduan, Yunnan, Aminyopini, *Niphades*.

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Introduction

Discovery of a new, bizarre and unclassified organism constitutes an intellectually challenging aspect of biodiversity research (Laumer et al. 2014). The single herein reported unusually shaped weevil (Fig. 1) was extracted from the forest litter on the southern slope of the Cang Shan Mountain Range in Yunnan, China. The combination of a few easily observable external characters (small size, tuberculate elytra with effaced shoulders, relatively straight and long rostrum) immediately set aside this otherwise suggestively "molytine" specimen as a potentially first representative of a new and deeply-divergent clade seemingly unknown from the region. Its taxonomic identification was attempted using morphological and DNA barcode data, while the specimen image was sent to colleagues seeking their suggestions. In spite of all these efforts, the beetle could not be placed in any named genus or tribe. The encountered lack of positive identification was, however, not surprising, since flightless weevils recently reported from Southwest China belong to inadequately known clades. Examples are the southern-most members of clades surviving the Holocene trapped on the mountaintops (such as the genera *Trichalophus* LeConte, 1876, *Catapionus* Schoenherr, 1842, and *Notaris* Germar, 1817; see Grebennikov 2015b, 2016a; Grebennikov & Kolov 2016, respectively), or first generic records for the country (such as the genera *Niphadomimus* Zherikhin, 1987, *Disphaerona* Jordan, 1902, *Cotasterosoma* Konishi, 1962 and *Tasactes* Faust, 1894; see Grebennikov 2014a, 2016b; Grebennikov & Morimoto 2016; Grebennikov 2018a, respectively), or genera outright new to science (such as *Morimotodes* Grebennikov, 2014; Grebennikov 2014b and *Devernodes* Grebennikov, 2018; Grebennikov, 2018b).

Remarkably, the herein reported specimen has a wide prosternal canal on the ventral surface of the prothorax (Fig. 2A) delimited posteriorly by contiguous procoxae. The prostenal canal is not to be confused with the normally much deeper and longer thoracic furrow of Cryptorhynchinae (Riedel et al. 2016) and a few other distantly related groups, such as the molytine tribe Aedemonini or the Afrotropical genus *Paocryptorrhinus* Voss, 1965 (Grebennikov 2015a). Thoracic furrow, when present, passes between the widely separate procoxae and terminates in a mesosternal receptacle (Fig. 2C). A much shallower and shorted prosternal canal (Figs 2E-H) is a characteristic feature of the molytine tribe Aminyopini, as defined by Alonso-Zarazaga & Lyal (1999, 2002) and Meregalli (2003), although Lyal (2014) defines it more broadly and calls it "Euderini". The tribe consists of about a hundred nominal species arranged in less than a dozen poorly understood genera distributed between New Guinea, Russian Far East and India and in the Afrotropical Region. The genus *Niphades* Pascoe, 1871 is distributed over the entire range of the tribe (Alonso-Zarazaga & Lyal 1999), while all other genera are limited to either Asia or Africa. The tribe unites both volant and flightless species associated with primary forests (*Falsanchonus* Zherikhin, 1987, *Niphades*, *Microplinthus* Zherikhin, 1987) and those restricted to the high altitude alpine zone (*Niphadonyx* Schenkling, 1932, *Niphadonothus* Voss, 1965, *Oreoscotus* Aurivillius, 1910). Even though some Asian Aminyopini have been recently revised (Meregalli 2003, 2004, 2013), the taxonomically implied monophyly of the tribe and all its genera has never been adequately test-

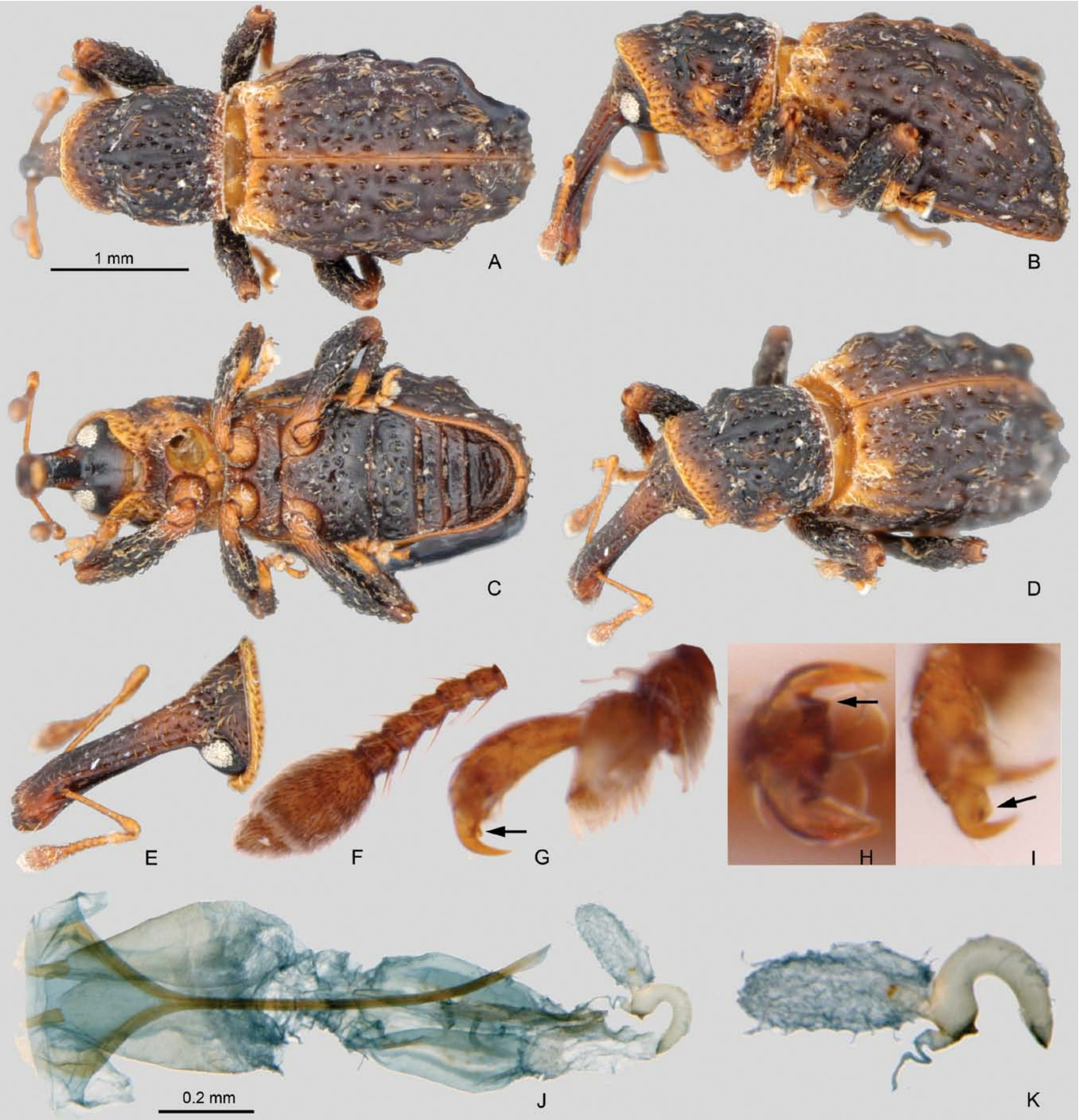

Fig. 1 – *Aater cangshanensis* **gen. et sp. nov. A-D**, habitus; **E**, head; **F**, antennal club and part of funicle; **G-I**, claws showing proximal tooth-like structure, hind (G), middle (H) and fore (I) leg; **J**, female genitalia; **K**, spermatheca.

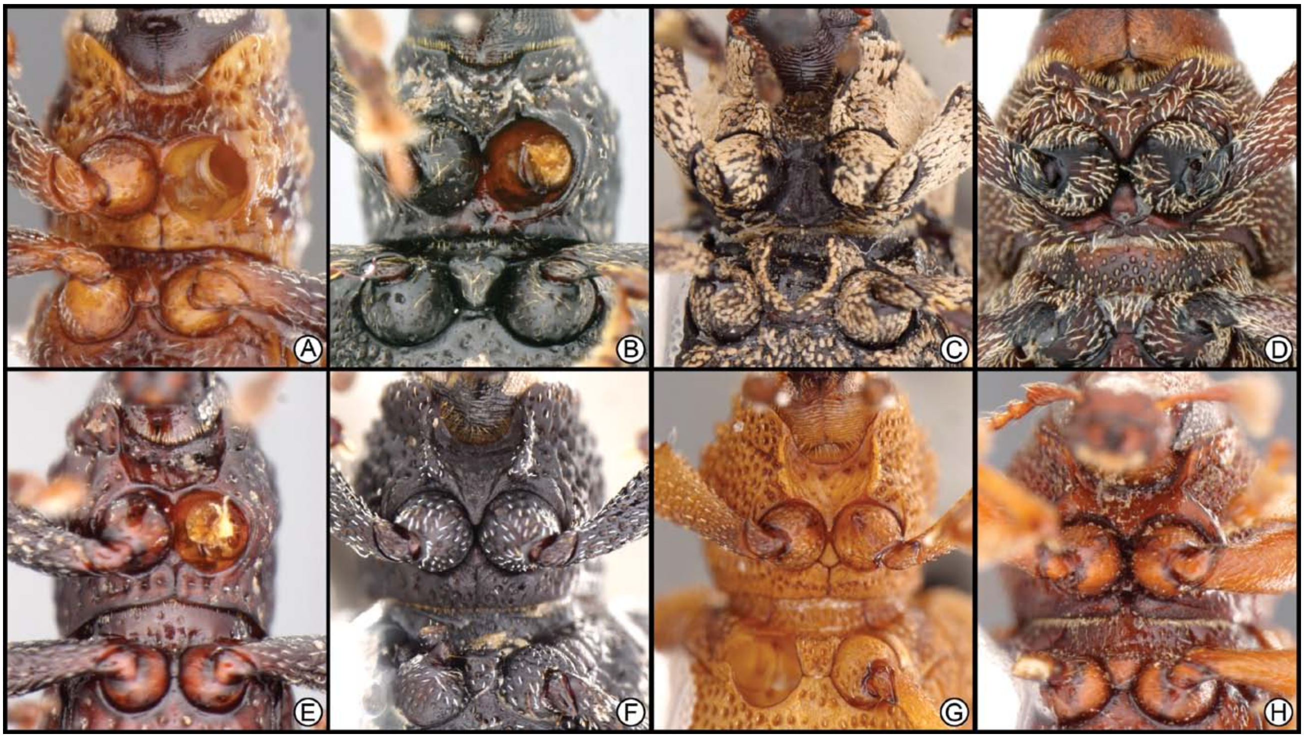

Fig. 2 – Thorax of Cryptorhynchinae (C) and Molytinae (A-B, E-H) in ventral aspect, exhibiting prosternal canal (A-B, D-H) or rostral furrow (C). **A**, *Aater cangshanensis* **gen. et sp. nov.**; **B**, *Niphadomimus maia* Grebennikov; **C**, *Cryptorhynchus lapathi* (Linnaeus); **D**, *Euderes lineicollis* (Wiedemann), © The Natural History Museum, London; **E**, *Falsanchonus emeishanicus* Meregalli; **F**, *Niphades verrucosus* Voss; **G**, *Niphades* from Tanzania; **H**, *Niphadonothus gentilis* Voss.

ed. At least two genera of Aminyopini (*Niphades* and *Microplinthus*) have been found within the radius of a kilometer from the type locality of the herein described taxon. This, as well as a tooth-like structure located at the base of the claws (Figs 1G-I) commonly found in Aminyopini, additionally suggests that the prosternal canal might perhaps be a synapomorphy linking the new find with the tribe. The molytine genus *Niphadomimus* Zherikhin, 1987, with eight high-altitude flightless species found in Nepal and Southern China (including the Cang Shan Mountain Range, Grebennikov 2014a) is yet another potential relative of the newly detected Yunnan beetle, since at least some *Niphadomimus* have a similar variously developed prosternal canal anterior of contiguous procoxae (Fig. 2B) and notably tuberculate elytra (Fig. 3).

The main goal of the present study, besides introducing to science the newly discovered and bizarre weevil from Yunnan, is to test the hypothesis that the prosternal canal in Molytinae is a diagnostically useful synapomorphy.

Material and Methods

All methods of specimen sampling and dissection are standard and were described in Grebennikov (2017) and references therein. DNA laboratory work followed the same procedure and targeted the same three markers, as in Grebennikov (2017): the mitochondrial DNA barcode fragment (5’COI) and two nuclear ribosome-coding regions: ITS2 and 28S. All details regarding lab work pertaining to DNA sequencing (such as DNA extraction, amplification, primers, PCR protocols), as well as images of the original electropherograms, habitus images and locality data of herein utilized specimens (see below) can be seen online in the Barcode of Life Database (=BOLD) dataset “Aater” at dx.doi.org/10.5883/DS-AATER.

To assess phylogenetic relationships of the newly discovered specimen, a phylogenetic matrix was constructed representing Aminyopini from Asia (five species, four genera) and Africa (four species, three genera), as well as two species of *Niphadomimus*. The outgroup was formed by 32 other Molytinae from a variety of nominal tribes (mainly utilizing data from Grebennikov, 2017) and excluding *Prothrombosternus* Voss, 1965, since in that study it unaccountably clustered with Entiminae, shedding doubts on the sequence identity. To root the topology, a representative of the likely monophyletic Cryptorhynchinae (Riedel et al. 2016) was added. The latter subfamily is likely more closely related to the majority of clades forming highly likely non-monophyletic Molytinae, than most

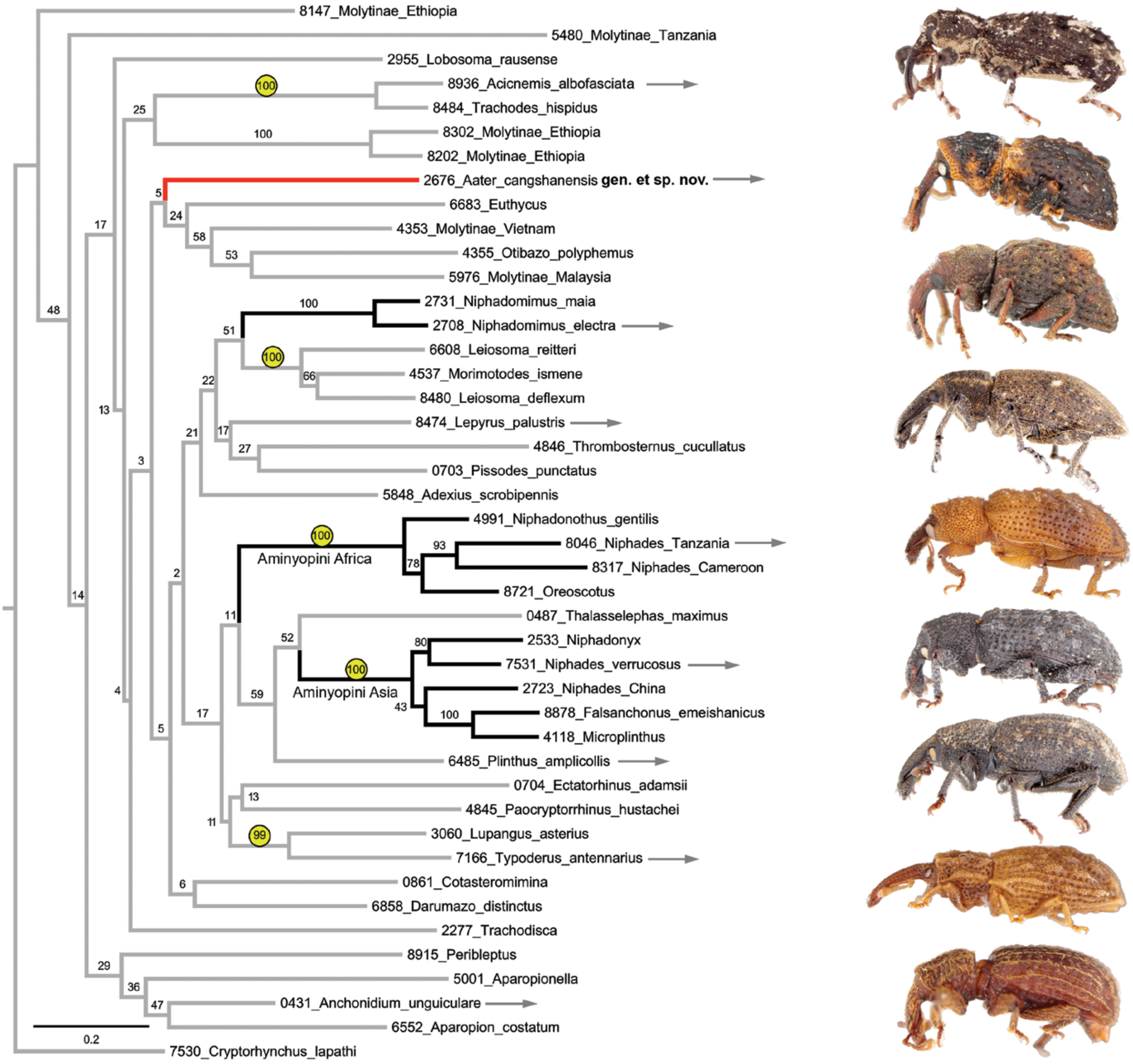

Fig. 3 – Maximum Likelihood inference phylogram. Terminal labels consist of a specimen ID (last four digits in the format label CNC-COLVG0000XXXX, see Table 2), followed by the taxonomic name of maximal precision (with a few likely unnamed genera represented only as "Molytinae"). Digits at internodes are bootstrap values; five high (>98%) bootstrap values for clades consisting two and more genera discussed in the text are in yellow circles. Branches in black represent other clades with prosternal canal.

of other weevils (McKenna et al. 2009; Haran et al. 2013). Alignment of the protein-coding COI was trivial and did not result in insertions/deletions (=indels), stop codons or frame shifts. Alignment of the ITS2 and 28S sequences was made using the MAFFT 7 online platform (Katoh et al. 2002; Katoh & Toh 2008a) with the Q-INS-i algorithm (Katoh & Toh 2008b) utilising the secondary structure information and resulted in introduction of 904 and 70 indels, respectively (Table 1). No parts of the alignment were excluded from the analysis. Three aligned single-fragment datasets were concatenated using Mesquite 3.11 (Maddison & Maddison 2011) into a matrix containing 43.5% of gaps (mainly due to indels in ITS2).

Phylogenetic analysis was conducted on the CIPRES Science Gateway online platform (Miller et al. 2010) using the Maximum Likelihood (ML) method. Phylogenetic trees were obtained using RAxML 7.2.7 (Stamatakis 2006), with default parameters unless otherwise stated. The concatenated matrix was partitioned into three fragments (Table 1) and an independent GTR+G model (the

Table 1 – DNA fragments used in the analysis.

Fragment	#	min	max	aligned	positions
COI	44	611	658	658	1 to 658
ITS2	41	223	724	1628	659 to 2286
28S	44	191	600	670	2287 to 2956

only one implemented in RAxML) was applied to each data partition. The best scoring ML tree was selected among 100 searches on the original alignment with different randomized parsimony starting trees. Support values were obtained with 1000 bootstrap (Felsenstein 1985) replicates. GenBank accession numbers for all 44 specimens are given in Table 2.

The herein presented analysis contains two limitations affecting its rigor. Firstly, not all Molytinae with prosternal canal could be sequenced, thus making the analysis to suffer from restricted taxon sampling. Most sensitive is the absence of the representatives of Euderini (sensu Alonso-Zarazaga & Lyal 1999) and of Cleogonini, particularly those of genus *Melanterius* Erichson, 1852 and its close relatives (Pinzón-Navarro et al. 2017). Secondly, due to technical reasons only three DNA markers could be sequenced, and this is likely to result in reduced statistical support for recovered clades. It should be, therefore, stressed that available molecular data are too fragmentary to adequately address phylogeny of Molytinae. Nevertheless, it appears justified to present the results of the DNA analysis as they are, since even in a reduced form they are likely to shed light on some among numerous and (with a few exceptions) taxonomically and phylogenetically neglected organisms vaguely assigned to the likely multiply non-monophyletic (Shin et al. 2017) "subfamily Molytinae".

Results

Maximum Likelihood analysis resulted in a poorly resolved topology having only five strongly supported clades (bootstrap 99–100%) formed by two and more genera: *Acicnemis* Fairmaire, 1849 + *Trachodes* Germar, 1824, *Leiosoma* Stephens, 1829 + *Morimotodes*, African Aminyopini, Asian Aminyopini and *Lupangus* Grebennikov, 2017 + *Typoderus* Marshall, 1953 (Fig. 3). The nominal tribe Aminyopini was recovered as two strongly supported and not most closely related Asia and African clades. The clade uniting *Aater cangshanensis* **gen. et sp. nov.** and its sister clade formed by four Asian genera have 5% and 24% bootstrap support, respectively (Fig. 3). Among the analysed beetles, species with a prosternum canal appear in four clades not most closely related to each other (Fig. 3).

Aater gen. nov.

Type species: *Aater cangshanensis* **sp. nov.**, here designated.

Diagnostic description. Female specimens of *Aater* can be immediately recognized among Molytinae weevils known from China and neighbouring countries by the unique combination of the following easily observed characters: body elongate and small (combined dorsal length of pronotum and elytra less than 5 mm); rostrum relatively long and straight (Fig. 3); antennal funicle with seven antennomeres; prosternum with canal and contiguous procoxae (Fig. 2A); femora without teeth-like projections; all claws with a ventral tooth-like structure at their base; elytra tuberculate, with effaced shoulders (Figs 1A-E); hind wings absent. Adults of the new genus might perhaps be confused with those of sympatric *Niphadomimus* (by sharing with the later the rostrum longer than wide, the postocular lobe on the pronotum, the prosternal canal and the appendiculate claws); the latter, however, have relatively shorter rostrum evenly curved in lateral view and notably lower ratio of elytral length to its maximal width (1.38 in *Aater cangshanensis* **gen. et sp. nov.** versus 0.97–1.17 in *Niphadomimus*).

Species composition and distribution. The genus *Aater* is monotypic and is known only from the Cang Shan Mountain Range in Yunnan, China.

Biology. The single known female of *Aater* was detected by sifting forest floor litter in primary broadleaf forest. Host plants, immature stages, parasites, or any other biological aspects remain unknown. The notably broad and ventrally pilose tarsi (Fig. 1G), along with the fact that no congeneric specimens were detected in Southwest China in spite of a sizable multi-year sifting effort (Grebennikov & Smetana 2015), suggest that these animals are perhaps arboreal, while their single detection in the forest floor litter might be an accident.

Etymology. The generic name is a meaningless combination of letters; gender masculine.

Aater cangshanensis sp. n. (Figs 1, 2A, 3)

Diagnostic description. With the morphological characters of the genus; dorsal body length between anterior edge of pronotum and elytral apex 3.4 mm; DNA data as in Table 2; color, proportion and all other relevant characters as in Figs 1, 2A, 3.

Material examined. Holotype (currently in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada; will be eventually deposited in the collection of Institute of Zoology, Chinese Academy of Science, Beijing, P.R. China), female: "**P.R. CHINA**,

Table 2 – GenBank accession numbers of sequences used in the analysis; those in **bold** are newly generated as compared to Grebennikov (2017).

Voucher#	Country	Taxonomy	COI	ITS2	28S
CNCCOLVG00000431	Morocco	*Anchonidium unguiculare*	HM417678	none	KY110382
CNCCOLVG00000487	Russia	*Thalasselephas maximus*	HM417677	KY110313	KY110375
CNCCOLVG00000703	China	*Pissodes punctatus*	HQ987002	none	KY110366
CNCCOLVG00000704	China	*Ectatorhinus adamsii*	HQ987003	KY110315	KY110377
CNCCOLVG00000861	China	*Cotasteromimina*	**HQ987100**	**MG648823**	**MG648736**
CNCCOLVG00002277	China	*Trachodisca*	KY110613	KY110321	KY110385
CNCCOLVG00002533	China	*Niphadonyx*	**MG648752**	**MG648826**	**MG648738**
CNCCOLVG00002676	China	*Aater congshanensis* **gen. et sp. nov.**	**MG648761**	**MG648835**	**MG648747**
CNCCOLVG00002708	China	*Niphadomimus electra*	KJ427734	KY110306	KY110368
CNCCOLVG00002723	China	*Niphades*	**MG648751**	**MG648825**	**MG648737**
CNCCOLVG00002731	China	*Niphadomimus maia*	KJ427744	KY110324	KY110389
CNCCOLVG00002955	Russia	*Lobosoma rausense*	KJ427738	KY110316	KY110378
CNCCOLVG00003060	Tanzania	*Lupangus asterius*	KY034280	KY250485	KY250480
CNCCOLVG00004118	China	*Microplinthus*	**MG648755**	**MG648829**	**MG648741**
CNCCOLVG00004353	Vietnam	Molytinae	**MG648754**	**MG648828**	**MG648740**
CNCCOLVG00004355	Vietnam	*Otibazo polyphemus*	KJ841732	KY110328	KY110393
CNCCOLVG00004537	China	*Morimotodes ismene*	KJ871649	KY110338	KY110403
CNCCOLVG00004845	Tanzania	*Paocryptorrhinus hustachei*	KJ841728	KY110333	KY110398
CNCCOLVG00004846	Tanzania	*Thrombosternus cucullatus*	KJ445714	KY110335	KY110400
CNCCOLVG00004991	Tanzania	*Niphadonothus gentilis*	KX360489	KY110336	KY110401
CNCCOLVG00005001	Tanzania	*Aparopionella*	KX360455	KY110318	KY110381
CNCCOLVG00005480	Tanzania	Molytinae	**MG648758**	**MG648832**	**MG648744**
CNCCOLVG00005848	Poland	*Adexius scrobipennis*	KJ445686	KY110305	KY110367
CNCCOLVG00005976	Malaysia	Molytinae	**MG648759**	**MG648833**	**MG648745**
CNCCOLVG00006485	Georgia	*Plinthus amplicollis*	KY110617	KY110331	KY110396
CNCCOLVG00006552	Georgia	*Aparopion costatum*	KJ445700	none	KY110387
CNCCOLVG00006608	Georgia	*Leiosoma reitteri*	KJ445698	KY110322	KY110386
CNCCOLVG00006683	Taiwan	*Euthycus*	KJ445702	KY110325	KY110390
CNCCOLVG00006858	Taiwan	*Darumazo distinctus*	KY110611	KY110317	KY110380
CNCCOLVG00007166	Tanzania	*Typoderus antennarius*	KY250487	KY250484	KY250479
CNCCOLVG00007530	Russia	*Cryptorhynchus lapathi*	KY110605	KY110303	KY110365
CNCCOLVG00007531	Russia	*Niphades verrucosus*	KY110610	KY110314	KY110376
CNCCOLVG00008046	Tanzania	*Niphades*	**MG648748**	**MG648821**	**MG648734**
CNCCOLVG00008147	Ethiopia	Molytinae	**MG648753**	**MG648827**	**MG648739**
CNCCOLVG00008202	Ethiopia	Molytinae	**MG648756**	**MG648830**	**MG648742**
CNCCOLVG00008302	Ethiopia	Molytinae	**MG648750**	**MG648824**	**MG669100**
CNCCOLVG00008317	Cameroon	*Niphades*	**MG648749**	**MG648822**	**MG648735**
CNCCOLVG00008474	Poland	*Lepyrus palustris*	KX360483	KY110332	KY110397
CNCCOLVG00008480	Poland	*Leiosoma deflexum*	KY110614	KY110326	KY110391
CNCCOLVG00008484	Poland	*Trachodes hispidus*	KX360436	KY110307	KY110369
CNCCOLVG00008721	Ethiopia	*Oreoscotus*	**MG648760**	**MG648834**	**MG648746**
CNCCOLVG00008878	China	*Falsanchonus emeishanicus*	**MG648757**	**MG648831**	**MG648743**
CNCCOLVG00008915	Vietnam	*Peribleptus*	KY110615	KY110329	KY110394
CNCCOLVG00008936	Russia	*Acicnemis albofasciata*	KY110609	KY110312	KY110374

Yunnan, Cang Shan at Dali, N25°41′07″ E100°06′58″, 02.vii.2011, 2714m, sift33, V.Grebennikov", "CNCCOL VG00002676".

Distribution. This species is known only from the type locality.

Etymology. The species epithet derives from the name of the type locality.

Discussion

The recovered topology (Fig. 3) has three most notable features. Firstly, the unresolved nature of the recovered Molytinae tree is not unexpected, since the current matrix contains the same DNA fragments and 29 (among 44) terminals, as those analysed in Grebennikov (2017), where a comparably unresolved tree had been recovered. The only notable difference is that the genera *Morimotodes* and *Leiosoma* form a strongly supported clade (as hypothesized in Grebennikov 2014b), while its non-monophyly in Grebennikov (2017) can be likely attributed to inadequate alignment.

Secondly, the obtained topology (Fig. 3) tends to reject the hypothesis that the prosternal canal might serve as a diagnostically useful synapomorphy. The prosternal canal has either evolved independently more than once, or reversed once or more, or both. The tribe Aminyopini, monophyly of which has never been explicitly doubted (mainly due to neglect, rather than to a conscious consent) collapsed into two geographically coherent and strongly supported clades: the Asian and the African ones. These results are novel and suggest that the notable habitual similarity between Asian and African species all attributed to the same nominal genus *Niphades* (Fig. 3) is perhaps a convergence.

Thirdly, the sister-group of *Aater cangshanensis* **gen. et sp. nov.** cannot be currently satisfactorily asserted, because the former and the next more inclusive clade have low bootstrap values and lack corroborating support from other data sources. The taxonomic interpretation of the resulting ML tree does not link the new genus with any of the three dozen poorly defined molytine tribes (Alonso-Zarazaga & Lyal 1999; Lyal 2014). Homology of the notably long and straight rostrum (Fig. 3) reminiscent of Australian elephant weevil (*Orthorhinus cylindrirostris* (Fabricius, 1775) and other Orthorhinina, Kuschel 2008; Anderson et al. 2018) cannot be currently tested due to unavailability of the latter; separate procoxae and non-overlapping distribution of Orthorhinina weaken this hypothesis. Considering all these uncertainties, the herein described taxon is considered as Molytinae *incertae sedis*.

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