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Flightless *Disphaerona* rediscovered in China: mtDNA phylogeography of the Yunnan clade and the sobering state of fungus weevil phylogenetics (Coleoptera: Anthribidae)

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Abstract
This paper reports discovery of the genus *Disphaerona* Jordan, 1902 in two widely separated regions in China: in three isolated highlands in Yunnan (the Cang Shan Range, Mt. Jizu and Mt. Haba) and in the Dabie Mountains of Hubei, at the border with Anhui. Till present the genus was known from China only from four specimens of *D. chinensis* (including its holotype) described from Sichuan in 1995. Sixteen specimens from each of the three newly detected localities in Yunnan were DNA barcoded and the data were made publicly available at dx.doi.org/10.5883/DS-DISPHAE. Temporal phylogenetic analysis revealed a topology suggesting monophyly and recent (0.2–0.4 Ma) origin of the populations on both Mt. Jizu and Mt. Haba. The population on the Cang Shan Range harbours representatives of both clades forming the ingroup, mtDNA of which diverged some 7.9 Ma. The habitus of the holotype of the only nominative Chinese *Disphaerona* species, *D. chinensis*, is illustrated, together with habitus and male and female genitalia of specimens newly discovered in both Yunnan and Hubei. All specimens of *Disphaerona* from Yunnan are seemingly conspecific and are taxonomically assigned to *D. chinensis*. Two similar males and one sympatric but dissimilar, smaller female from the Dabie Mountains do not have associated DNA barcode data. It remains unknown whether the three Dabie Mountains specimens are conspecific or even congeneric; pending this uncertainty they are tentatively treated as *Disphaerona* without a Linnaean name. *Disphaerona* population in the Dabie Mountains, if indeed a member of this hypothesised clade, forms the easternmost record of the genus. Monophyly and sister group of *Disphaerona* are briefly discussed and both are shown as unknown and unverifiable. A brief overview of the state of phylogenetic knowledge of Anthribidae is given, which is practically non-existing and with neither the family, nor any of its tribes and the vast majority of genera tested as monophyletic.

Key words: *Disphaerona*, CO1, DNA barcode, phylogeography, weevils.

Introduction

Reporting discoveries among neglected taxa is an awkward job. On one hand the discoverer is eager to present the recently detected and evolutionary intriguing organisms with newly generated morphological, geographical, biological and/or DNA data. These finds, on the other hand, have to be placed, or rather forced, in the framework of the often acutely inadequate pre-existing knowledge. This framework often entirely lacks any phylogenetic basis and represents merely a taxonomic arrangement, as it was given in the last catalogue of names. This taxonomic arrangement is, in turn, historically inherited and is based on arbitrary concepts of the more inclusive taxa (genera, tribes, subfamilies) introduced in the pre-Hennigian time and of doubtful monophyly. Various later authors subsequently assigned their new species to these more inclusive taxa, often based on varying and inadequate evidence. Many, if not all, of the species-group names are often based on the type series only, and even those are inadequately documented (not illustrated, not dissected, no DNA sequence, vague geo-data). Thus, unless the modern author undertakes a highly-demanding cleanup of the backlog of accumulated names with little information linked to them, his reports of the recent discoveries must be somehow incorporated into the pre-existing taxonomic framework.

The present paper is an example of such a report on understudied organisms. It was triggered by the first discovery made in 2008 when sifting forest litter in China. Series of fungus weevils (Anthribidae) with characteristically rounded elytral shoulders were discovered in two mountainous localities of Yunnan and Hubei some 1,600 km apart (Fig. 1). Morphologically, these beetles were attributable to the subfamily Anthribinae (sensu Alonso-Zarazaga & Lyal 1999), although the latter is likely non-monophyletic (see Discussion). Further identification attempts came to a standstill, since Anthribidae fauna of China is inadequately known. Eventually the specimens were found best matching definition of *Disphaerona* Jordan, 1902 by using a key to the Oriental genera (Morimoto 1972), further assisted by the adult habitus illustrations there and elsewhere (Rheinheimer 2004; Frieser 2008).

This genus consists of 25 nominal species, all but one restricted to Sri Lanka and India (Rheinheimer 2004; Frieser 2008). The remaining species, *D. chinensis* Frieser, has been relatively recently described from Sichuan in China (Frieser 1995). Its type locality is less than 200 km away from where some of the herein reported specimens were recently collected. No alternative generic assignment was readily evident and, moreover, no convincing evidence existed to hypothesise an unnamed genus. The genus *Disphaerona*, poorly known as it is, therefore became the least inclusive pre-existing Linnaean entity to taxonomically incorporate the new finds.

The goals of this paper are: (1.) to report the discovery of specimens in Southwest China attributable to the fungus weevil genus *Disphaerona*; (2.) to perform a mtDNA phylogeographical analysis of specimens from Yunnan, for which mtDNA data are available; (3.) to attribute them to a Linnaean species; (4.) to record three seemingly congeneric specimens from Hubei forming the easternmost distributional record for the genus; (5.) to document the phylogenetic and nomenclatorial uncertainties encountered during this study, and (6.) to highlight the remarkable degree of phylogenetic neglect characteristic to the beetle family Anthribidae as a whole.

Material and methods

Museum abbreviations, followed by the name of the curator:

CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (P. Bouchard);
ZSM	Zoologische Staatssammlung Munich, Germany (A.D. Balke).

Specimens sampling and dissecting

This work is based on examination of 31 adult specimens of *Disphaerona* (CNC) newly sampled by the author in China:

Disphaerona chinensis **Frieser, 1995** (Figs 2–5): 28 exx in total from three localities in Yunnan (Fig. 1): Cang Shan Range (16 exx collected in May 2008 and in May and June 2010 at about N25°40'13.2» E100°07'54.8», 2728 m), Mt. Juzu (10 exx collected in June 2008 and June and July 2011 at about N25°59'02» E100°20'20», 2689 m), and Mt. Haba (2 exx collected on 29.vi.2012 at about N27°22'05» E100°06'25», 3272 m).

Disphaerona **sp.** (Figs 6, 7): 3 exx in total, two males (specimens 0314 and 0315, Fig. 6) and one female (specimen 0313, Fig. 7): Hubei, Dabie Mountains (collected on 11–21.vi.2008 at about N31°06.013' E115°47.300', 640 m).

All these specimens were detected by sifting forest leaf litter with a standard hand-held sifter (except for sample CN01 taken with a novel suspended a mega-sifter, Fig. 8 and Grebennikov 2016), with subsequent specimen extraction using Winkler funnels. To dissect genitalia, specimens were broken at the junction between pro- and mesothorax and placed overnight in warm solution of Proteinase K in buffer ATL, as described in "DNeasy Blood & Tissue Handbook". This procedure softened specimens and by means of the lysis process cleared most of muscle and other soft tissue, thus facilitating genitalia extraction. Disarticulated body parts were glued together, while pieces of the abdomen (including genitalia) were embedded in Canada Balsam on a card pinned under respective specimen.

DNA barcoding

Sixteen specimens of *Disphaerona* from Yunnan from all three localities were DNA barcoded (plus a specimen of European *Anthribus nebulosus* Forster, 1770 but not the *Disphaerona* specimens from the Dabie Mountains because they did not respond to attempted DNA barcoding). These 17 specimens received unique identifier label in the format CNCCOLVG0000XXXX; the latter four X correspond to a unique four digit number shown on the topology linked to a GenBank accession number (Fig. 8). Sequences of all 17 specimens were of full DNA barcode length (658 bp) and without ambiguous reads. All details regarding DNA sequencing, primers, PCR protocols, original electropherograms, habitus images and exact locality data of 17 genetically barcoded specimens can be seen online in the Barcode of Life Database (=BOLD) public dataset "Disphaerona", doi: dx.doi.org/10.5883/DS-DISPHAE.

DNA analyses

Two DNA analyses were run, each using 16 mtDNA barcoding sequences of *Disphaerona* from Yunnan, plus that of *A. nebulosus* as an outgroup. The first analysis (**A1**) was designed to date evolutionary events of Yunnan *Disphaerona* using BEAST v1.8.0 software (Drummond et al. 2012) utilizing the Bayesian inference approach. Analysis parameters were as follows: no *a priori* grouping or rooting, all options at their default, HKY+G nucleotide substitution model (the nearest match for the T92+G model detected in a separate model-searching analysis in MEGA 6 as having the best fit, Tamura et al. 2013), strict linear molecular clock and nucleotide substitution rate of 0.018 substitutions per site per million years per lineage (Papadopoulou et al. 2010). The latter rate has been detected for Tenebrionidae beetles and was, therefore, chosen for *Disphaerona* as that of the nearest known relative. Tracer 1.6 (Rambaut et al. 2016) was used to graphically determine stationarity and to check convergence of runs. TreeAnnotator v1.8.0 was used to create consensus topology (Fig. 8) and the "burn in" option was not implemented in a belief that arbitrary discarding "suboptimal" trees introduces more uncertainty, than otherwise; instead chain was run longer (10,000,000) to accumulate adequate statistics re-

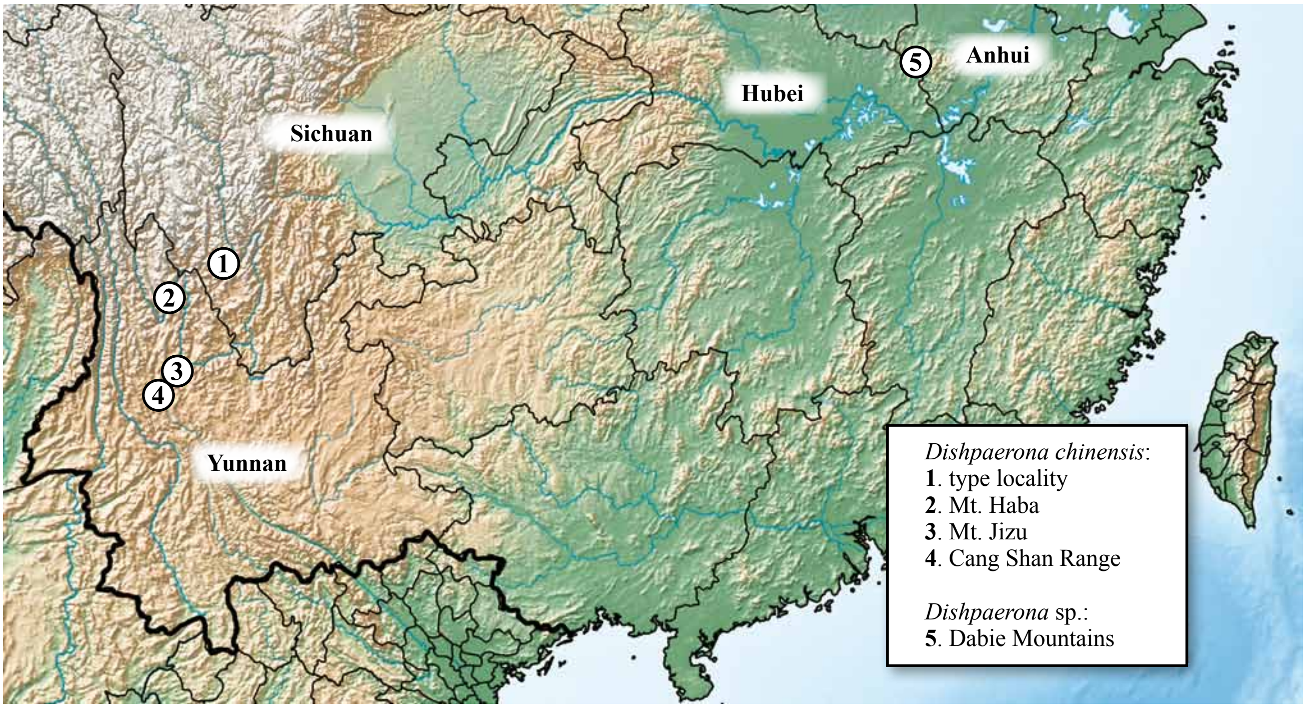

Fig. 1 – Distribution of *Disphaerona* fungus weevils in China. The underlying map was generated using the online SimpleMappr tool (Shorthouse 2010).

sistant to the presence of "suboptimal" topologies. The second analysis (**A2**) was aimed to test constancy and robustness of the **A1** topology by bootstrapping the Maximum Likelihood tree with 500 repetitions, as implemented in MEGA 6 and using the HKY+G nucleotide substitution model. Consensus topologies from each analysis were visualized in FigTree v1.4 (Rambaut 2016) and the **A1** topology (Fig. 8) was exported to imaging software for plate preparation.

Phylogenetic and taxonomic uncertainties, data limitations and practical solutions

Necessity to keep this project within accomplishable size imposed certain limitations. The study, therefore, is limited to reporting new finds of peculiar beetles found in China and most likely attributable to the genus *Disphaerona* (an entity of questionably phylogenetic identity, i.e. not demonstratively monophyletic), and to providing evolutionary interpretation of this find. Testing monophyly of the genus would require significant additional efforts and, therefore, was not attempted. Furthermore, no morphological study of *Disphaerona* specimens from outside of China was undertaken, neither specimens of the genera potentially closely related to *Disphaerona* (see Discussion) were studied. None among the four type series specimens of the only named Chinese *Disphaerona* species, *D. chinensis*, were studied, while the dorsal and lateral views of the holotype (and the original labels, Fig. 5) were taken by the Curator of ZSM. Male and female genitalia were dissected from four specimens, two from the Yunnan clade (Figs 2, 3) and two found in the Dabie Mountains (Figs 6, 7); these four specimens are thought to be adequately representative for all current practical purposes of identification.

To complete this paper, a large number of unevenly-distributed uncertainties had to be dealt with. For example, DNA barcodes remain unknown for all but one *Disphaerona* species, and this excluding its holotype and other topotypical specimens from Sichuan. The shape of male and female genitalia, on the other hand, is unknown for all but the Chinese congeners, and again, expect for the type series of the only nominal species. While it is likely that all *Disphaerona* specimens from Southwest China can be attributed to the same Linnaean species (see Discussion), all three specimens from the Dabie Mountains lack DNA barcodes and are from two markedly distinct morphological groups (two large males as in Fig. 6 versus one small female in Fig. 7). Although the latter data could be random, it could also suggest existence of two sympatric species or/and sexual dimorphism, phenomena that are not infrequent in Anthribidae (see, for example, size difference in *Systaltocerus platyrhynus* Labram & Imhoff, 1840; Mattos et al. 2014). Moreover, no adequate data are available to test relations of the Hubei specimens to *D. chinensis*, while the geographical gap of at least 1,400 km strongly suggest separate evolutionary histories likely worthy of separate Linnaean names. Available data are, however, inadequate to decide on the formal taxonomic status of three speci-

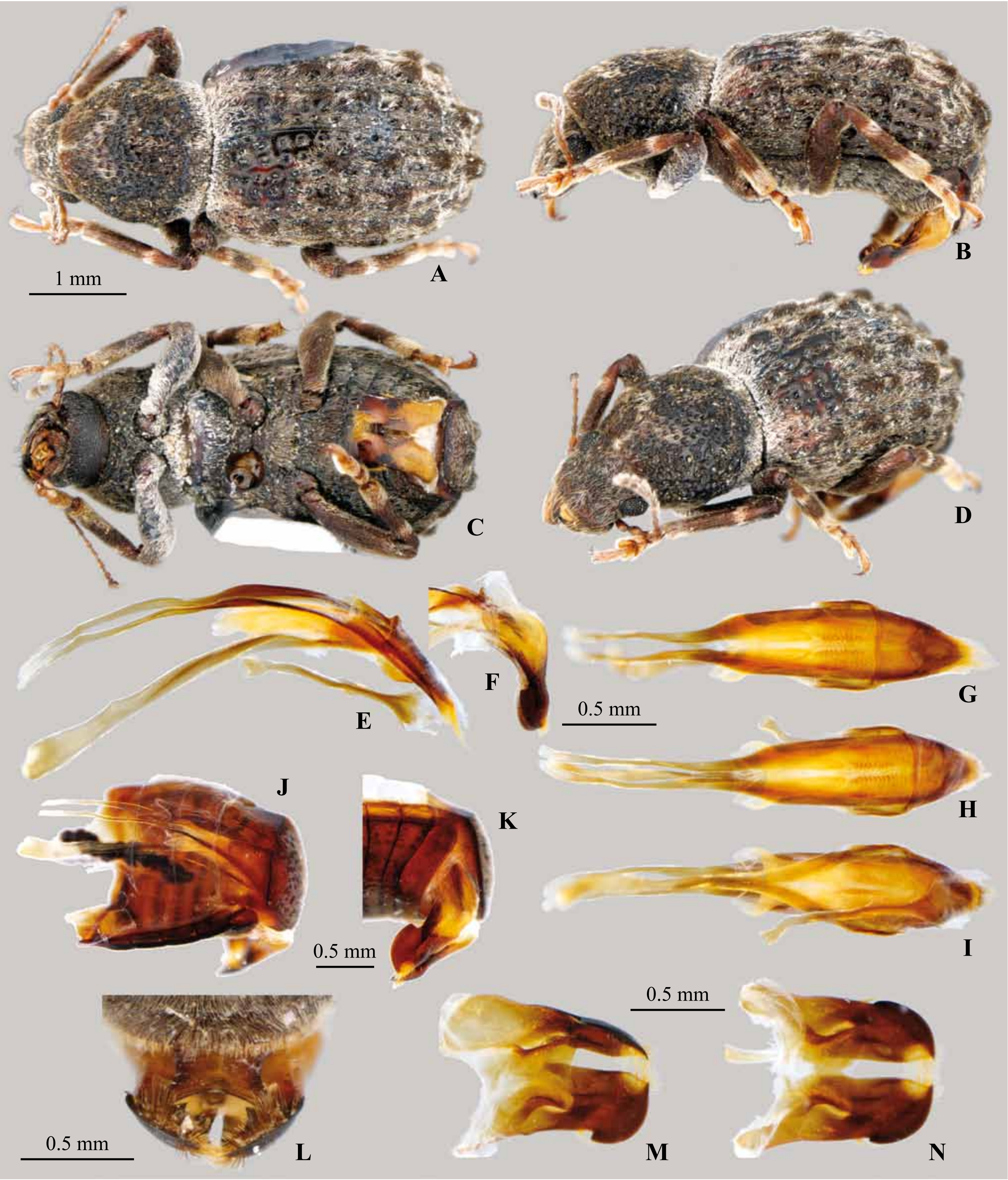

Fig. 2 – *Disphaerona chinensis*, specimen 4562, male, Mt. Haba. **A-D**, habitus (note everted segment 8 on lateral and ventral views); **E-I**, aedeagus, tegmen, sternite 9 (**F**: with segment 8), lateral (**E**, **F**), dorsal (**G**, **H**) and ventral (**I**); **J-K**, abdomen showing internal arrangement of gut and genitalia with everted segment 8, left dorso-lateral (**J**), right ventro-lateral (**K**) and posterio-ventral; **M-N**: segment 8, left ventro-lateral (**M**) and ventral (**N**).

mens from Hubei and, therefore, pending further research, they remain unassigned to a nominal Linnaean species (although extensively illustrated herein).

Disphaerona Jordan, 1902

Jordan, 1902: 77 (species included: *punctata*). Type species: *Disphaerona punctata* Jordan, 1902, by original designation.

Diagnosis

Characteristic habitus of a medium-sized fungus weevil with variously effaced elytral shoulders is the most practical external morphological character to recognize adults of *Disphaerona* among all Anthribidae in China. Biologically, all *Disphaerona* species are thought to dwell in the forest leaf litter, a habitat which is uncommon (although not unique) for Anthribidae and, therefore, also diagnostic. Since the genus has never been revised, its only published morphological diagnosis is the original generic description

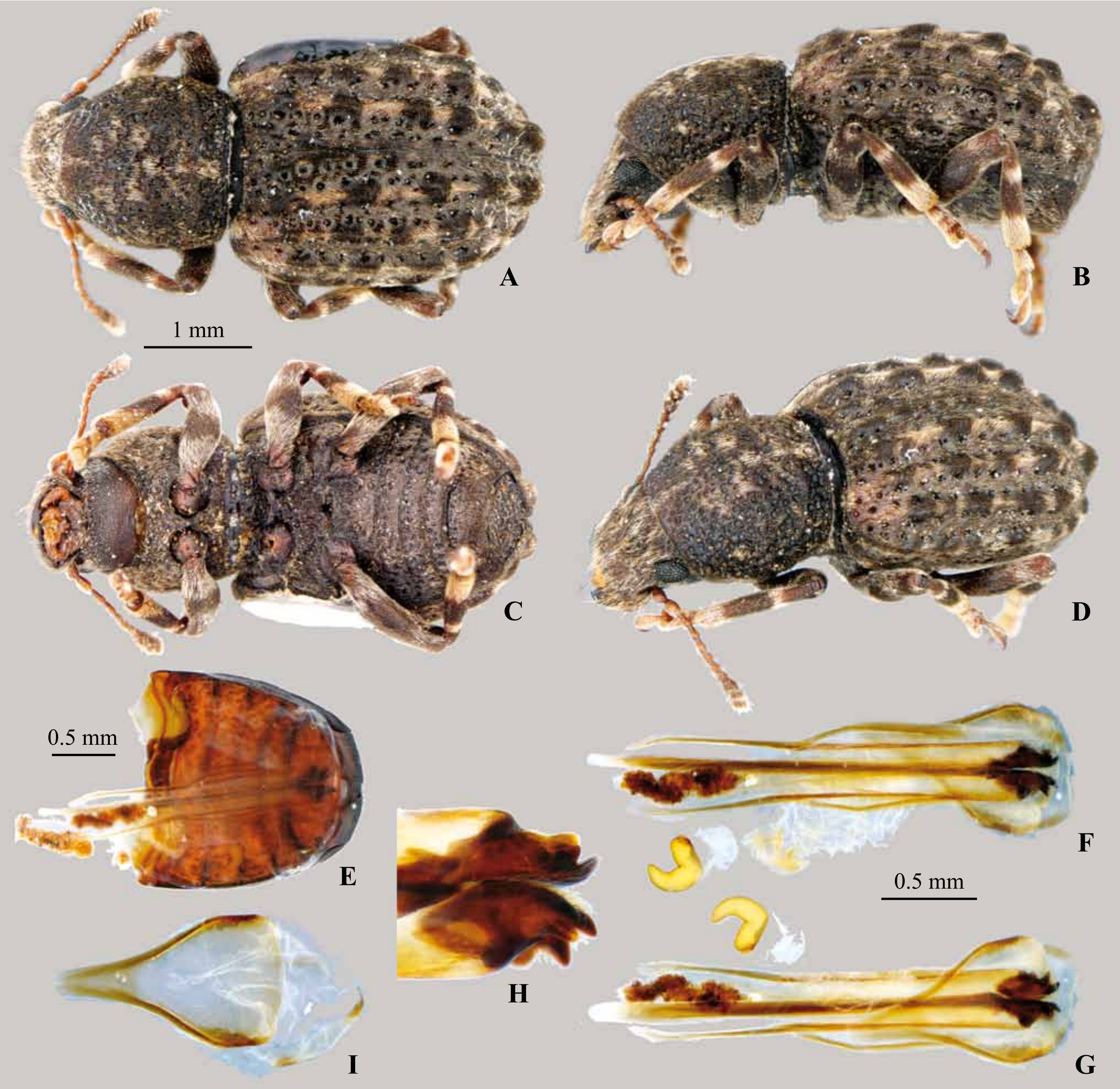

Fig. 3 – *Disphaerona chinensis*, specimen 4561, female, Mt. Haba. **A-D**, habitus; **E**: abdomen showing internal arrangement of gut and genitalia, dorsal; **F**, **G**, genitalia and segment 8, dorsal (**F**) and ventral (**G**); **H**, hemisternites 9, each formed by a larger toothed basal part ("coxite") and a small digit-shaped apical part ("stylus"); **I**, segment 8, with large sternite 8 connected by membrane to two small sclerotized plates likely homologous to tergite 8.

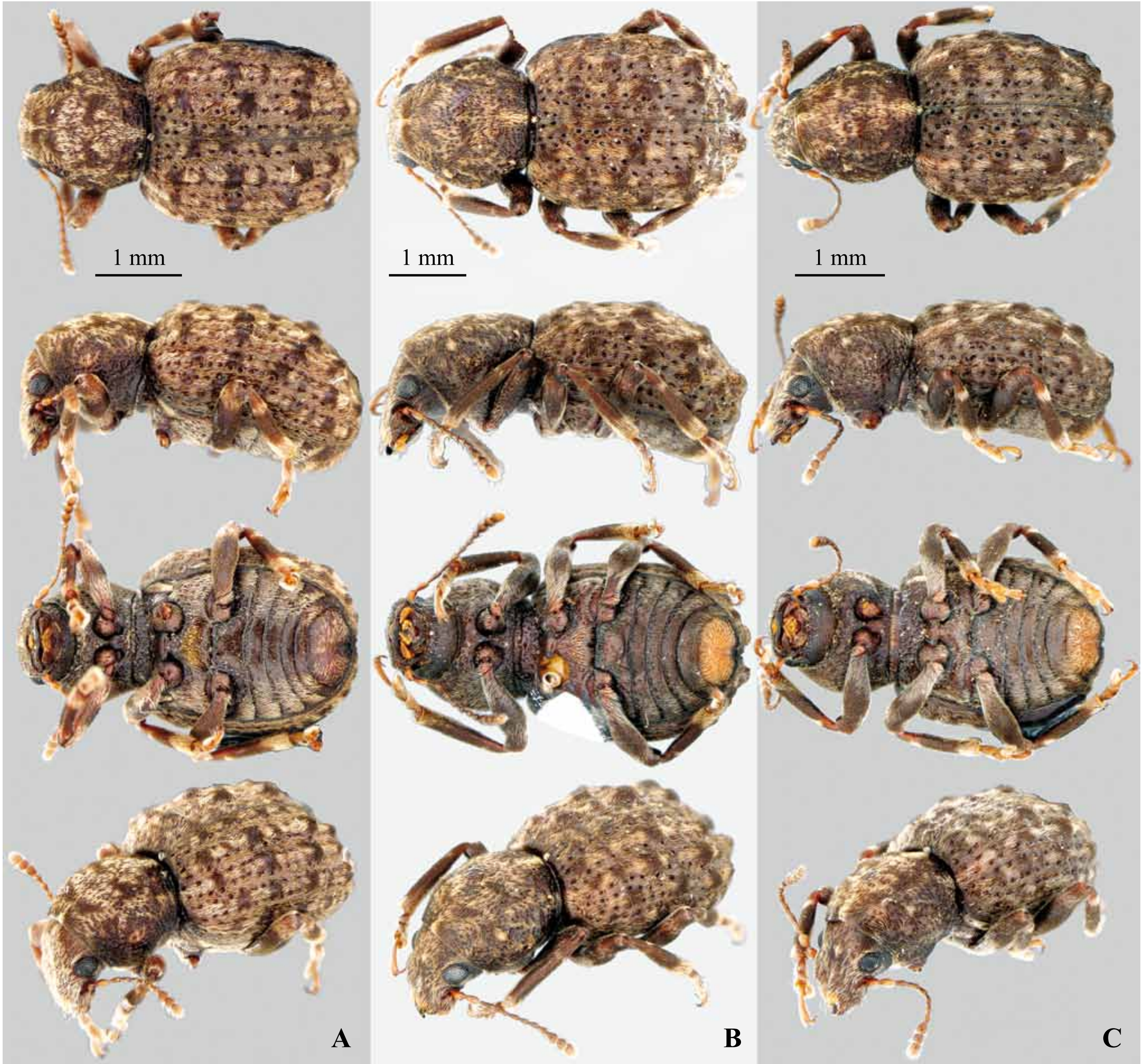

Fig. 4 – *Disphaerona chinensis*, **A**, specimen 0746, Cang Shan Range; **B**, specimen 2679, Cang Shan Range; **C**, specimen 2579, Mt. Jizu.

Fig. 5 – *Disphaerona chinensis*, holotype (courtesy Ditta Amran Balke).

in eight lines made based on the female holotype of the type species (Jordan 1902) from "Anuradhapura" (likely a major city with the same name in Sri Lanka). The illustrated keys to Oriental Anthribidae (Morimoto 1972), or to those from the Indian subcontinent (Frieser 2008), are the best generic diagnostic tools currently available to distinguish *Disphaerona* adults from all other fungus weevils.

Results

Temporal analysis in BEAST (analysis **A1**, Fig. 8) placed the root of the obtained topology between *A. nebulosus* and the rest. The basal-most split within the *Disphaerona* clade separating the specimen 0746 is dated at about 7.9 Ma. The second basal-most split between the specimens

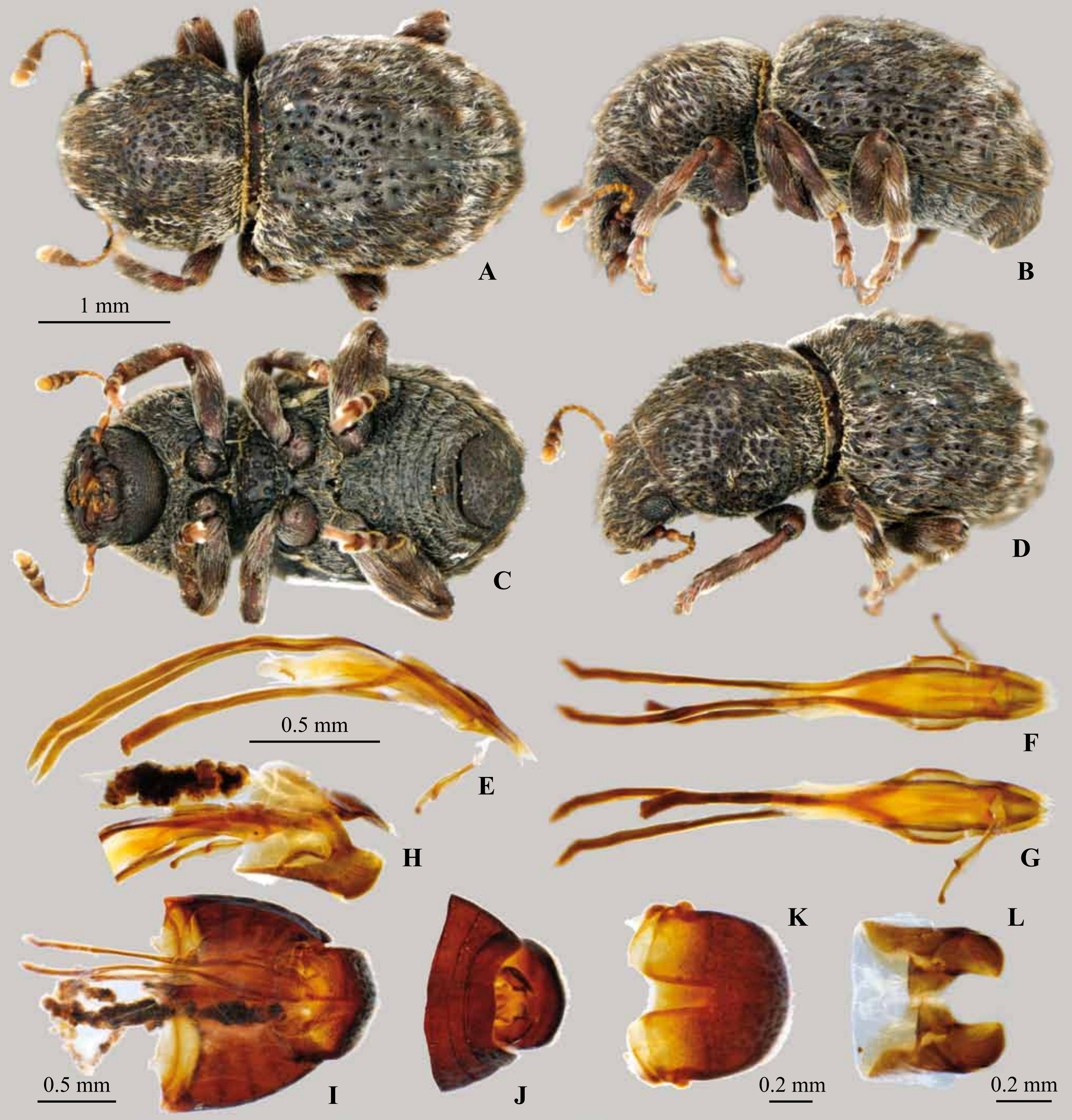

Fig. 6 – *Disphaerona* sp., specimen 0315, male, Dabie Mountains. **A-D**, habitus; E-G, aedeagus, tegmen and sternite 9, lateral (**E**), dorsal (**F**) and ventral (**G**); **H**: aedeagal apex with segment 8, left dorso-lateral; **I**, **J**, abdomen showing internal arrangement of gut and genitalia with opened tergite 7 (= pygidium) and partly everted segment 8, dorsal (**I**) and ventral (**J**); **K**, tergite 7 (= pygidium), dorsal; **L**: segment 8, ventral.

from Mt. Haba and the rest of the clade (consisting of the remaining specimens from the Cang Shan Range and those from the nearby Mt. Jizu) is dated at about 4.7 Ma. All *Disphaerona* specimens from Mt. Jizu and all those from the Cang Shan Range (except for specimen 0746) are reciprocally monophyletic, and their separation is dated at about 1.4 Ma. Unlike both Mt. Haba and Mt. Jizu each supporting a monophyletic *Disphaerona* lineage, the Cang Shan Range is a home to two distant *Disphaerona* clades, one of them formed by the specimen 0746.

The best ML tree (analysis **A2**, not illustrated) had the highest log likelihood of –2122.6807 and topology identical to that obtained in the **A1** analysis, except that the specimen 2679 from Cang Shan Range formed a sister group in a weakly (20%) supported clade with all specimens from Mt. Jizu and all other but one (0746) specimens from Cang Shan Range. Except for this weakly supported clade, all recovered clades had high (>89%) bootstrap support, with values superimposed on identical clades recovered in **A1** (Fig. 8).

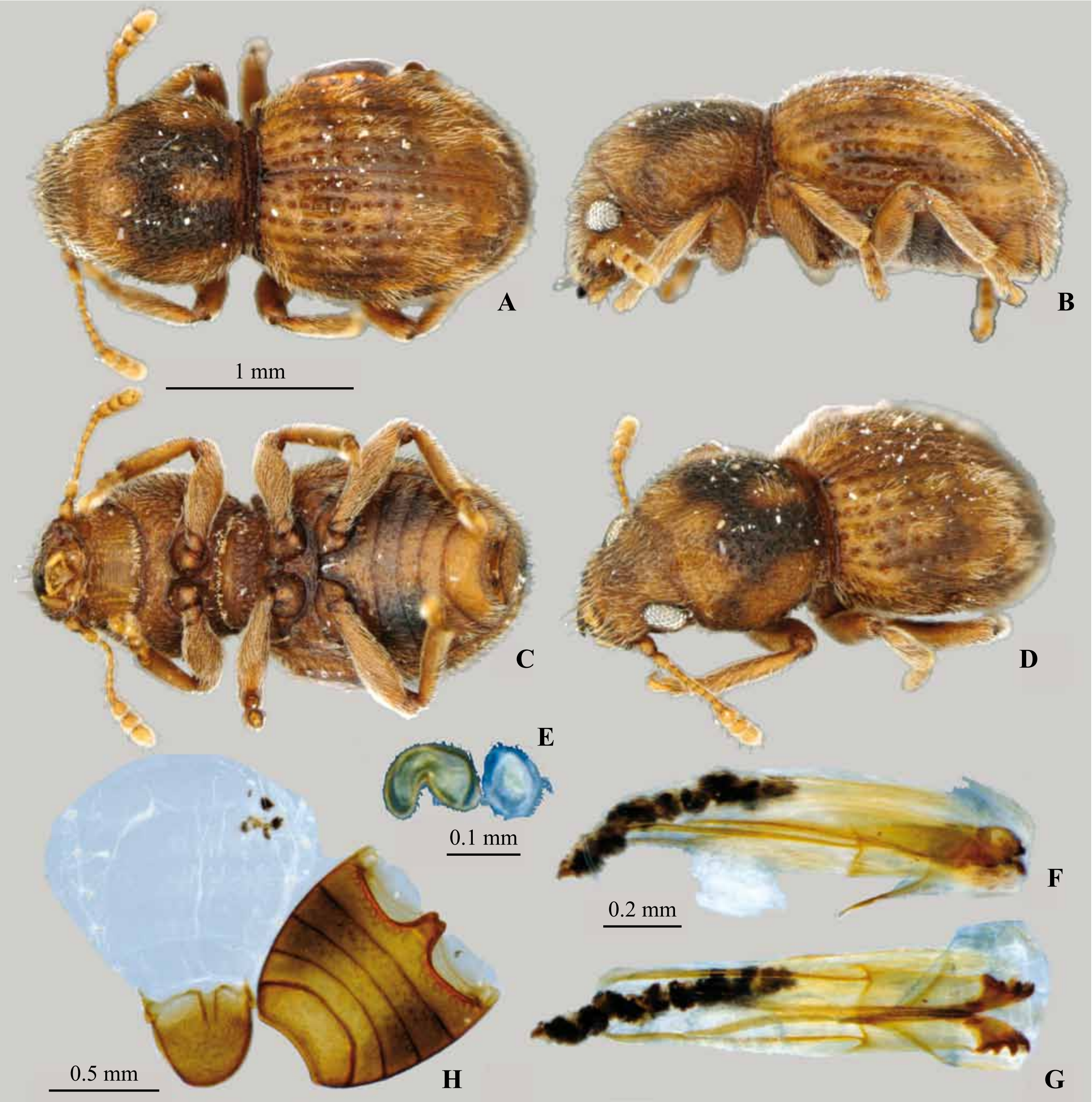

Fig. 7 – *Disphaerona* sp., specimen 0313, female, Dabie Mountains. **A-D**, habitus; **E**, spermatheca and gland; **F**, **G**, genitalia and segment 8, lateral (**F**) and ventral (**G**); **H**, tergites (up to tergite 7, =”pygidium”) and sternites 3-7.

Discussion

All Disphaerona *from Southwest China are assignable to* D. chinensis

Before discussing *Disphaerona* from China, identity of *D. chinensis*, the only nominal species known from this country, needs to be established. The species was described in German by Frieser (1995, no illustrations, no genitalia characters) based on two males and two females collected in 1991 in Sichuan (Fig. 1). The holotype (Fig. 5) is in ZSM. The type locality is relatively near to three localities in Yunnan (Fig. 1), where herein reported populations of *Disphaerona* have been discovered. The description of *D. chinensis* and the holotype images (Fig. 5) do not offer reliable characters to distinguish this nominal species from the herein reported Yunnan specimens. The latter are remarkably similar externally and have DNA barcodes sufficiently similar to consider them conspecific. Available evidence are, therefore, consistent with the simplest taxonomic solution, that is to treat all known *Disphaerona* from Southwest China as the same Linnaean species, for which the name *D. chinensis* is available. Such conservative approach was consistently implemented for allopatric (*Trichalophus* LeConte, 1876 by Grebennikov 2015, *Notaris* Germar, 1817 by Grebennikov & Kolov 2016) and sometimes sympatric (*Morimotodes* Grebennikov, 2014 by Grebennikov 2014) populations of flightless weevils in Southwest China and in situations when available evidence were inadequate and/or conflicting to offer a more fragmented taxonomic arrangement.

Monophyly and relationships of Disphaerona

The genus *Disphaerona* has never been a subject of a phylogenetic analysis and, therefore, its monophyly is an untested hypothesis implied by the continuous taxonomical recognition. Judging by the habitus similarity and geographic proximity (Rheinheimer 2004), at least two other genera might be closely related to, or perhaps nested within, *Disphaerona*: *Disphaeronella* Frieser, 1991 with two species from Malaysia and *Botriessa* Jordan, 1928 with two species from Myanmar and Nepal, respectively. If indeed monophyletic, the current assignment of *Disphaerona* to the tribe Corrhecerini (Alonso-Zarazaga & Lyal 1999) containing 38 predominantly Old World genera might be considered as the best available and yet never tested hypothesis, since neither the tribe, nor any of its genera have ever been a subject of a phylogenetic analysis.

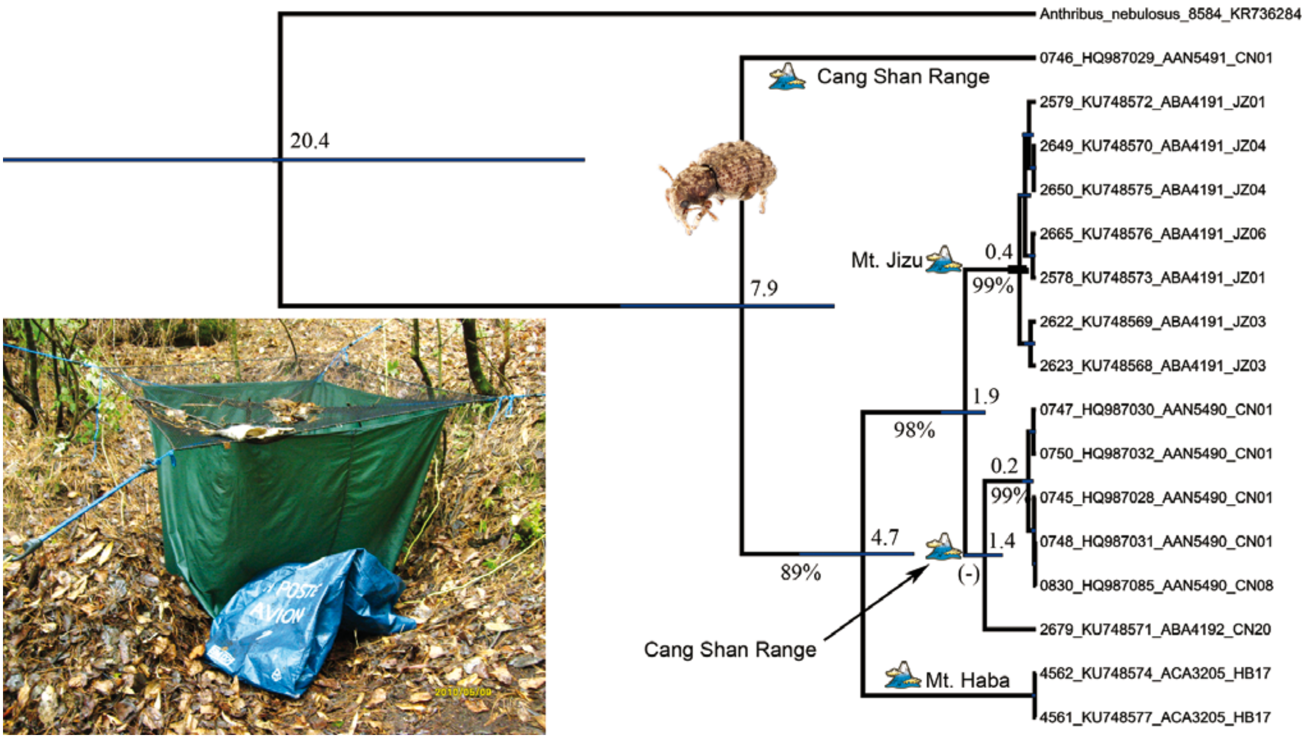

Fig. 8 – Ultrametric time tree obtained from analysis **A1** using BEAST software to date evolutionary events of the *Disphaerona chinensis* from Yunnan. Numbers at nodes are million years before present. Blue node bars represent 95% confidence interval of the age estimate. Bootstrap statistical support from analysis **A2** is indicated in per cents for clades consistently recovered in both analyses. Terminal numbers are specimen number (four first digits), followed by GenBank accession, followed by BIN (= Barcode Index Number, Ratnasingham & Hebert 2013), followed by sample number. Habitat insert shows a newly developed mega-sifter (Grebennikov 2016) in operation when taking sample CN01 on the Cang Shan Range on May 9, 2010; numerous *Disphaerona* specimens were extracted from the pile of leaf litter visible on the foreground.

Flightlessness of Disphaerona

No biological data are available for the genus, other than the collecting circumstances of the adults and their apparent flightlessness expressed in the loss of hind wings. Holloway (1982) in her detailed treatment of the New Zealand Anthribidae fauna gave a brief overview of the phenomenon of flightlessness in the family. She noted that 24 of the 27 species of St. Helena are apterous (Basilewsky 1972), while apparently all of the Japanese species are fully winged (Morimoto 1981); both territories are exceptionally species-rich in relation to their size. Like *Disphaerona*, adults of flightless Anthribidae are predominantly linked to edaphic habitat. Examples are numerous and include mainly unnamed Choraginae such as *Styphlocharagus* Frieser, 1978 and its allies sifted from the leaf litter in most of wet Afrotropical forests. Exceptions, however, are infrequent, like the genus *Dasyanthribus* Holloway, 1982 with two minute (1.5–2.1mm) flightless canopy-dwelling species from New Zealand and New Caledonia, respectively (Kuschel 1998). These diversified and seemingly repeatedly acquired biological strategies expressed in the loss of flight offer fertile field for further research (see, for example, Grebennikov & Kolov 2016).

Phylogeography of Disphaerona *in Yunnan*

Limited as it is, this study is the first attempt to use fungus weevils for phylogeographic (Avise 2000) purposes. Three neighbouring (Fig. 1) and yet discrete Yunnan montanous forested localities supporting *Disphaerona* populations are separated by vast areas of lowlands, devoid of forests and seemingly unsuitable for flightless *Disphaerona*. While *Disphaerona* populations of Mt. Jizu and Mt. Haba are both monophyletic and each suggests a single colonization event younger than 0.5 Ma, specimens from the Cang Shan Range form either two (**A1**) or three (**A2**) clades, one of them (specimen 0746) consistently recovered as the sister to the rest of the ingroup. Remarkably, this genetically odd and morphologically somewhat different (Fig. 4A) specimen was discovered in the same sifting sample CN01 together with some other herein analysed congeners. Available data are insufficient to offer explanation of this sympatric coexistence of specimens so markedly different in their DNA barcode sequences. A number of scenarios can be suggested, ranging from existence of a separate species to any of various causes resulting in mtDNA species non-monophyly (Funk & Omland 2003).

Anthribidae, a phylogenetically neglected family

The cosmopolitan family Anthribidae contains 3,861 species, 378 genera, 31 non-nominative tribes and three subfamilies (Mermudes & Leschen 2014). Regional faunas of Anthribidae are relatively well documented for the Nearctic region (Valentine 1998), the Palaearctic region (Trýzna & Valentine 2011), Russian Far East (Egorov in Egorov et al. 1996), Japan (Morimoto 1981), the Indian subcontinent (Frieser 2008), Madagascar (Frieser 2010), surprisingly species-rich Saint Helena (Basilewsky 1972), New Caledonia and Vanuatu (Kuschel 1998), Southern Polynesia (Zimmerman 1938), Australia (Zimmerman 1994) and New Zealand (Holloway 1982). Among these works those on Japan by Morimoto (the last forth part published in 1981) and on New Zealand by Holloway (1982) are, perhaps, the most detailed and best illustrated. Rheinheimer (2004) provides the World catalog of 3,779 Recent Anthribidae species with habitus illustrations of 288 of them. Anthribidae DNA barcode libraries are available for mainly Nearctic and Palaearctic species, with the pivotal work by Hendrich et al. (2015) introducing 56 barcodes for 14 species of the German fauna. On the other hand, phylogeny of Anthribidae is markedly neglected. For example, the monophyly of the family is highly unlikely, since Urodontinae consistently fail to form a clade with the rest of Anthribidae (McKenna et al. 2009, Lawrence et al. 2011). Perhaps even more consistently the subfamily Anthribinae is found paraphyletic with respect to Choraginae (Kuschel 1995, McKenna et al. 2009, Gunter et al. 2016). None among the tribes and less than five relatively small and either southern African (Oberprieler 1999; the cycad-associated genus *Apinotropis* Jordan, 1945) or Neotropical (by Mermudes and his co-authors, references in Mermudes & Leschen 2014) genera have ever been analysed with formal phylogenetic procedure employing exclusively adult morphological characters. The lack of phylogenetic attempts is even more surprising because adult exoskeletal characters seem to be diversified, relatively easy to observe and at least some of them, such as pronotal carinae (Holloway 1984) or male sexual patches (Holloway 1985), were documented in broad comparative studies. Summing up, Anthribidae might easily be the champions among the medium-sized beetle families in degree of their phylogenetic neglect (or, alternatively, in degree of unexplored research opportunities).

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