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Neglected *Trichalophus* (Coleoptera: Curculionidae): DNA barcode and phylogeography of high-altitude flightless weevils rediscovered in Southwest China

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Abstract. *Trichalophus* LeConte weevils are rediscovered in Southwest China (Yunnan and Sichuan) after last being collected in 1915. Populations are all found at high altitudes (3704–4158 m) and are attributed to three species: *T. caudiculatus* (Fairmaire, 1886) (= *compressicauda* Fairmaire, 1887, syn. n.), *T. scylla* sp. n. and *T. tibetanus* (Suvorov, 1915). Type specimens of all four species-group names are illustrated. A DNA barcode library of five *Trichalophus* species (29 sequences) is presented at doi: dx.doi.org/10.5883/DS-TRICHAL. All examined species of *Trichalophus* are flightless. Phylogenetic relationships of Southwest China *Trichalophus* based on Maximum Likelihood and Maximum Parsimony analyses suggest their monophyletic origin and monophyly of each species. Results of the temporal analysis are consistent with the basic Quaternary expansion-contraction model of altitudinal range change. The warm period following the Last Glacial Maximum (26,000–19,000 years before present) is linked to the present day high altitude *Trichalophus* refugium in Southwest China, but not for the lineage diversifications, which are much older (8.08–5.17 Mya). An illustrated overview of ten extant Alophini genera is provided.

Key words. New species, new synonym, Yunnan, Sichuan, CO1, Entiminae, Alophini, Father Delavay

INTRODUCTION

The exclusively Holarctic weevil genus *Trichalophus* LeConte, 1876 consists of 51 valid species (Yunakov 2013). Adults of *Trichalophus* are believed to be flightless and brachypterous (Anderson 1997; Fig. 1). Loss of flight ability is commonly observed in a number of unrelated edaphic, alpine, high latitude, subterranean, island, or litter-inhabiting insects. Examples from weevils include Macaronesian *Laparocerus* Schönherr, 1834 (Machado et al. 2008), Polynesian *Rhyncogonus* Sharp, 1885 (Machado 2007), predominantly Oriental *Trigonopterus* Fauvel, 1862 (Riedel 2011), Middle American *Theognete* Champion, 1902 (Anderson 2010), an assemblage of likely unrelated Old World genera historically placed in Molytini (Grebennikov 2014b) and the Western Palaearctic genera of former "Cryptorhynchinae (Lyal 2014) traditionally linked to *Acalles* Schoenherr, 1825 (Astrin & Stüben 2008). The reduced dispersal capacity predisposes such evolutionary lineages to become hostages of their habitats and, therefore, subject to more frequent bottleneck effects. These conditions favour allopatric speciation (Grant & Grant 2006; Ikeda et al. 2012; Vogler & Timmermans 2012) seemingly accompanied by an accelerated rate of DNA evolution (Bromham 2008), as compared to their flight-capable relatives (Mitterboeck et al. 2013). Such biological characteristics make flightless weevils a model group for phylogeographical studies on such dynamic terrains as oceanic islands (Tänzler et al. 2014; Toussaint et al. 2015) or mountaintops (Grebennikov 2014a), if it were not for their often highly inadequate taxonomy. The latter, if not updated, either lacks names for newly detected evolutionary lineages (= new species), or has too many names for the same clade (= synonyms), or a combination of both. In such situations the historical burden of Linnaean names impedes, rather than advances evolutionary studies (Riedel et al. 2013a, b).

The genus *Trichalophus* has a trans-Beringian distribution range, with species found on the Pacific sides of both Asia and North America, evoking the Bering land bridge hypothesis (Berman et al. 2011). All but one species are restricted to either Asia or North America; the exception being the Nearctic *T. hylobinus* (LeConte, 1876) recently reported from North Korea (Yunakov 2013). Trans-Beringian distributions are commonly observed in a number of weevil genera: *Alaocybites* Gilbert, 1956 (Grebennikov 2010), *Thalasselephas* Egorov & Korotyaev, 1977, *Emphyastes* Mannerheim, 1852, *Lepyrus* Germar, 1817, *Lobosoma* Zimmermann, 1964, or *Lepidophorus* Kirby, 1837 (Egorov et al. 1996; Bousquet et al. 2013). Indeed, all but one (Yunakov et al. 2012) Palaearctic records of *Trichalophus* pertain to Siberia, Mongolia, Central Asia and the northern part of the Pacific Asia including Japan, while the Nearctic species are predominantly found in Alaska, the western USA, and Canada west of Ontario (Anderson 2002; Bousquet et al. 2013). Yunakov (2013)

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listed 43 *Trichalophus* species and one non-nominal subspecies (*T. vittatoides striola* Reitter, 1913) for the Palaearctic region, while Anderson (2002) mentioned eight North American congeners. Since then the Nearctic diversity of *Trichalophus* has lost two species names due to synonymy (*T. seriatus* Mannerheim, 1843 and *T. brunneus* Van Dyke, 1927) and has gained two others through the recently synonymized genus *Acmaegenius* LeConte, 1876 (Bright & Bouchard 2008). As a result, eight Nearctic species are currently recognized (*T. arcuatus* Fall, 1907, *T. hylobinus* LeConte, 1876, *T. planirostris* LeConte, 1876, *T. seminudus* Van Dyke, 1938, *T. granicollis* Van Dyke, 1927, *T. didymus* LeConte, 1854, *T. simplex* LeConte, 1876, and *T. alternatus* Say, 1832), the latter four being recorded from Canada (Bright & Bouchard 2008).

Despite the relatively large size of these beetles and their occasional abundance in suitable habitats, biological data on *Trichalophus* are remarkably scarce. Adult beetles appear highly polyphagous (Anderson 2002) being found on a number of shrubs and herbs (personal observation). North American *T. didymus* was mentioned as an occasional pest of strawberries (*Fragaria* sp.) in Washington State (see references in Bright & Bouchard 2008). Immature stages and larval host plants are adequately known only for a widely distributed Siberian species *T. leucon* Gebler, 1841. Larvae of this species feed externally on the roots of *Ribes* L. (Grossulariaceae) as well as on a few other shrubs and take two years to complete development (Krivets & Burlak 1986; Krivets 2006). The host plant record is of potential economic significance, since the host genus includes cultivated currants and a number of ornamental plants. The genus *Ribes* also includes alternate hosts for the White Pine Blister Rust (*Cronartium ribicola* J.C.Fischer, Cronartiaceae), a fungus accidentally introduced to North America about 1900 from Europe or Asia, which causes significant damage to American white pines (*Pinus* spp.; Maloy 2001).

Nothing is known about the evolutionary history of *Trichalophus* and the phylogenetic relationships of this taxon. Flightlessness is not unique for *Trichalophus*, but it is found in some other genera of Alophini (Bright & Bouchard 2008), including the West Palaearctic *Graptus* Schoenherr, 1823 (Davidian & Arzanov 2004). The latter genus has long been known under its synonymous name *Alophus* Schoenherr, 1826 and was widely used in original combinations for Palaearctic *Trichalophus* prior to Reitter's generic revision (1913). No members of either *Trichalophus* or any other Alophini were subjected to a phylogenetic analysis so far. The taxonomic recognition of either the genus or the tribe, along with a few diagnostic characters used in the keys (i.e. Anderson 2002) are, therefore, the only hints of their possible monophyly. Since the genus *Trichalophus* was historically linked to *Graptus*, they both might form a clade, even if paraphyletic with respect to the North American *Plinthodes* LeConte, 1876 (Bright & Bouchard 2008) and perhaps other oligotypic Holarctic genera of Alophini (*sensu* Alonso-Zarazaga & Lyal 1999, with subsequent modifications of Bright & Bouchard 2008 and Alonso-Zarazaga et al. 2010; see also below). DNA data for *Trichalophus* are exceptionally scarce, with only four public partial CO1 sequences (>400 bp) of *T. alternatus* presently available from either Barcode of Life Database (BOLD) or GenBank.

LeConte (1876) established the genus for six nominal Nearctic species known to him, four of them having been described earlier as *Alophus* (*A. didymus*, *A. constrictus* LeConte, 1857, *A. alternatus*, *A. seriatus*) plus two newly described (*A. simplex*, *A. planirostris*). Six other currently valid Palaearctic species (Yunakov 2013) described prior to 1876 were added later; one of them was originally described as *Hypsonotus* Germar (*H. boeberi* Schoenherr, 1826) and five others as *Alophus* (*A. albonotatus* Motschulsky, 1869, *A. humeralis* Gebler, 1834, *A. lineatus* Gebler, 1841, *A. quadriguttatus* Gebler, 1829, *A. rudis* Boheman, 1842). After 1876, the Palaearctic part of the genus grew quickly in size. By the year 1915 *Trichalophus* included all but six of its 44 currently valid Palaearctic species-group taxa (Yunakov 2013). This notable increase was mainly due to the efforts of Johannes K.E. Faust and Edmund Reitter who, together with a few others, introduced 30 currently valid species-group names described from specimens collected on the Asian frontiers of the rapidly growing Russian Empire (Siberia, Russian Far East, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan, Mongolia, Xinjiang Uyghur Autonomous Region of China; Pierce 1960; Bajtenov 1974). Oddly enough, two new *Alophus* species, *A. caudiculatus* and *A. compressicauda*, were reported by Fairmaire (1886, 1887, respectively) from geographically distant Yunnan situated on the extreme southwest of China. The latter records, if indeed belonging to *Trichalophus*, would extend the genus' range for over 1,000 kilometers southwards. In 1913 Reitter described 13 species-group taxa in a key to all Palaearctic species known to him. Until now Reitter's revision has remained the most comprehensive single publication on *Trichalophus* weevils.

For the following hundred years the genus was neglected and only six new species-group names were introduced. Among them are both species recorded from Japan: *T. rubripes* Zherikhin & Nazarov, 1990 and *T. nutakkanus* Kôno, 1936; the former also found on the continent, while the latter is endemic to Hokkaido. Two other species were named from the mountains of the former Soviet Central Asia (*T. lixomorphus* Bajtenov, 1974 and *T. krauseanus* Bajtenov, 1975), while one (*T. korotyaevi* Zherikhin & Nazarov, 1990) was described from Sakha Republic (=Yakutia). Additionally, Suvorov (1915) established a monotypic genus *Pseudalophus* for his new species *P. tibetanus* described from an unknown number of syntypes collected during Pyotr K. Kozlov's (1863–1935) Mongol-

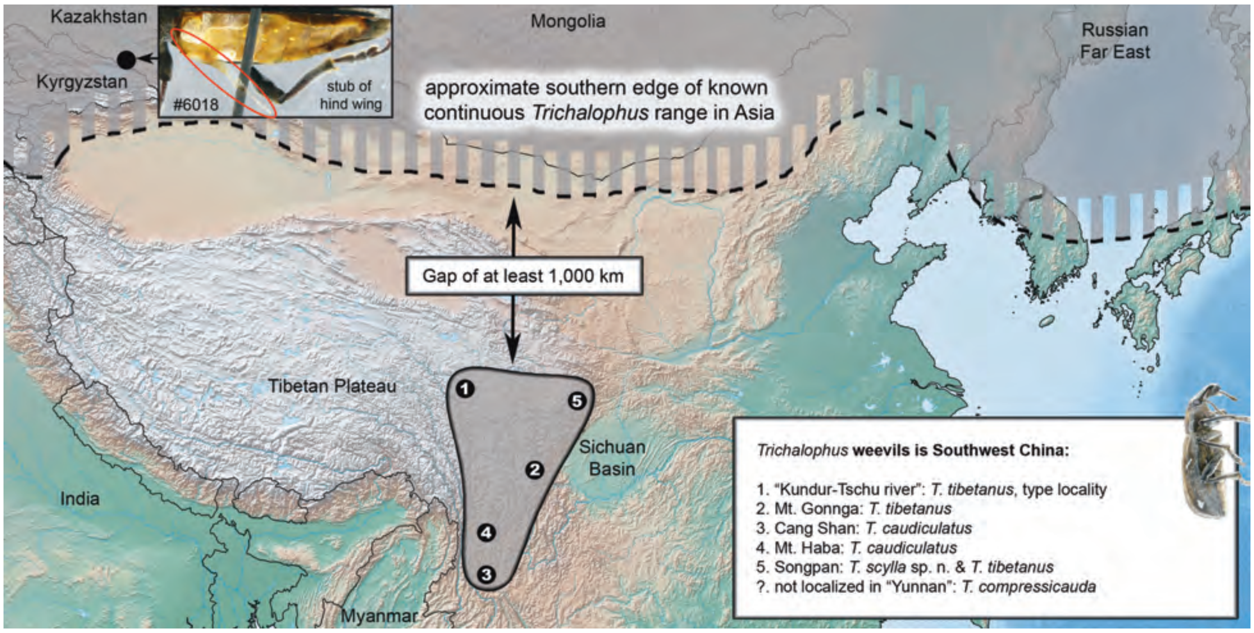

Fig. 1. Known geographic distribution of *Trichalophus* is Southwest China. Inserted image of female specimen #6018 from Kazakhstan shows hind wing brachyptery in *Trichalophus*.

Tibetan expeditions 1899–1901. The published temporal and geographical data of this species are identical with those of *Notaris kozlovi* Korotyaev, 1979 (Grebennikov & Kolov, unpublished) and the type locality is in the present day extreme northwest of Sichuan (Fig. 1). The four-line description of the new genus hinged on two characters distinguishing it from "*Alophus*", namely (a.) elytra strongly compressed "internally" (i.e. as if a force was applied in the horizontal plane therefore flattening elytra in the vertical plane) and (b.) elytral surface "naked" (= lacking vestiture). The former character is known to occur in Palaearctic *Trichalophus* and was used by Fairmaire (1887) to derive the name *compressicauda* for a species from nearby Yunnan, while the latter character might perhaps be attributed to abrading. Suvorov's original description was suggestive of a *Trichalophus* species, and, not surprisingly, Yunakov (2013) synonymized both generic names.

This project began on May 19, 2010, when the first two *Trichalophus* specimens (#0713 & #0714, Figs 3, 5), among those reported below were found under stones in the alpine zone of the Cang Shan Mountain Range in Yunnan (Fig. 1). The find was most inspiring and seemingly supportive of Fairmaire's historical claim that the genus was present so far south. During the next two years additional specimens were recovered in the same and three other high altitude localities in Yunnan (Mount Haba) and Sichuan (Mount Gongga and Songpan, the latter seemingly supporting two sympatric species). Phenetic similarities and subsequent analysis of DNA barcodes suggested that those were indeed species of *Trichalophus*. The wide gap seemingly separating these *Trichalophus* of Southwest China from their congeners in the north (Fig. 1) became partly bridged when the former "*Pseudalophus*" *tibetanus* was transferred to *Trichalophus* (Yunakov 2013). At that stage it became evident that *Trichalophus* was indeed present in Yunnan and Sichuan. The discovery of the high-altitude and the extreme southern representatives of a widely distributed trans-Beringian genus suggests a refugial distribution since the last glacial period (Darwin, 1859: 373–382). The goals of the present paper, therefore, are (1.) to attempt unfolding the evolutionary past of the newly sampled *Trichalophus* specimens from Southwest China using mainly mtDNA data and (2.) to report these findings in the framework of ranked Linnaean classification. Additionally, an attempt is made to provide an illustrated overview of all ten extant genera of Alophini and, therefore, to bring attention to this poorly defined, and taxonomically disorganized weevil tribe.

MATERIAL AND METHODS

Museum abbreviations, followed by the curator's name:

CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (P. Bouchard)
IZCAS	Institute of Zoology, Chinese Academy of Science, Beijing, P.R. China (R. Zhang)
MNHN	Muséum National d'Histoire Naturelle, Paris, France (H. Perrin, A. Mantilleri)

Fig. 2. Habitats of *Trichalophus* spp. in Southwest China. A–C: *T. scylla* sp. n., Songpan, Sichuan; D–F: *T. tibetanus*, Songpan, Sichuan; G–I: *T. caudiculatus*, Cang Shan, Yunnan; J–L: *T. caudiculatus*, Mt. Haba, Yunnan.

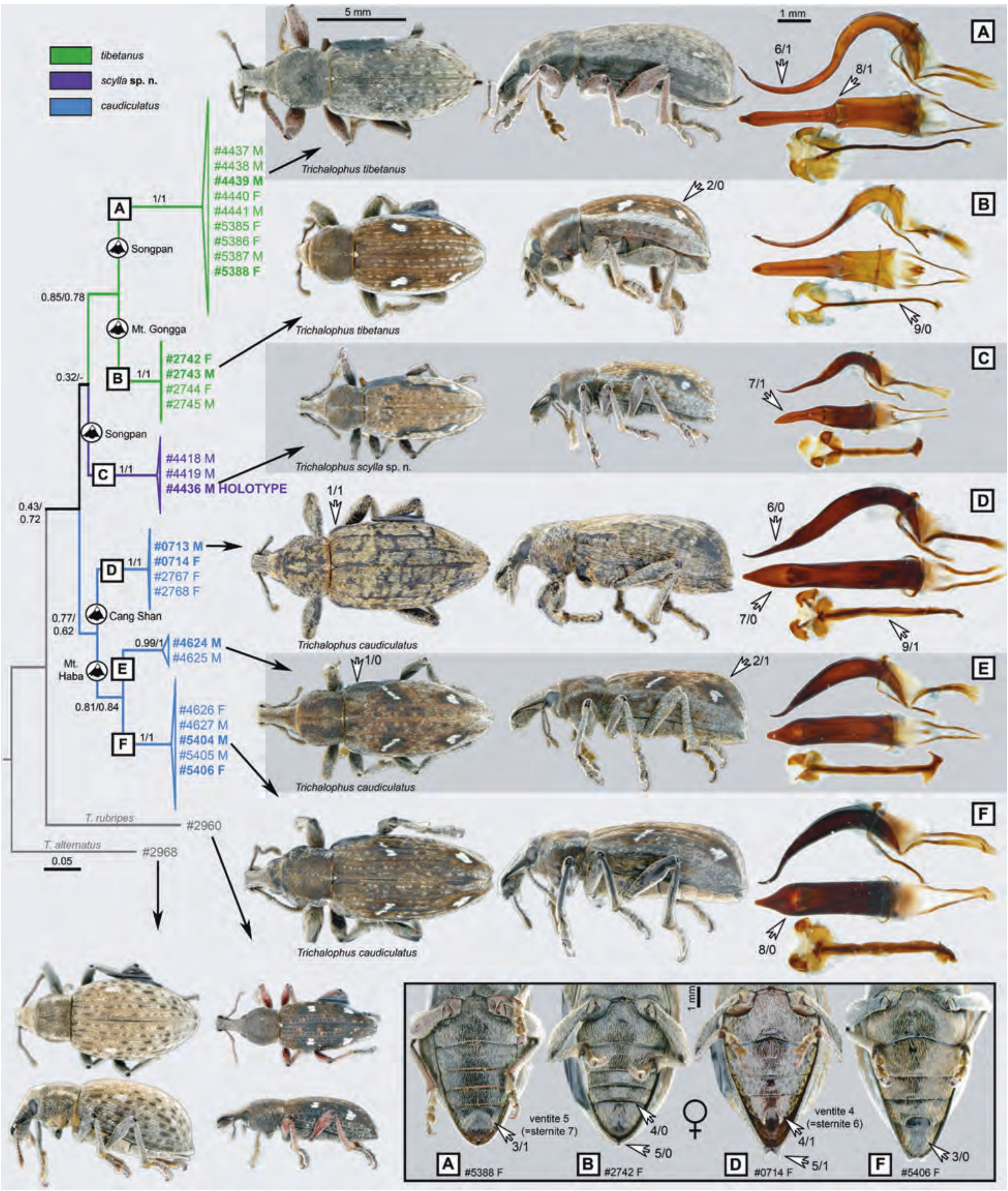

Fig. 3. Maximum Likelihood inference phylogram of *Trichalophus* weevils from Southwest China using the 658 bp of the mtDNA barcoding CO1 gene fragment. The tree is rooted on *Graptus circassicus* (Entiminae: Alophini; not shown); two extraterritorial outgroup *Trichalophus* (#2960 & #2968) are in grey. Digits at internodes are ML/MP bootstrap values. Six geographical evolutionary groups of *Trichalophus* are marked as clades A–F in white squares; note that Mount Haba and Songpan each harbours two evolutionary groups. Black long arrows link respective terminal clades with an image of their representative. Specimen numbers in bold are those of imaged males (M, to the left of the tree) or females (F, in the insert showing ventral view). Black and white short arrows indicate morphological characters and, after a slash, their states (Table 1).

MTD	Senckenberg Naturhistorische Sammlungen, Dresden, Germany (K.-D. Klass, O. Jäger)
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (B.A. Korotyaev)

The length of the body was measured in dorsal aspect from the elytral apex to the anterior edge of the pronotum. Distribution map (Fig. 1) is generated using the on-line SimpleMappr tool (Shorthouse 2010). The chronostratigraphic timing follows Cohen et al. (2013). Nomenclature of male genitalia follows that of Wanat (2007). The term "Southwest China" is delimited to two Chinese provinces, Yunnan and Sichuan. The term "base pair" is abbreviated as bp when referring to sequence length; abbreviations "syn. n" and "sp. n." denote new synonym and new species, respectively.

Specimen sampling, handling and gathering DNA data

Except for two specimens #4418 and #4419 sifted from *Rhododendron* L. leaf litter, all newly collected *Trichalophus* were handpicked from under stones (Figs 2A–L) in the alpine zone (Fig. 2J), or on a glade in the upper forest zone (Fig. 2D) in Southwest China. In total 38 adult *Trichalophus* beetles were collected in the following four localities (Fig. 1; in brackets are the total number of specimens followed after a slash by the number of those successfully sequenced for DNA barcode >400 bp): the Cang Shan Mountain Range (4/4), Mount Haba (12/7), Mount Gongga (4/4), and the vicinity of Songpan township (18/12). A leg was removed from a specimen for DNA extraction. All specimens used for DNA barcoding have at least one unique identifier label with the code CNCCOLVG0000XXXX; this format is shortened to the last four digits #XXXX when a specimen is referred to (Figs 3, 4). Specimen images, geographical data, primers, original electropherograms and other relevant data pertaining to all 35 matrix-forming sequences can be seen online in the publicly accessible dataset "*Trichalophus* 35 [DS-TRICHAL]" on the Barcode of Life Database portal (doi: dx.doi.org/10.5883/DS-TRICHAL). Genitalia of six males each representing a terminal cluster (=evolutionary group) as detected in the phylogenetic analyses (see below) were dissected, imaged (Fig. 3) and stored in microvials with glycerol pinned with the specimens.

DNA analyses and matrix construction

Three separate DNA analyses were performed. The **Maximum Likelihood** (ML) and the **Maximum Parsimony** (MP) analyses attempted to place the diversity of

Table 1. Discrete morphological characters for diagnostics of *Trichalophus* weevils in Southwest China (Fig. 3)

1. Elytral shoulders and elytral sides in basal 2/3, dorsal view: shoulders rounded, sides evenly widening posterad (0); shoulders angular, sides subparallel (1).
2. Elytral dorsal and posterior profile (=declivity), lateral view: evenly and gently rounded throughout (0); flattened dorsally and abruptly curved (1).
3. Female, ventrite 5, bumps and depressions on surface, ventral view: absent (0); present (1).
4. Female, ventrite 4, two sharp points at posterior edge, ventral view: absent (0); present (1).
5. Female, posterior projections of elytral apices, ventral view: absent (0); present (1).
6. Male genitalia, long, thin, and curved apical lamella of aedeagus (lateral view): absent (0); present (1).
7. Male genitalia, aedeagus, dorsal view: symmetrical (0); asymmetrical (1).
8. Male genitalia, aedeagus, notch in lateral outline, dorsal view: absent (0); present (1).
9. Male genitalia, sternal apodeme 9, dorsal view: thin (0); thick (1).

clade	species	Locality	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
A	*tibetanus*	Songpan	0	0	0	1	0	1	0	1	0
B	*tibetanus*	Mt. Gongga	0	0	0	1	0	1	0	1	0
C	*scylla* sp. n.	Songpan	0	0	?	?	?	0	1	0	1
D	*caudiculatus*	Cang Shan	1	1	1	0	1	0	0	0	1
E	*caudiculatus*	Mt. Haba	0	1	?	?	?	0	0	0	1
F	*caudiculatus*	Mt. Haba	0	1	1	0	1	0	0	0	1

Trichalophus from Southwest China into phylogenetic and geographical perspective. Both ML and MP used the same matrix of 35 DNA barcodes with a minimum and maximum length of 400 bp and 658 bp, respectively. The ingroup consisted of 27 *Trichalophus* specimens from Southwest China, while the outgroup included two extraterritorial *Trichalophus* specimens representing *T. rubripes* from the Russian Far East and *T. alternatus* from Canada (Fig. 3). The rest of the outgroup was formed by six specimens of *Graptus circassicus* Solari, 1945 from Georgia: Abkhazia. Both ML and MP analyses were implemented using MEGA 6 (Tamura et al. 2013), including (a.) topology building, (b.) statistical support test by using 1000 repetitions of bootstrapping and (c.) search for the best substitution model for ML analysis (T92+G). The root was consistently placed between *Graptus* and *Trichalophus*. The GenBank accessions for these 35 sequences are KM538655–86, KJ445708, KJ445709, KJ445712; all of them are new, except for the three latter *Graptus* sequences.

The third DNA analysis was performed to date the ingroup branching events and to re-test the phylogenies suggested by the ML and MP analysis. The original matrix of 35 sequences was reduced to include only 23 full-length DNA barcodes (658 nt; except for the sequence of *T. alternatus* with 609 bp). The second analysis was performed in BEAST v1.8.0 (Drummond et al. 2012) utilizing the Bayesian inference (BI) approach with no *a priori* grouping, all default priors and options, GRT+G+I nucleotide substitution model (instead of the T92+G+I not offered in the software; the latter model was detected in a separate model-searching analysis in MEGA 6 as having the best fit), strict linear molecular clock and nucleotide substitution rate of 0.018 (Papadopoulou et al. 2010). Tracer 1.6 (Rambaut et al., 2014) was used to graphically determine stationarity and to check convergence of runs. The "burn in" option was implemented eliminating the first 2500 of the 10000 obtained trees. The resulting topologies from each of three analyses (ML, MP, BI) were visualized in FigTree v1.4 (Rambaut et al. 2014).

Contribution from morphology

Morphological data are not expected to contribute decisively in DNA-dominated phylogenetic analysis, particularly in shallow branches of the tree of life (Ward 2011) conventionally called "species" in ranked classification (Hey 2001). Consequently, no effort was made to merge the DNA matrix with a few morphological characters scored for the ingroup (Table 1). Instead, DNA-determined *Trichalophus* clusters (= evolutionary groups by Hey 2001 or *clades A-F* on Fig. 1) were *a posteriori* scrutinized in search of diagnostic morphological characters (Maddison 2014), not necessarily synapomorphic (Ward 2011). The easily observable dorsal color pattern, being either too variable or subject to abrasion, was judged as unreliable for diagnostic purposes in *Trichalophus*. An additional effort was made to explore structures of male genitalia by dissecting a single male per each of six clades detected on the phylogenetic tree (Fig. 3).

Integrating molecular phylogenetic results into taxonomy

In biodiversity studies taxa are normally named first and then their phylogeny and boundaries are analysed, if ever. This approach, although logically awkward, has strong historical roots from the times when (a.) phylogenetic theory was not practiced by taxonomists, and (b.) researchers lacked adequate data to perform sufficiently detailed analyses when naming their new species. Advent of Hennigian principles coupled with availability of DNA sequences challenges this classical and logically deficient approach (Ward 2011). A modern student of biodiversity is expected to (A.) delimit evolutionary groups through a formal analysis, then (B.) make a balanced, responsible and subjective judgement using all available evidence sources as to which clades need names (Hey 2001) and then (C.) conservatively apply formal names, either preexisting or newly proposed. In other words whenever possible, taxa naming should not be done before but after the analysis and discussion, not to abuse logic by putting the cart before the horse. Through most of the present paper all six tree-delimited clades representing candidate species (Fig. 3) are referred to by using informal non-taxonomic names (*clades A-F*, italicized). Therefore, the taxonomic part of this paper using three valid species-group names (two previously used and one new) and synonymizing one name follows the Results section and most of the Discussion.

RESULTS

The Maximum Likelihood (ML) analysis produced the best tree (Fig. 3) with the highest log likelihood of –3265.92. All *Trichalophus* specimens from Southwest China formed a weakly supported clade with highly resolved internal structure consisting of six *clades A–F*. The Maximum Parsimony (MP) analysis resulted in seven best trees (length: 558, consistency index: 0.64, retention index: 0.90; topologies are not shown) also recovering the same six *clades A–F* (as in Fig. 3). In both analyses the ingroup was recovered as a clade. The only backbone topological difference of the MP strict consensus tree (as compared to the ML topology, Fig. 3) was that the *clade C* was recovered as the sister to the rest of *Trichalophus* from Southwest China.

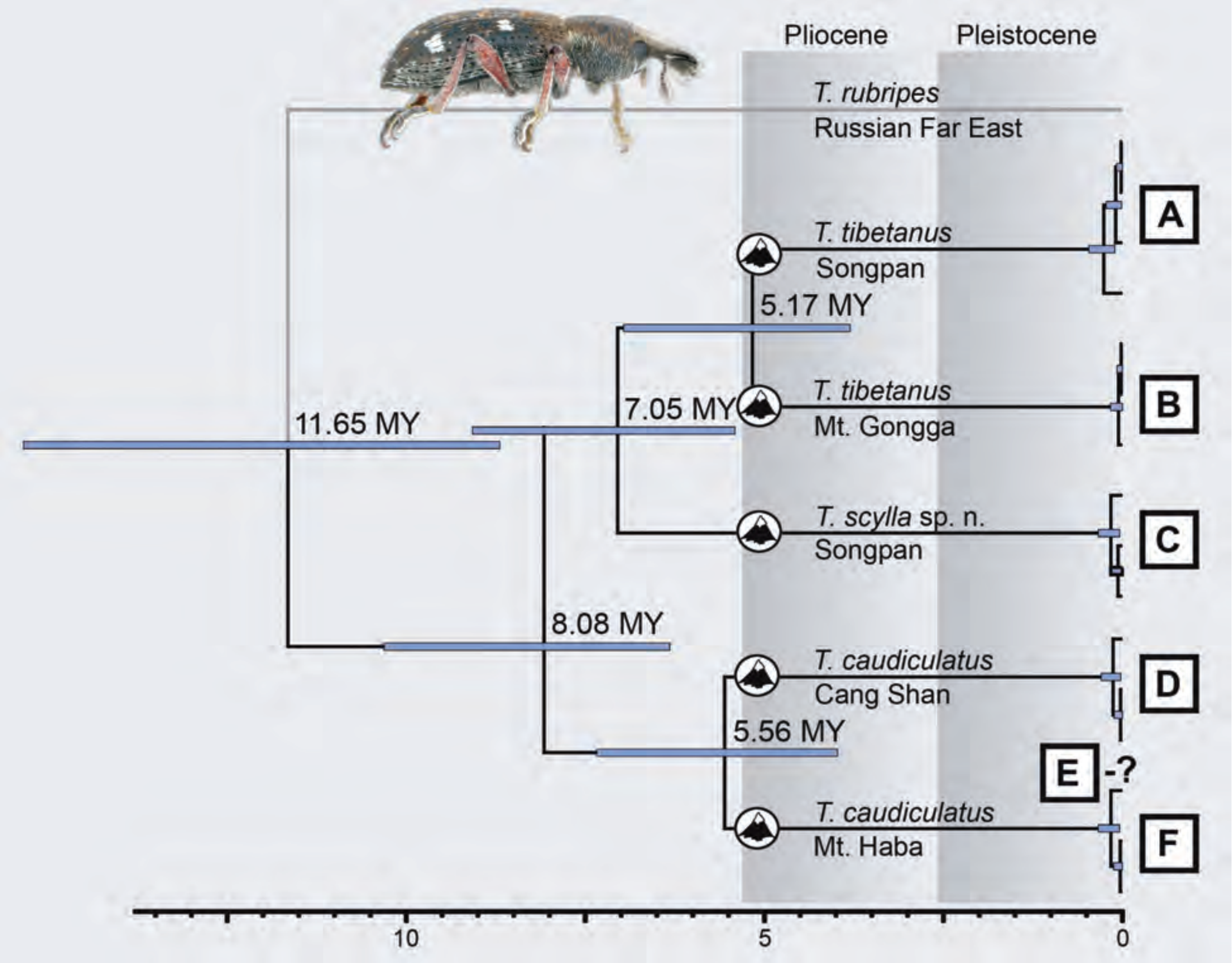

Fig. 4. Ultrametric tree dating evolutionary events of *Trichalophus* beetles in Southwest China. Digits at nodes and on the scale below are million years before present. Node bars represent 95% confidence intervals of the age estimate.

Temporal analysis in BEAST (Fig. 4) recovered all *Trichalophus* specimens from Southwest China in a clade with the same internal backbone topology as in the ML analysis (Fig. 3, although some specimens and the entire *clade E* were not represented in the BEAST analysis due to inadequate sequence length). The inferred timing of the origin of the Southwest China *Trichalophus* is 11.65 MY, while the clade's diversification leading to the five *clades A–D* and *clade F* range between 8.08 MY and 5.17 MY (Fig. 4).

DISCUSSION

mtDNA phylogeny and phylogeography of *Trichalophus* in Southwest China

Recovery of a monophyletic *Trichalophus* radiation in Southwest China (Figs 3, 4) should be treated with caution, since limitations in the number of the in- and outgroup representatives did not permit a rigorous test. Little other evidence is available to challenge this hypothesis. The entire *clade A-F* has a compact range allopatric to that of the rest of the genus (Fig. 1), although the disjunct distribution might be plausibly attributed to the lack of adequate sampling effort to bridge the gap. Morphologically *Trichalophus* beetles from Southwest China are seemingly large-bodied compared to other two species (Fig. 3), although adding more *Trichalophus* in the analysis might challenge this pattern. Nearly all of the ingroup morphological characters (Table 1) cannot be adequately matched with those for the rest of the genus due to the lack of comparative data. Summing up, compact distribution (Fig. 1) of monophyletic *Trichalophus* of Southwest China (Figs 3, 4) is a weakly supported hypothesis to be eventually retested. Internal structure of six ingroup clades (Fig. 3) is mainly consistent with limited geographical (Fig. 1) and morphological (Table 1) data and is further discussed when Linnaean species are delimited (see below).

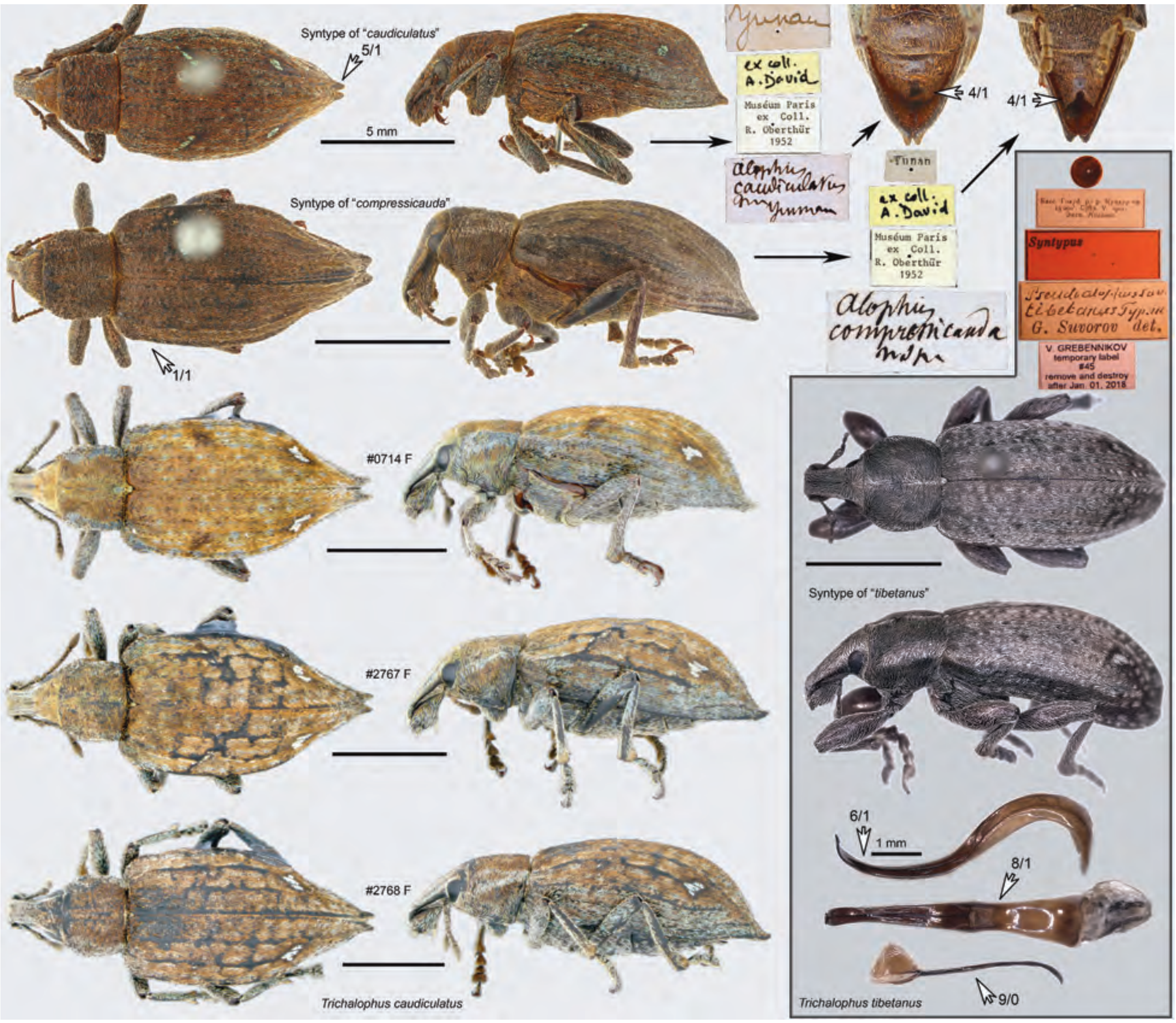

Fig. 5. Type specimens and original labels of three historical *Trichalophus* species names from Southwest China (*caudiculatus*, *compressicauda*, *tibetanus* currently assigned to two valid species *T. caudiculatus* and *T. tibetanus*), together with three *T. caudiculatus* females (#0714, #2767, #27678) sequenced for DNA barcode (Fig. 1). Black and white arrows indicate morphological characters and their states (Table 1, separated by a dash). Images of *caudiculatus* and *compressicauda* syntypes and their labels: Antoine Mantilleri, © MNHN.

Unlike at least some of its more northern congeners, *Trichalophus* in Southwest China inhabit high altitudes (3704–4158 m). Such a characteristic of the southern-most representatives of a temperate northern hemisphere clade of low-dispersing organisms is consistent with the basic Quaternary expansion-contraction model of latitudinal range change (Qiu et al. 2011). The latter stipulates extensive latitudinal range shifts in the form of southward movement during glacials followed by rapid expansions northwards during interglacials (Qiu et al. 2011). If so, distribution of *Trichalophus* in Southwest China (Fig. 1) is a direct result of the last warming following the Last Glacial Maximum (26,000–19,000 ybp). More specifically, the observed data are consistent with at least three subhypotheses (numbering after Qiu et al. 2011): (iii) long-term isolation and survival in multiple localized refugia (*clades A–D* and *clade E+F* in Fig. 3), (ii) population isolation and endemism due to river course dynamics (*clade D* versus *clade E+F*) and (iv) glacial *in situ* survival of some hardy alpine species on the Tibetan plateau itself (population of *T. tibetanus* represented by the type specimens, Fig. 5). Like the hypothesis on monophyly of *Trichalophus* in Southwest China, all phylogeographical inferences are highly preliminary due to material and data limitations.

With no suitable fossils to calibrate a *Trichalophus* molecular clock, the temporal aspect of *Trichalophus* evolution in Southwest China (Fig. 4) relies on the *a priori* mtD-

NA substitution rate of distantly related Tenebrionidae (Papadopoulou et al. 2010). The obtained dates of the *Trichalophus* cladogenesis (Fig. 4) are comparable to those of the sympatric and similarly high-altitude and flightless weevil genus *Niphadomimus* Zherikhin, 1987 (Grebennikov 2014a). Both agree that the lineage divergence took place well before the onset of the Pleistocene climate fluctuations. Both time estimations were based, however, on identical methods and substitution rates, which might have biased them both. Exact substitution rates may significantly vary depending on population size, founder effects, and a number of other less well-understood factors and, therefore, markedly differ from the assumed 0.018 substitutions per site per million years. In other words application of the user-friendly BEAST software and the obtained clear-cut dates (Fig. 4) should be treated carefully, since we are far from understanding the molecular clock (Lanfear et al. 2010), even for such relatively simplified and recent scenario as that of *Trichalophus* weevils in Southwest China.

Delimitation of Linnaean species for *Trichalophus* in Southwest China

The practical task of assigning Linnaean species names to the newly discovered *Trichalophus* from Southwest China, even with the help of a tree (Fig. 3), is far from being trivial. It involves at least one theoretical and two practical difficulties. First, imposing ranked classification on the continuum of the tree of life cannot be objectivised (Hey 2001; Ward 2011) and, therefore, involves arbitrary decisions (Sites & Marshall 2004). Second, despite sampling and analytical efforts, relatively little data on *Trichalophus* are available. For example, the relatively well-resolved DNA tree (Fig. 3) is that of a very short fragment of a fast-evolving mitochondrial maternally inherited gene and, therefore, only a proxy to organismal evolutionary history. Third difficulty is the existence of three available historical names, which have nomenclatorial priority and have to be interpreted and used, if considered as valid. These three issues have to be considered before the freshly sampled *Trichalophus* in Southwest China might be incorporated into the existing taxonomic scheme (Yunakov 2013). The first difficulty, concerning the issue of what a *Trichalophus* "species" is, will be resolved in this passage, while both practical issues are considered further below.

A "species" as a taxonomic category is purely and solely a label routinely and often inconsistently assigned to the shallow branches of the tree of life ever since Linnaeus. As such, "species" is no more real than other taxonomic categories like "genus", "family" or "phylum" (Hey 2001). Like every other taxonomic category, a "species" is a mere convenience required by the human mind to categorize and count biological diversity. Acceptance of this basic philosophical and methodological principle denies "species" reality in the same sense at it denies reality "genera" or other "higher" taxonomic categories. In practical terms a species is nothing more than a morphologically (or otherwise) diagnosable group of organisms preferably forming a clade and, most importantly, considered practically worthy of being called a species (Hey 2001). If to follow such an approach, decision on species boundaries almost fully rests with the revising author, which, in turn, results in the splitters versus lumpers issues, particularly in regard to a clade of allopatric populations. The authors normally feel free to either split them into as many species as possible, or lump them into a single one. The first approach is an example of unnecessary taxonomic inflation (Isaac et al. 2004) adding nothing but unnecessary names. The alternative lumping approach using a single species name and a geographic reference would label every allopatric evolutionary group equally well, while avoiding unnecessary additions to the already heavy nomenclatorial burden. Moreover, a scramble to call a "species" an allopatric evolutionary group, even if accompanied by correlating morphological and other differences, can be misleading when linked to the phenomenon of Sisyphean evolution (McKay & Zink 2014). Summing up, introduction of new species names should be done only when all alternative options have been shown as inadequate. Such a careful and reserved approach would not have created the multitude of meaningless and cryptic taxa (Riedel et al. 2013a, b; Vences et al. 2013).

Two among six terminal clades representing *Trichalophus* evolutionary groups (Fig. 3) are allopatric to all other ingroup clades (*clade B* and *clade D* from Mt. Gongga and Cang Shan, respectively). They should, therefore, be first assessed if each of them can be merged together with its strongly supported sister-group into a more inclusive clade to merit a species name. Indeed, *clade B* is strongly linked to the allopatric *clade A* (Fig. 3), so the *clade A+B* might itself be considered a candidate species. *Clade C* is recovered in the ML analysis as a sister to *clade A+B* (Fig. 3), but in MP analysis the sister group of *clade A+B* was the *clade D+E+F*. Remarkably, specimens of both *clade A* and *clade C* occur in sympatry in Songpan (or at least in parapatry; their two geographically closest samples were taken a few hundred meters apart). Moreover, while males and females of both *clade A* and *clade B* share all eight morphological character states (Table 1), their males differ in three genitalia characters from those of *clade C*. Such considerations strongly suggest that *clades A+B* and *clade C* (Fig. 3) should be treated as two separate species, respectively, and the former one as consisting of at least two geographically and morphologically unique evolutionary groups (*clade A* and *clade B*, Fig. 3). It is possible that in the future each *clade A* and *clade B* might be considered as separate species, but not until the current nomenclatorial lumping arrangement is refuted as impractical.

The *clade D+E+F* emerges as the third and the last one to be designated as a Linnaean species among those represented in the ingroup (Fig. 3). Remarkably, *clade E* and *clade F* from Mount Haba, although genetically distinct, are formed by morphologically and geographically indistinguishable specimens (Fig. 3). This notable genetic dimorphism accompanied by full sympatry and morphological similarity is perhaps linked to incomplete lineage sorting (Funk & Omland 2003). The *clade E+F* is strongly supported as a sister to the geographically closest *clade D* and both share all but one morphological character (Table 1). Like the *clade A+B*, the *clade D+E+F* (Fig. 3) might also later require two Linnaean species, but not before the present conservative nomenclatorial decision is shown as inadequate.

Matching historical names with the tree-delimited *Trichalophus* Linnaean species

The most significant practical constraint is how to link three clades delimited for designation as Linnaean species (*clade A+B*, *clade C* and *clade D+E+F*, Fig. 3) with three available historical names (*T. caudiculatus*, *T. compressicauda* and *T. tibetanus*). The type specimens of the latter are well preserved and available for study (Fig. 5). Matching the type specimens of three historical names with three evolutionary groups in Fig. 1 can be done using three sources of evidence: (a.) similarity in body shape and in male genitalia, (b.) geographical proximity and (c.) biological characteristics expressed through the altitude of the type locality. No attempt was made to extract DNA from the type specimens, mainly because they were judged too old to warrant an attempt.

Of the three historical names, only the type specimen of *T. tibetanus* has information available from all three sources. Its type locality can be traced precisely (Figs 1, 5), while habitus and shape of male genitalia of a syntype (Fig. 5) match most closely those of the *clade A+B* (Fig. 3). The name *T. tibetanus* is, therefore, used to designate the *clade A+B* (Fig. 1). Such matching is far less straightforward with the both Fairmaire's names.

The most significant uncertainty with both names *caudiculatus* and *compressicauda* is that their type localities are imprecise, originally given as "Yunnan". The years when the types were collected are also unknown. Only the younger of these two names, *compressicauda*, has the collector's name stated: Père Jean Marie Delavay (=Father Delavay). It seems, however, plausible that Father Delavay also collected the type series of *caudiculatus*. Even though Fairmaire cited Armand David (= Father David) as the type specimen source for species described together with *caudiculatus* in the 1886 paper, Father Delavay was likely the original collector of at least some of them, since Fairmaire in the same paper also named *Cicindela delavayi* Fairmaire, 1886 in his honour. Indeed, the years before both species were described (1886, 1887) correspond with Delavay's second stay in China (1882–1891) (Anonymous 2014). This trip took place after Father Delavay's meeting with Father David in 1881, the latter convincing the former to collect specimens for the Muséum national d'histoire naturelle (Anonymous 2014). During his second stay in China, Delavay was mainly based in a Yunnan village somewhere between Lake Erhai and Lijiang township given as "Dapingzi" (Anonymous 2014). Delavay had two favourite climbing spots nearby: "Mount Heishanmen" (or "Ma'an Shan", west of "Dapingzi", see Handel-Mazzetti 2014; not definitely located, but distinct from the Cang Shan Mountain Range) and the Cang Shan Mountain Range along the western shore of lake Erhai (Lancaster 1993, Anonymous 2014). Besides these two high mountain localities, Father Delavay is definitely known to have collected in the alpine zone around Deqin in northwestern Yunnan, from where numerous alpine *Carabus* were sampled (T. Deuve, personal communication). It is highly probable that Father Delavay visited many other alpine localities in Yunnan, however those three were apparently most frequently visited and/or sampled for high altitude beetles.

Both *caudiculatus* and *compressicauda* were described from an unknown number of syntypes. Curatorial searches in MNHN in 2014 revealed a single syntype for each for these names (Antoine Mantilleri, personal communication). Their syntype status is corroborated by the fact that both specimens bear original identification labels and, moreover, fully agree with relatively detailed descriptions of both nominal species (Antoine Mantilleri, personal communication). Both syntypes, although not dissected, appear to be females by possessing posterior projections on elytral apices (character 5/1, Fig. 5) and posterior projections of ventrites 4 (character 4/1, Fig. 5). These two syntype characters match with those of the female specimens from *clade D* (Fig. 3); the other being angular elytral shoulders and subparallel elytra in their basal 2/3 (Table 1). Specimens from *clade D* inhabit the Cang Shan Mountain Range, which was visited on many occasions by Father Delavay, including altitudes above 4,000m (Lancaster 1993). Both Fairmaire's names, therefore, represent the best fit for the Linnaean species represented on Fig. 3 by the *clade D+E+F*, which, in turn, suggests their synonymy proposed below.

Taxonomic overview of *Trichalophus* in Southwest China

Trichalophus LeConte, 1876

Type species: *Alophus didymus* LeConte, 1854, fixed by subsequent designation (Bright & Bouchard 2008: 57).

Trichalophus caudiculatus (Fairmaire, 1886)

(Figs 2, 3, 5)
caudiculatus Fairmaire 1886: 353 (*Alophus*)

Type locality. Yunnan.

Type specimens. Syntype (MNHN, Fig. 5), likely female, examined from images in Fig. 5, labels in Fig. 5. Described from unknown number of syntypes.

= *compressicauda* Fairmaire, 1887: 129 (*Alophus*) **syn. n.**

Type locality. Yunnan.

Type specimens. Syntype (MNHN, Fig. 5), likely female, examined from images in Fig. 5, labels in Fig. 5. Described from unknown number of syntypes.

Diagnosis. This species is recognized by presence of apical elytral projections in females (character 5/1, Fig. 3).

Intraspecific variation. GenBank accessions: KM538662, KM538665, KM538667–68, KM538670–71, KM538676–77, KM538681–82, KM538684. Length: 12.3–14.5 mm (Cang Shan), 11.1–11.8 mm (Mount Haba, *clade E*) and 11.4–14.5 mm (Mount Haba, *clade F*). Specimens from both sampled localities (Fig. 1) slightly differ in dorsal coloration, shape of elytral shoulders and arrangement of posterior projection on ventrite 4 of females (Fig. 3). Aedeagus of a single male known from the Cang Shan Mountain Range is less curved and more elongate, as compared to those of two males dissected from Mount Haba (Fig. 3), while female posterior projections on elytral apices of the Cang Shan specimens are noticeably longer than those from Mount Haba (Fig. 3).

Additional material examined. 16 exx in total: 2 exx #0713–0714 (CNC) “P.R. CHINA, Yunnan, E slope Cangshan at Dali, N25°39’54.7” E100°06’04.5”, 19.v.2010, 3815m, turn rock, V.Grebennikov”; 2 exx #2767–2768 (CNC) “P.R. CHINA, Yunnan, Cang Shan at Dali, N25°39’51” E100°06’05”, 04.vii.2011, 3815m, under stone, V.Grebennikov”; 12 exx #4623–4628, #5403–5406, #6207–6208 (CNC) “CHINA, Yunnan, Haba Shan, N27°20’51” E100°05’33”, 27.vi.2012, 4158m, under rock, V. Grebennikov”.

Distribution. This species is known from the Cang Shan Mountain range and nearby Mount Haba, both in Yunnan (Fig. 1). Elevation: 3815–4158 m.

Trichalophus scylla sp. n.

(Figs 2, 3)

Diagnosis. Specimens of this species are unique among known congeners in Southwest China by two characters: they are the smallest and possess asymmetrical aedeagus in dorsal view (character 7/1, Fig. 3).

Description. Holotype, male (Fig. 3). GenBank accession: KM538655. Length: 9.4 mm. Combination of other morphological characters as in Table 1.

Intraspecific variation. GenBank accessions: KM538656, KM538679. Length: 9.0–9.4 mm.

Material examined. Holotype (Fig. 3) male (IZCAS): #4436: “CHINA, Sichuan, 23km E Songpan, N32°38’07” E103°49’10”, 24.v.2012, 3704m, under rock, V. Grebennikov”. Paratypes (CNC): 2 males #4418 and #4419 “CHINA, Sichuan, 23km E Songpan, N32°37’38” E103°50’03”, 26.v.2012, 3791m, sifting 09, V. Grebennikov”.

Distribution. This species is known only from the type locality some 20 km E of Songpan, Sichuan (Fig. 1), where it is found sympatrically with *T. tibetanus*. Elevation: 3704–3791 m.

Etymology. The species epithet is the Latinized Greek mythical name of Scylla, one of the Nereids, transformed by Circe into a six-headed monster and who, together with its counterpart Charybdis, threatened Odysseus’ crew on their return voyage from Troy to Ithaca; noun in apposition.

Trichalophus tibetanus (Suvorov, 1915)

(Figs 2, 3, 5)
tibetanus Suvorov 1915: 338 (*Pseudalophus*)

Type locality. China, basin of the Blue river (=the Yangtze), the Kundur-Tschu river, 13200’.

Type specimens. Syntype (ZIN, currently on loan in MTD, Fig. 5), male, dissected by Rüdiger Krause, labels as in Fig. 5. Described from unknown number of syntypes. Twenty other similar specimens collected together with the imaged syntype are also likely part of the type series; of them four specimens each have a golden circle as in Fig. 5.

Diagnosis. This species is best distinguished by the presence of elongate and curved apical labella of aedeagus (character 6/1, Fig. 3) and relatively thick apodeme of male sternite 9 (character 9/0, Fig. 3).

Intraspecific variation. GenBank accessions: KM538657, KM538658, KM538659, KM538661, KM538663–64, KM538672–75, KM538680, KM538685–86. Length: 11.5–13.3 mm (Songpan) and 10.3–12.1 mm (Mount Gongga). Each elytron with single indistinct apical spot (Fig. 5), two indistinct spots, or two distinct spots (Fig. 3). Specimens from Mount Gongga have a long white longitudinal stripe laterally on each elytron (Fig. 3).

Additional material examined. 19 exx in total: 4 exx #2742–2745 (CNC) "P.R. CHINA, Sichuan, NE slope Gongga Shan, N25°53'53" E102°01'49", 8.vi.2011, 4085m, under stone, V.Grebennikov"; 15 exx #4437–4441, #5385–5388 and six not numbered specimens in ethanol (CNC) "CHINA, Sichuan, 23km E Songpan, N32°38'07" E103°49'10", 24.v.2012, 3704m, under rock, V. Grebennikov".

Distribution. Besides the type locality in the extreme north-western Sichuan, this species is also known from Mount Gongga and from vicinities of Songpan, both in Sichuan (Fig. 1); in the latter locality this species is found sympatrically with *T. scylla* sp. n. Elevation: 3704–4085 m.

Generic overview of the tribe Alophini

The proposed amalgamation of Alophini (as delimited below) with the tribe Tropiphorini (*sensu* Alonso-Zarazaga & Lyal 1999) by Zherikhin & Egorov (1991), for which a synonymous name Leptopiini was used by Marvaldi et al. (2014), is not followed here. Neither taxonomic arrangement was phylogenetically tested, therefore none is better than the other. Additionally, dissolving the compact and predominantly Holarctic Alophini in the much larger cosmopolitan Tropiphorini would discourage any practical effort to shed light on the genera involved, as attempted below.

The tribe Alophini was first proposed by LeConte (1876: 115) to incorporate the Palaearctic species grouped then in *Alophus* Schoenherr and species belonging to six Nearctic genera, five of them newly established: *Triglyphus* LeConte, *Plinthodes* LeConte, *Acmaegenius* LeConte, *Trichalophus* LeConte, *Lophalophus* LeConte and *Lepidophorus* Kirby, 1837. By the end of the millennium the tribe consisted of 15 valid genera, including three described from the Oligocene of the USA (*Centron* Scudder, 1893, *Geralophus* Scudder, 1893 and *Limalophus* Schudder, 1893, see Alonso-Zarazaga & Lyal 1999). Since then Bright & Bouchard (2008) synonymised the genus *Acmaegenius* under *Trichalophus* and reviewed the Alophini of Canada and Alaska. Alonso-Zarazaga et al. (2010) demonstrated that the sole known specimen of the monotypic genus *Ctenolobus* Desbrochers des Loges, 1892 from Morocco is conspecific with the type species of the otherwise strictly South American genus *Strangaliodes* Schoenherr, 1842 (Tropiphorini). As a result, *Strangaliodes* was transferred to the otherwise strictly Palaearctic Alophini and was keyed out against three other Mediterranean genera: *Graptus*, *Rhytideres* and *Seidlitzia* (Alonso-Zarazaga et al. 2010). Finally, Yunakov (2013) synonymized *Pseudalophus* under *Trichalophus*. At present the following 10 extant genera constitute the tribe Alophini:

***Graptus* Schoenherr, 1823** (Figs 6A, B) with 37 species-group taxa is distributed in Western Palaearctic (Yunakov 2013). Davidian & Arzanov (2004) revised and keyed 10 *Graptus* species from Russia and adjacent lands, including two newly described ones, and mentioned that many poorly known nominal species have been reported from the West Palaearctic.

***Lepidophorus* Kirby, 1837** (Figs 6C, D) consists of 11 brachypterous species found in western North America (Anderson 1997, 2012; Bright & Bouchard 2008), two of which, *L. inquinatus* Mannerheim, 1852 and *L. lineaticollis* Kirby, 1837, are also found on the Asian side of the Bering Strait (Yunakov 2013). Another extant North American species, *L. thulius* Kissinger, 1974, is known from numerous subfossil records on both side of the Bering Strait and, therefore, extant populations might perhaps be discovered in the northern Pacific Asia (as *Vitatitus* Kissinger, 1974 in Egorov et al. 1996 and in Anderson 1997). Anderson (2002) mentions that the genus cannot be reliably distinguished from *Dirotognathus* Horn, 1876 (Tropiphorini *sensu* Alonso-Zarazaga & Lyal 1999), giving support to a notion to synonymize both tribes (Zherikhin & Egorov 1991; Marvaldi et al. 2014).

***Plinthodes* LeConte, 1876** (Figs 6E, F) consists of two North American species, *P. foveirostris* Chittenden, 1925 from Ohio, North Carolina, Tennessee and Virginia and *P. taeniatus* LeConte, 1857 from British Columbia, Washington and Oregon (Anderson 2002). Bright & Bouchard (2008) questioned the distinctness of this genus from *Trichalophus*.

***Pseudobarynotus* Desbrochers des Loges, 1891** (Fig. 8) contains a single mysterious species *P. laticeps* (Desbrochers des Loges, 1875) known only from the type series and described from "Pyrénés". The type series could have been mislabelled, while Kazakhstan was suggested as its true origin (Alonso-Zarazaga et Lyal 1999). The later possibility is not unlikely, since the depicted syntype (Fig. 8) resembles a species of *Trichalophus* and might perhaps be later demonstrated as such.

Fig. 6. Type species of the Alophini genera. A–B: *Graptus triguttatus* (Fabricius, 1775), Austria, Wien, date and collector unknown, CNC; C–D: *Lepidophorus lineaticollis* Kirby, 1837, USA, Alaska, Wasilla, 1.viii.1988, J.Pilny, CNC; E–F: *Plinthodes taeniatus* LeConte, 1857, Canada, British Columbia, Victoria, 6.vii.1962, B.Carr, CNC; G–H: *Rhytideres plicatus* (Oliver, 1790), no collecting data, CNC. Scale: 2 mm.

Rhytideres **Schoenherr, 1823** (Figs 6G, H) includes three species widely distributed around the Mediterranean Sea (Yunakov 2013).

Seidlitzia **Desbrochers des Loges, 1891** (Figs 7A, B) consists of two species and one non-nominal subspecies from Spain and Morocco (Yunakov 2013).

Strangaliodes **Schoenherr, 1842** (habitus image in Alonso-Zarazaga et al. 2010, figs 1A, B) includes nine species from the South American Cordillera, all of them found in Chile and a few in neighbouring countries (Wibmer & O'Brien 1986); one of them also questionably recorded from Morocco (Alonso-Zarazaga et al. 2010). This is the only non-Palaearctic member of Alophini.

Trichalophus **LeConte, 1876** (Figs 7C, D) consists of 51 species and one non-nominal subspecies distributed on both sides of the Bering Strait; for more details see the current paper.

Triglyphulus **Cockerell, 1906** (Figs 7E, F) consists of two species, *T. ater* LeConte, 1876 and *T. nevadensis* Van Dyke, 1938 from the western part of the USA (Anderson 2002).

Xeralophus **Korotyaev, 1992** (Figs 7G, H) was established to accommodate *Alophus cretaceus* Reitter, 1894, described from present day Ulan Bator, Mongolia. Besides

Fig. 7. Type species of the Alophini genera. A–B: *Seidlitzia maroccana* (Fairmaire, 1868), Morocco, date and collector unknown, MNHN, image: Antoine Mantilleri, © MNHN, original image showing right lateral view was digitally flipped horizontally to appear as left; C–D: *Trichalophus didymus* (LeConte, 1854), Canada, British Columbia, Kitsumkalum Lake, 16.vi.1960, B.S.Heming, CNC; E–F: *Triglyphulus ater* (LeConte, 1876), USA, Idaho, Bear, 26.vii.1977, B.Carr, CNC; G–H: *Xeralophus cretaceus* (Reitter, 1894), Russia, Tyva, Kyzyl, 6.v.1974, B.A.Korotyaev, ZIN, image: Andrey Frolov. Scale: 2 mm.

the type series, four more specimens were later reported, all found dead in sandy steppe of the neighbouring Tyva Republic of Russia (Korotyaev 1992). Korotyaev (1992) hypothesised that this xerophilic taxon is phylogenetically nested within the predominantly mesophilic "*Alophus*" (= *Graptus*). This hypothesis, if corroborated, would render the name *Xeralophus* a junior subjective synonym of *Graptus*.

CONCLUDING REMARKS

It seems worthy of reiterating some important and perhaps not too obvious generalities emerging from this study. First, if the genus *Trichalophus* does exist in the phylogenetic sense, then its presence has been reconfirmed in Southwest China for the first time since Suvorov (1915). Second, the last glacial retreat is likely responsible for the

Fig. 8. *Pseudobarynotus laticeps* (Desbrochers, 1874), syntype, MNHN, image: Antoine Mantilleri, © MNHN.

present day high altitude presence of *Trichalophus* in the high mountains of Yunnan and Sichuan, but not for the diversification of the lineages leading to the extant populations. Third, in spite of the large body size and relative ease of sampling, *Trichalophus* is among the least understood genera of the Holarctic weevils. Such neglect is partly due to the abundance of ambiguous historical species names, particularly in Central Asia, which creates a nomenclatorial impediment and hinders further research. Fourth, relationships of *Trichalophus* in Alophini, and the overall phylogenetic validity of this tribe and most of its genera (particularly *Plinthodes*, *Pseudobarynotus* and *Xeralophus*) remain untested. When adequately studied, however, the genus *Trichalophus* is expected to be of significant biogeographic potential, similarly to other clades of low-dispersing organisms most suitable to reveal the geographical component on their evolutionary past (Murienne et al. 2014; Tänzler et al. 2014; Toussaint et al. 2015).

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