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Subterranean species of *Anemadus* Reitter: systematics, phylogeny and evolution of the Chinese "*Anemadus smetanai*" species group (Coleoptera: Leiodidae: Cholevinae: Anemadini)

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Abstract

The "*Anemadus smetanai*" species group (Coleoptera: Leiodidae: Cholevinae: Anemadini) is revised. The species group is redefined, including *Anemadus smetanai* Růžička, 1999, *A. kabaki* Perreau, 2009 from China: Sichuan province and five new species: *A. grebennikovi* sp.n. (Yunnan province: Jizu Shan Mts.), *A. haba* sp.n. (Yunnan province: Haba Xue Shan Mt.), *A. hajeki* sp.n. (Yunnan province: Cang Shan Mt., Yulong Xue Shan Mts.), *A. imurai* sp.n. (Sichuan province: Mt. Mianya Shan) and *A. tangi* sp.n. (Xizang autonomous region: Linzhi county). The species of this group show gradual morphological modifications linked to their endogean life. The conditions of this subterranean evolution and the link with high altitudinal biotopes are discussed. A phylogenetic analysis based on morphological characters is presented. A key for identification of species is provided and the geographical distributions of the seven species are mapped. A new synapomorphy (female genital annulus) is presented. It may provide a significant tool to understand the phylogeny of the Anemadini.

Key words

Coleoptera, Leiodidae, phylogeny, taxonomy, new species, morphology, microphthalmy, anophthalmy, China, Palaearctic region.

1. Introduction

1.1. The subtribe Anemadina and the genus *Anemadus*

The tribe Anemadini contains four subtribes (Anemadina, Paracatopina, Nemadina and Eunemadina) and is believed to be the least derived tribe of the Leiodidae: Cholevinae (Newton 1998; Perreau 2000); however, no formal phylogenetic analysis, morphological or molecular, has ever been performed on the subtribes of Anemadini. The monophyly of the subtribe Anemadina is presently weakly supported. Newton (1998: 102) in a key to subtribes of Anemadini listed only two characters to separate Anemadina from Nemadina + Eocatopina: (1) male mesotarsus with basal two tarsomeres dilated in Anemadina (with at most one basal tarsomere dilated in the other two subtribes); and (2) epistomal suture present in Anemadina (usually absent in the other two subtribes). However, these characters are highly homoplastic in other subfamilies of Leiodidae.

Anemadina contains four genera, two of them are Oriental (*Anemadiola* Szymczakowski, 1963 with four species, *Cholevodes* Portevin, 1928 with a single species), one is western Palaearctic (*Speonemadus* Jeannel, 1922 with 12 species in Western Europe and Northern Africa), and *Anemadus*, with 44 species, is widely distributed throughout the Palaearctic region (Giachino & Vailati 1993; Perreau 2000, 2002, 2004, 2009, 2015, 2016; Giachino et al. 2013; Wang & Zhou 2016; Reboleira et al. 2017). After a general revision by Giachino & Vailati (1993), three additional species were described by Giachino & Vailati (2000) and Giachino et al. (2013) from Greece, Turkey and Syria, an additional nine species were described from Nepal, China, Taiwan and Japan (Perreau 1996, 2002, 2004, 2009; Růžička 1999), one species was synonymized by Perreau (2004), and four recently added (Wang & Zhou 2016; Perreau 2016).

The genus *Anemadus* Reitter, 1884 is divided into 12 species groups (Giachino & Vailati 1993; Perreau 2000), three of which are endemic to the Oriental region. The "*asperatus* species group" contains six species distributed along the Himalayan ridge, in India (*A. kuluensis* (Champion, 1927): Himachal Pradesh; *A. asperatus* Champion, 1923: Uttaranchal and Meghalaya); Pakistan (*A. besucheti* Giachino & Vailati, 1993: Chitral); Nepal (*A. weigeli* Perreau, 2004: Kathmandu); China (*A. turnai* Perreau, 2016: Henan); and one Japanese species: *A. nipponensis* Perreau, 1996. The "*taiwanus* species group" (Perreau 2000, 2002, 2004) from mainland China and Taiwan has recently been revised (Wang & Zhou 2016) and presently contains seven species. The third: the "*smetanai* species group" is the subject of this paper. Presently, it contains two species: *A. smetanai* Růžička, 1999 and *A. kabaki* Perreau, 2009. We describe here five new species from the Sichuan and Yunnan provinces and the Xizang autonomous region (= Tibet). The group is redefined, a key to identification of its members is provided, and a phylogenetic analysis based on morphological characters is presented. The distribution of all species is summarized and mapped. All the species of this group show morphological modifications generally linked to subterranean biotopes.

1.2. Subterranean evolution

Subterranean organisms are those living underneath the surface of Earth; in subterranean space from large caves to close fissures (microvoids) and in the superficial subterranean habitats (also called *mesovoid shallow substratum* or *milieu souterrain superficiel*, MSS) (Camacho 1992; Giachino & Vailati 2010; Romero 2009). MSS sometimes plays the role of an ecotone in which both epigean and truly subterranean organisms occur (Gers 1998).

Biospeologists have been fascinated by morphological modifications of these organisms, present in diverse groups of beetles (e.g., Juberthie & Decu 1998). Christiansen (1962) introduced the term troglomorphy to describe both regressive and progressive evolutionary features associated with cave life. Much controversy is associated with regressive modifications; several hypotheses try to explain their mechanisms. Most recent studies have invoked either an increase in the number of neutral genes having a disruptive and/or reductive effect on functionless organs or associative selection (Christiansen 2005).

Generally, terminology describing ecological classification of subterranean organisms is quite confusing and sometimes controversial (see review of its historical and current development in Sket 2008 and Ortuño et al. 2014). Here we follow White & Culver (2012) and Solodovnikov & Hansen (2016), simply using "hypogean" to describe species adapted to crevices (from microvoids to large caves) as opposed to "endogean" which means adapted to life "within soil." Endogean and hypogean beetles are often characterized by reduction in the size of the eyes (microphthalmy to anophthalmy), reduction to absence of metathoracic wings and reduction of pigmentation. The reduction of wings in ground and carrion beetles has been discussed in a general evolutionary context (Darlington 1943, 1971; Brandmayr 1991; Kavanaugh 1985; Ikeda et al. 2008, 2012). These adaptations clearly developed independently many times in Coleoptera, and also in some soil and leaf litter living groups. For example, significant recent treatments have been provided for the following groups: Carabidae (e.g. Jeannel 1926; Darlington 1943, 1971; Brandmayr 1991; Kavanaugh 1985; Sokolov et al. 2004; Ortuño & Gilgado 2011; Sokolov 2013; Às Vanin 2014), Dytiscidae (e.g., Balke et al. 2004; Watts & Humphreys 2006; Miller et al. 2013), Elmidae (e.g., Hayashi et al. 2013), Agyrtidae (e.g., Newton 1997), Staphylinidae (e.g., Thayer 1992; Assing 2001, 2002, 2006, 2012, 2013; Ferro & Carlton 2010; Park & Carlton 2013; Peng et al. 2013; Jałoszyński 2015), Silphidae (e.g., Ikeda et al. 2008, 2012), Bothrideridae (e.g., Dajoz 1977), Limnichidae (e.g., Hernando & Ribera 2003), Tenebrionidae (e.g., Aalbu & Andrews 1985; Schawaller 2001), and Curculionidae (e.g., Gilbert & Howden 1987; Howden 1992; Grebennikov 2010).

Leiodidae are exceptionally successful in the colonisation of subterranean habitats. Taxa with morphological modifications to subterranean environments (eye and/or wing reduction, depigmentation of the cuticle, etc.) occur in most of the six subfamilies: all species of Catopocerinae are anophthalmous (Peck 1975; Perreau & Růžička 2007; Peck & Cook 2011); Coloninae: *Colon* Herbst, 1797 (Nishikawa 2010); Leiodinae: *Agathidium* (Angelini & De Marzo 1986a,b; Hoshina 2000; Hoshina et al. 2003; Miller & Wheeler 2005; Švec 2012), *Zelodes* Leschen, 2000 (Leschen 2000); Cholevinae: Anemadini: *Dissochaetus* Reitter, 1885 (Jeannel 1936), *Mesocolon* Broun, 1911 (Jeannel 1936), *Speonemadus* Jeannel, 1922 (Giachino & Vailati 1993), Cholevini: *Apterocatops* Miyama, 1985 (Miyama 1985; Harusawa 2005), *Catops* Paykull, 1798 (Peck & Cook 2002), *Choleva* Latreille, 1796 (Růžička & Vávra 2003; Bordoni 2005), *Cholevinus* Reitter, 1901 (Jeannel 1936; Perkovsky 1999), *Dzungarites* Jeannel, 1936 (Jeannel 1936), *Rybinskiella* Reitter, 1906 (Frank 1988; Lafer et al. 2001), Eucatopini: *Eucatops* Portevin, 1903 (Szymczakowski 1963; Peck & Cook 2005), Leptodirina: all genera except one (Jeannel 1924), Oritocatopini: *Oritocatops* Jeannel, 1921 (Jeannel 1964), Ptomaphagini: *Adelopsis* Portevin, 1907 (Jeannel 1936), *Proptomaphaginus* Szymczakowski, 1969 (Peck 1973a), *Ptomaphagus* Hellwig, 1795, *P.* (*Adelops*) Tellkampf, 1844 (Peck 1968, 1973a,b, 1977, 1978, 1979; Peck & Gnaspini 1997; Peck & Wynne 2013; Friedrich 2013), *P.* (*Appadelopsis*) Gnaspini, 1996 (Peck 1979) and *Ptomaphagus* s.str. (Blas & Vives 1983; Nishikawa 1993), *Ptomaphaginus* Szymczakowski, 1969 (Peck 1981), Sciaphyini: *Sciaphyes* Jeannel, 1910 (Perkovsky 1989; Hoshina & Perreau 2008; Fresneda et al. 2011).

Some species of *Anemadus* are known to be associated with cave environments, such as *Anemadus leonhardi* Reitter, 1904 in the Balkans and *Anemadus lucarellii* Giachino, Latella & Vailati, 2013 in Turkey. Currently, both species have been recorded mainly from caves (Giachino & Vailati 1993; Giachino et al. 2013; Perreau 2016). However, these species are winged and have fully developed eyes. The first depigmented, apterous and microphthalmous species of the genus: *A. smetanai* was described by Růžička (1999). The "*smetanai* species group" was subsequently introduced to accommodate this species (Perreau 2000). More recently, Perreau (2009) described *A. kabaki*, an anophthalmous species sharing many morphological characters with *A. smetanai* (not only those linked to subterranean evolution). The remarkable characters of these species appear to be shared by the five additional species described here, and are the basis of a morphological phylogenetic analysis that supports the monophyly of this group. Moreover, we observe a new apomorphic character shared by all genera of Anemadina which may be useful in phylogenetic analyses of Anemadini.

2. Material and methods

2.1. Microscopic observations

Male genitalia were cleaned in a hot 10% KOH solution, and embedded in Euparal or DMHF for permanent mounts on microslides. Female genital segments were cleaned in hot 10% KOH solution, stained with a diluted ethanolic solution of Azoblack (Carayon 1969) and embedded in DMHF for permanent mounts on microslides. Photographs of genitalia were taken using a Spot Insight IN1820 camera attached to a Leitz Diaplan microscope. Habitus photographs were taken using a Canon macro photo lens MP-E 65mm on a Canon 550D. Multiple layers of focus were combined using Zerene Stacker 1.04 (http://www.zerenesystems.com/cms/stacker) for the habitus images, and Helicon Focus 4 (http://www.heliconsoft.com/heliconsoft-products/helicon-focus/) for the genital slide preparation images. High resolution photonic pictures of the external morphology of the pronotum and elytra were taken with a Keyence VHX5000 microscope with a VH-Z250T lens. High resolution electronic pictures of external morphology were taken using the Hitachi S-3700N environmental electron microscope at the National Museum, Praha.

2.2. Measurements

External morphological characters were measured using cellSens Entry 1.6 (Olympus, Tokyo, Japan) with a DP73 camera attached to Olympus SZX16 stereomicroscope. Length of pronotum was measured along the median line (as posterior angles are slightly prolonged in some species); length of elytra was measured from the posterior margin of the scutellum to the tip of the elytra in dorsal view. Total body length was measured from the anterior margin of the labrum (with head in extended position) to the apex of elytra.

2.3. Distribution maps

The distribution map was produced and edited in ESRI ArcMap 10.2 of ArcGIS Desktop 10.2 suite. For map layers, free level 0 and level 1 data from Global Administrative Areas (http://www.gadm.org/world) and the World Shaded Relief (goo.gl/Nv15HR) with 60% transparency over the GEBCO08_hillshade (goo.gl/KRku0x) were used.

2.4. Phylogenetic analysis

Phylogenetic analyses were performed using a matrix (Table 1) comprising seven terminal taxa of the ingroup with two additional taxa for the outgroup, and 31 characters (23 of which are parsimony informative) based on external adult morphology. The matrix was compiled in WinClada version 1.00.08 (Nixon 2002), and analysed by exhaustive search ("implicit enumeration" option) of maximum parsimony approach using TNT ver. 1.1 (Goloboff et al. 2008). Standard bootstrap analysis (with 1000 replicates) was executed in TNT; tree visualization and character mapping were done in WinClada. Character 5 was retained in the matrix, although it was finally treated as inactive in both analyses, because of its potential significance for the forthcoming phylogenetic analysis of *Anemadus*.

Presently, there is no phylogenetic hypothesis available for the 44 species of *Anemadus*. The division of this genus into 12 species groups (Giachino & Vailati 1993) is based on pre-Hennigian classification. Cladistic analysis of this group is under development (M. Perreau unpubl. data). The two species used as outgroups in the present analyses were selected to represent two large Western Palaearctic species groups: *Anemadus strigosus* (Kraatz, 1852), the type species of *Anemadus*, belonging to the "*strigosus* species group" (containing 6 species); and *A. acicularis* (Kraatz, 1852), belonging to the "*acicularis* species group" (containing 7 species).

Two analyses were performed. Analysis 1 contains most of the characters, with only character 5 treated as inactive (because it could be evolutionarily linked with character 8). All characters were equally weighted and most of multi-state characters were treated as unordered. The only exception was character 1, which was treated as ordered, since its states probably represent a transformation series.

Analysis 2 was run on modified character set, with characters 1 – 9 treated as inactive. This analysis is intended to test homoplasy of these derived character states as a result of parallel/convergent evolution in geographically isolated lineages. Most of these character states represent regressive modifications, possibly linked with subterranean life style of members of this species group. The remaining characters represent a potentially unique synapomorphy of this group within *Anemadus* (character 10, but see discussion below) and characters on male and female abdominal terminalia and genitalia (characters 11 – 31), which are probably less influenced by their ecology.

2.5. Abbreviations and labelling

The following abbreviations are used for collections (curators names are given between parentheses): **BMNH** – Natural History Museum, London, United Kingdom (M.V.L. Barclay); **JRUC** – collection of Jan Růžička, Praha, Czech Republic; **JVAC** – collection of Jiří Vávra, Ostrava, Czech Republic; **MHNG** – Muséum d'histoire naturelle, Genève, Switzerland (G. Cuccodoro, I. Löbl); **MNHN** – Muséum national d'Histoire naturelle, Paris, France (A. Taghavian); **MNIC** – collection of M. Nishikawa, Ebina, Japan; **MPEC** – collection of Michel Perreau, Paris, France; **MSCC** – collection of Michael Schülke, Berlin, Germany; **NMPC** – Národní muzeum, Praha, Czech Republic (M. Fikáček, J. Hájek); **NSMT** – National Museum of Nature and Science, Tsukuba-shi, Ibaraki, Japan (S. Nomura); **OUMNH** – Oxford University Museum of Natural History, Oxford, England (D.J. Mann); **RMNH** – Naturalis Biodiversity Center, Leiden, The Netherlands (M. Schilthuizen); **SHNU** – Department of Biology, Shanghai Normal University, Shanghai, China (L. Tang); **ZMHB** – Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany (J. Frisch).

Specimens of the newly described species are provided with one red printed label "HOLOTYPE or PARATYPE (male or female symbol) / [*Name of the taxon*] sp. nov. / Jan Růžička et Michel / Perreau det. 2015". Exact label data are cited for all material. Separate lines on labels are indicated by "/", separate labels by "//". Author's remarks and comments are enclosed in square brackets, [p] – preceding data are printed.

The following abbreviations are used throughout the text: **HT** – holotype; **PT** – paratype; **a7** – **a10** – antennomeres 7 to 10; **ap** – apodeme; **co** – coxite; **ee** – elytral epipleuron; **en** – endophallus; **ga** – genital annulus; **hr** – humeral region of elytron; **ml** – median lobe; **os** – outer seta; **pa** – paramere; **pl9** – pleurite 9; **pla9** – apex of pleurite 9; **set** – setation; **sv** – spiculum ventrale; **t2** – **t10** – tergites 2 to 10; **v4** – **v8** – ventrites 4 to 8. Morphological terminology generally follows Lawrence & Ślipiński (2013).

2.6. Morphological terminology of female genitalia

There are basically two concepts of homologies concerning the terminology of female genital sclerites (belonging to abdominal segments 9 and 10) of beetles. According to Tanner (1927), followed by many specialists (Naomi 1989; Lawrence et al. 2011; Lawrence & Ślipiński 2013), the dorsal sclerite (when a single one occurs) of the female genitalia is tergite 10, and the two lateral sclerites, anteriorly apposed to the appendicular parts, are lateral parts of a presumably longitudinally divided tergite 9. In the second interpretation, according to Deuve (1993, 2001) the dorsal sclerite is tergite 9, and the lateral parts are epipleurites 9 (that is belonging to the pleural field and not the tergal one). Certainly the latter has been deduced from detailed (and strongly argued) investigations of Caraboidea and a transposition *ipso facto* to Staphylinoidea is not obvious. However it appears that the plesiomorphic state of female genitalia of Caraboidea is clearly similar to that of basal lineages of Scarabaeoidea (Dupuis 1991) and also of Staphylinoidea (Agyrtidae, Leiodidae, Silphidae …). So there is no reason why homologies should be different. For this reason, the second concept has been used in many works on Leiodidae. Nevertheless, to allow a more direct comparison with other works on Staphylinoidea, we will follow here the practice of most of specialists (Naomi 1989; Lawrence et al. 2011) and follow Tanner's nomenclature.

3. Phylogeny

3.1. Characters

Thirty-one characters are used for the seven taxa of the "*smetanai* species group". The list of characters is given below, illustrated in Figs. 1–114. The resulting matrix of characters is given in Table 1.

1. Eye size and development: (0) large, with hemispherical arrangement of > 130 distinct facets (Fig. 89); (1) minute, with hemispherical arrangement of 15–10 distinct facets (Figs. 85, 86); (2) minute, with flat or even concave arrangement of < 15–10 facets, which are hard to distinguish (Figs. 81–84); (3) absent, without any trace of facets (Figs. 87, 88).

2. Antenna, length: (0) short, with antennomere 8 slightly to distinctly transverse, ca. 0.4–0.9× as long as wide (Figs. 14–15, 110–111); (1) elongate, with antennomere 8 ca. 2.0× as long as wide (Fig. 17).

3. Pronotum shape: (0) transverse, flat, widest posteriorly (Fig. 6); (1) flat, widest at basal third (Giachino & Vailati 1993: 83, fig. 149); (2) slightly to distinctly cordate, regularly convex, widest behind the mid-length (Figs. 1–5); (3) reduced, trapezoidal to subquadrate, widest at mid-length, significantly narrower than elytra (Figs. 7, 8, 114).

4. Pronotum and elytra setation: (0) short, recumbent (Figs. 112–113); (1) longer, semierect (set, Fig. 114).

5. Elytra, coalescence: (0) each elytron free, independently movable (Fig. 6); (1) elytra coalescent, joined also with scutellum (e.g., Figs. 5 and 8).

6. Elytra, humeral region in dorso-lateral view: (0) laterally distinctly expanded, prominent to a sharp carina (Fig. 112); (1) laterally only slightly expanded, more rounded (Fig. 113); (2) not expanded, distinctly rounded (Fig. 114).

7. Elytra, elytral epipleuron in lateral view: (0) narrow (Fig. 9); (1) wide (Fig. 10).

8. Metathoracic wings: (0) fully developed, functional; (1) absent.

9. Abdominal tergites 2 to 6: (0) normally sclerotized, visible (Fig. 72); (1) very weakly sclerotized, transparent (Fig. 73).

10. Abdominal ventrites 4 to 7: (0) antero-lateral part simple (Fig. 13); (1) laterally with anteriorly developed pair of rectangular apodemes, which are overlapping with latero-posterior parts of adjacent antecedent segment (ap, Figs. 11, 12).

Male terminalia

11. Tergite 8, anterior margin in dorsal view: (0) prominent, rounded medially, emarginated laterally (Fig. 45); (1) simply transverse medially, regularly rounded laterally (Figs. 75, 76).

12. Tergite 8, posterior margin in dorsal view: (0) weakly notched (Fig. 45); (1) regularly rounded (Fig. 75), (2) truncate (Fig. 76).

13. Ventrite 8 medially, in ventral view: (0) narrow, widely notched anteriorly and prominent posteriorly (Fig. 46); (1) wide, regularly arched on both anterior and posterior margin; (2) narrow, regularly arched on both anterior and posterior margin (Figs. 74, 77).

14. Tergum 9 of genital segment: (0) apex triangular (Figs. 44, 53); (1) apex regularly rounded (Figs. 47–50); (2) apex truncate (t9 with arrow, Fig. 52).

15. Pleurites 9 of genital segment in ventral view, base: (0) widely joined posteriorly (Giachino & Vailati 1993: 160, fig. 288; arrow, Fig. 54); (1) only in narrow contact (Figs. 47–52).

16. Pleurite 9 of genital segment in ventral view, apex: (0) wide, regularly rounded (Giachino & Vailati 1993: 160, fig. 288; Fig. 54); (1) wide, emarginate on medial margin (Giachino & Vailati 1993: 85, fig. 156; pla9 with arrow, Fig. 53); (2) narrower, truncate or subtruncate (Figs. 47–51); (3) narrow, sharply pointed (pla9 with an arrow, Fig. 52).

17. Median lobe, shape in dorsal view: (0) robust, compact, 3.5–3.8× as long as wide (Giachino & Vailati 1993: 160–161, figs. 283–284, 289–291; Figs. 18, 20, 28, 36); (1) slender, elongate, around 4.5× as long as wide (Figs. 22, 31).

18. Median lobe, length/width ratio of basal part in ventral view: (0) 2.7; (1) 2.0; (2) 1.3–1.6.

19. Median lobe, apex in lateral view: (0) prolonged short, knob-like tip (Giachino & Vailati 1993: 85, figs. 154–155; 160, fig. 285); (1) straight, narrow point (Figs. 19, 21); (2) robust, obtuse tip (Fig. 23); (3) prolonged into dorsally bent tip (Figs. 29, 30, 37).

20. Median lobe, shape and structure of endophallus: (0) baso-medial sclerotized structures divided into two parts, more or less overlapping: basal one, consisting of two parallel differentiated rows of weak or strong teeth, and median one, consisting of two parallel phanerae of undifferentiated spines (Giachino & Vailati 1993: 85, fig. 151; 160, figs. 283–285; Figs. 30–31, 40, 42); (1) two baso-medial parallel rows of strong teeth, not differentiated into two parts (Figs. 28–29, 36–37); (2) two medio-apical rows of moderately developed teeth, basally joined with larger, oval teeth (Figs. 18–21); (3) uniformly dispersed, weak, undifferentiated spines (Figs. 22–23).

21. Paramere, proportion in dorsal view: (0) wide basally, narrowed near the base (before 1/4 of its length) (Figs. 18, 20, 22, 40, 42); (1) wide basally and around midlength, narrowed only in apical half (Fig. 28, 31, 36).

22. Paramere, subapical modifications of apex: (0) without or with indistinct subapical constriction in dorsal view; straight in lateral view (Giachino & Vailati 1993: 85, figs. 151, 154; Perreau 2009: 8, fig. 10; Figs. 18, 20, 22, 31, 40, 42); (1) with a clear subapical constriction in dorsal view; sinuate in lateral

Table 1. Morphological data matrix for the phylogenetic analysis of the "*smetanai* species group".

Species / Character	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**
A. strigosus (outgroup)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
A. acicularis (outgroup)	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	2	1	0	0	0	0	1	0
A. grebennikovi sp.n.	2	0	2	0	1	1	0	1	1	1	1	1	2	1	1	2	0	2	1	2	0	0	3	1	1	1	1	0	0	0	0
A. haba sp.n.	2	0	2	0	1	1	0	1	1	1	?	?	?	1	1	1	0	2	3	1	1	1	2	2	0	1	1	1	0	1	1
A. hajeki sp.n.	2	0	2	0	1	1	0	1	1	1	1	1	2	1	1	2	0	2	1	2	0	0	3	2	1	1	1	0	0	0	0
A. imurai sp.n.	3	0	3	1	1	2	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	1	1
A. kabaki Perreau, 2009	3	1	3	1	1	2	1	1	1	1	1	1	1	1	1	2	1	2	2	3	0	0	3	2	0	1	1	0	1	1	1
A. smetanai Růžička, 1999	1	0	2	0	1	1	0	1	1	1	1	1	2	1	1	2	0	2	3	1	1	1	2	2	0	1	2	1	0	0	1
A. tangi sp.n.	1	0	2	0	1	1	0	1	1	1	1	2	2	2	1	3	1	2	3	0	1	0	2	2	0	1	2	0	0	0	1

view (Růžička 1999: 625, figs. 6, 7; Figs. 28–29, 36–37).

23. Paramere, shape of apex in dorsal view: (0) reversed outwards into rounded point (Giachino & Vailati 1993: 160, fig. 286; Figs. 42, 43); (1) widely bent inwards into flattened, regularly rounded apex (Giachino & Vailati 1993: 85, fig. 152; Figs. 40, 41); (2) nearly straight, slightly convergent inwards at the apex, not thickened, the apical setae pointed inwards in orthogonal position (Figs. 32, 34, 38); (3) nearly straight, slightly convergent inwards at the apex, thickened, the apical setae pointing inwards in oblique position (Figs. 22, 24, 26).

24. Paramere, configuration of setae in dorsal view: (0) small, but distinct outer seta is present (Giachino & Vailati 1993: 160, fig. 286; Fig. 43); (1) minute apical outer (external) seta is present (Fig. 24); (2) outer seta is absent (Růžička 1999: 625, fig. 7; Figs. 22, 26, 32, 34, 38).

25. Paramere, relative length compared to length of median lobe: (0) moderately longer than the median lobe of the aedeagus (Giachino & Vailati 1993: 160–161, figs. 283, 284, 289–291; Figs. 22, 23, 28–31, 36, 37); (1) significantly longer than the aedeagus (Giachino & Vailati 1993: 85, figs. 151, 154–155; Figs. 18–21, 40, 42).

26. Basal lobe and median lobe of aedeagus, length: (0) similar length (Figs. 40, 42); (1) basal lobe distinctly shorter than median lobe (Figs. 18, 20, 22, 28, 31, 36).

Female terminalia

27. Ventrite 8, shape of spiculum ventrale: (0) with convergent sides, widely triangular (Fig. 62); (1) with parallel sides, narrow (ca. 1/4 of width of ventrite) (Figs. 55–59); (3) with divergent sides, wide (ca. 1/2 of width of ventrite) (Figs. 60, 61).

28. Ventrite 8, posterior margin: (0) regularly rounded (Figs. 55, 57–59, 62); (1) widely truncate (Růžička 1999: 625, fig. 9; Figs. 56, 60).

29. Tergite 10, posterior margin: (0) regularly rounded, with setae of fairly uniform size regularly dispersed (Figs. 63–68, 71, 109); (1) truncate, with one large pair of setae and several small setae only laterally (Fig. 69).

30. Coxite, ventral view: (0) basal seta absent (Figs. 64–67, 70, 71); (1) basal seta present (Figs. 63, 68, 69).

31. Genital annulus: (0) small: diameter < 1/3 of the maximal width of the tergite 10 (Figs. 63–65, 67): (1) large: diameter ≥ 2/3 of the maximal width of the tergite 10 (Figs. 66, 68–71).

3.2. Result of analyses

Analysis 1 (with only character 5 inactive) resulted in a single most parsimonious tree with a length of 56 steps (consistency index = 0.87, retention index = 0.82) (Fig. 124). The analysis supports the "*smetanai* species group" as monophyletic (with bootstrap of 100), based on derived states of 14 characters. Within the group, *A. grebennikovi* sp.n. and *A. hajeki* sp.n. were recovered as a clade (without significant support) based on three characters (1-2, 19-1, 20-2; the former being homoplasious). The remaining five species form another clade (with bootstrap of 66) based on two characters (25-0, 31-1). Within this clade, *A. imurai* sp.n. and *A. kabaki* form a subclade (bootstrap = 99) based on five characters (1-3, 3-3, 4-1, 6-2, 30-1; the latter being homoplasious), and *A. tangi* sp.n. + (*A. haba* sp.n. + *A. smetanai*) form another subclade (without significant support), based on three characters (19-3, 21-1, 23-2). Here, *A. haba* sp.n. + *A. smetanai* form another subclade (with weak bootstrap of 51) based on three characters (20-1, 22-1, 28-1).

Analysis 2 (with characters 1–9 inactive) resulted also in a single most parsimonious tree, with identical branching pattern as in Analysis 1. Resulting tree has a length of 45 steps (consistency index = 0.77, retention index = 0.75) (Fig. 125). The analysis also supports the "*smetanai* species group" as monophyletic (bootstrap = 100), based on derived states of 10 characters. Within the group, *A. grebennikovi* sp.n. and *A. hajeki* sp.n. were recovered as a clade (bootstrap = 65) based on two characters (19-1, 20-2). The remaining five species form again another clade (bootstrap = 95) based on the same two characters as in Analysis 1. Within this clade, *A. imurai* sp.n. and *A. kabaki* form a subclade (bootstrap = 85) based on a single homoplasious character (30-1). *Anemadus tangi* sp.n. + (*A. haba* sp.n. + *A. smetanai*) form another subclade (with weak bootstrap of 55) based on the same three characters as in Analysis 1. Here, *A. haba* sp.n. + *A. smetanai* form again another subclade (bootstrap = 85) based on the same three characters as in Analysis 1. Generally, the bootstrap support of the tree in Analysis 2 is higher in most nodes than in Analysis 1. The phylogenetic hypothesis presented here probably fits better the natural relationships of these species, being less influenced by homoplasies caused by convergent evolution of independent lineages.

4. Ecology

Most of the species of this group inhabit deep litter and perhaps soil in the upper forest and lower alpine zones with an altitude between 2700–4100 m, with ca. 3800 m being optimal (V.V. Grebennikov pers. comm.). They are mostly collected by sieving, sometimes individually under large rocks (V.V. Grebennikov pers. comm., I.I. Kabak pers. comm.) or using baited pitfall traps.

5. Taxonomy

5.1. Diagnosis of the "*smetanai* species group"

Adults of the species belonging to this species group can be characterized as follows: (1) Head microphthalmous or anophthalmous (Figs. 81–88). (2) Elytra coalescent, joined also with scutellum. (3) Elytra with humeral region laterally only slightly or not expanded, more rounded or fully rounded in dorso-lateral view (Figs. 9, 10). (4) Elytral surface with only fine transverse microsculpture or glabrous (only in *A. imurai* sp.n.). Punctures granulate, arranged into transverse, irregular rows (elytral type "a" according to Giachino & Vailati 1993: 31, fig. 56a). (5) Metathoracic wings absent. (6) Abdominal tergites 2 to 6 very weakly sclerotized, transparent (Fig. 73; cfr. Fig. 72 for more distinctly sclerotized tergites in *A. acicularis*). (7) Abdominal ventrites 4 to 7 laterally with anteriorly developed pair of rectangular apodemes, which are overlapping with lateroposterior parts of adjacent preceding segment (Figs. 11, 12). Surface of ventrites with very fine setation. (8) Ventrite 8 with pair of short, lateral apodemes (Fig. 77). *Male*. (9) Pleurites 9 of genital segment in narrow contact at base in ventral view (Figs. 47–52). (10) Median lobe of aedeagus in ventral view with short and robust basal part, its width/length ratio ca. 1.3–1.6.

5.2. Diagnosis and (re-)description of species

Anemadus grebennikovi **sp.n.**
(Figs. 1, 18, 19, 24, 25, 47, 55, 65, 81, 91, 92, 122)

Type locality. China: Yunnan province, Jizu Shan, summit plateau, 37 km NE Dali, 25°58′30″N 100°21′36″E, 3150 m.

Type material. Holotype ♂ (MSCC, later will be deposited in ZMHB): 'CHINA: Yunnan [province], Dali Bai Aut. Pref., / Jizu Shan, summit plateau, 37 km NE Dali, 25°58′30″N, 100°21′36″E, / 3150 m, mixed forest, sifted from litter, / moss & mushrooms, 5.IX.2009, / leg. M. Schülke (CH09-28) [p]'. Paratypes: 4 ♂♂, 5 ♀♀ (JRUC, MPEC, MSCC): same data as holotype; 3 ♀♀ (RMNH – voucher specimen to DNA isolates No. RMNH.INS.63348): 'P. R. CHINA, Yunnan [province], / Jizu Shan, N25°58′ / 39″ E100°21′14″, / 28.vi.2011, 3216m, / sift27, V. Grebennikov [leg.] [p]'.

Description. ***Measurements*****:** Total body length 2.53–2.80 mm in males (2.78 mm in HT) and 2.46–2.87 mm in females, maximum body width 1.10–1.30 mm in males (1.23 mm in HT) and 1.13–1.33 mm in females. Pronotum 1.55–1.59× as wide as long in males (1.55× in HT), 1.49–1.60× in females. Pronotum 1.90–2.20× as wide as head in males (1.93× in HT), 1.90–2.10× in females. Elytra 1.29–1.39× as long as wide (1.30× in HT) and 0.97–1.06× as wide as pronotum (1.06× in HT) in males; 1.22–1.35× as long as wide and 1.06–1.09× as wide as pronotum in females. ***External morphology*****:** Pronotum and elytra with short, recumbent, yellow setation. Head, pronotum and elytra with distinct, transverse microsculpture, more dense on elytra (Figs. 81, 91, 92). Eye minute, with flat or even concave arrangement of < 15 facets, which are hard to distinguish (Fig. 81). Antenna short, with antennomere 8 slightly transverse, ca. 0.8× as long as wide. Pronotum cordate, regularly convex, widest behind the mid-length (Fig. 1). Elytra with humeral region only slightly expanded laterally, more rounded in dorso-lateral view (Fig. 1). Elytral epipleuron narrow in lateral view. ***Male terminalia*****:** Posterior margin of tergite 8 regularly rounded in dorsal view. Ventrite 8 medially narrowed, regularly arched on both anterior and posterior margin in ventral view. Tergum 9 of genital segment with apex regularly rounded (Fig. 47). Pleurite 9 with truncate apex in ventral view (Fig. 47). Aedeagus. Length of median lobe 0.14 mm, length of median lobe with parameres 0.17 mm (both in HT). Ratio of apical/basal part of median lobe 1.88. Ratio of length/width of basal part of median lobe 1.33. Median lobe robust, compact in dorsal view (more robust than in *A. hajeki* sp.n.) (Fig. 18), apex with obtuse, narrow point in dorsal view (Fig. 18), robust in lateral view (Fig. 19). Endophallus with two medio-apical rows of moderately developed teeth, basally joined with larger, oval teeth (Fig. 18). Paramere wide basally, narrowed near the base (before 1/4 of its length) (Fig. 18); with indistinct subapical constriction in dorsal view; straight in lateral view (Figs. 18–19); apex nearly straight, slightly convergent inwards at the apex, thickened, the apical setae pointing inwards in oblique position (Fig. 24); more distinctly sclerotized and dorsally prominent than in *A. hajeki* sp.n. (Figs. 24–25), with two inner and two apical setae and one smaller outer seta (Fig. 24). ***Female terminalia***: Ventrite 8 with spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite, but slightly less elongate than in *A. hajeki* sp.n.), with anterior emargination (Fig. 55). Ventrite 8 with posterior margin regularly rounded (Fig. 55). Tergite 10 regularly rounded posteriorly, with setae of fairly uniform size regularly dispersed along posterior margin (Fig. 65). Coxite only with 3 subapical setae in ventral view (Fig. 65). Genital annulus diameter approximately 0.4 × width of tergite 10 (Fig. 65).

Differential diagnosis. *Anemadus grebennikovi* sp.n. is very similar to *A. hajeki* sp.n. (Fig. 120), both species can be differentiated from other species of the "*smetanai* species group" in males by the aedeagus with paramere distinctly longer than median lobe of aedeagus (Figs. 18, 20), apex of the paramere thickened in dorsal view (Figs. 24, 26), the endophallus of aedeagus with two medio-apical rows of moderately developed teeth, basally joined with larger, oval teeth (Figs. 18, 20). Females of both species are characterized by the ventrite 8 with posterior margin regularly rounded in combination with the spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite), with anterior emargination (Figs. 65, 67); genitalia with the female genital annulus small, approximately 0.4 × width of tergite 10 (Figs. 65, 67). *Anemadus grebennikovi* sp.n. differs from *A. hajeki* sp.n. by more robust shape of the median lobe of aedeagus in dorsal and lateral view (Figs. 18–19) and the apex of paramere more distinctly sclerotized and dorsally prominent (Figs. 24–25); aedeagus is more slender (Figs. 20–21) and apex of paramere is less sclerotized and less dorsally prominent (Figs. 26–27) in *A. hajeki* sp.n. In females, the ventrite 8 with spiculum ventrale is wider (Fig. 55) in *A. grebennikovi* sp.n., and more elongate (Fig. 57) in *A. hajeki* sp.n.

Etymology. Patronymic, named after Vasily V. Grebennikov (Ottawa, Canada), an enthusiastic coleopterist interested in many kinds of minute, mostly endogean beetles (Carabidae: *Antireicheia* Basilewsky, 1951; Ptiliidae: *Discheramocephalus* Johnson, 2007; Leiodidae: *Fusi* Perkovsky, 1989 and *Sciaphyes* Jeannel, 1910; Staphylinidae: *Pseudopsis* Newman, 1834; Curculionoidea: *Alaocybites* Meregalli & Osella, 2007 etc.), with great collecting skills, who sieved a substantial portion of *Anemadus* specimens on several high mountain localities in Yunnan.

Collecting circumstances. The new species was found in mixed forest; sifted from litter, moss and mushrooms (M. Schülke pers. comm.), or sifted in deciduous forest on the top (similar to Fig. 115), with trees not very large (V.V. Grebennikov pers. comm.).

Distribution. Presently known only from Jizu Shan Mt. in the north-western part of Yunnan province (Fig. 122).

Anemadus haba **sp.n.**
(Figs. 2, 11, 36–39, 48, 56, 66, 84, 93, 94, 109, 122)

Type locality. China, Yunnan province, Haba Xue Shan Mt., 27°21′20″N 100°06′36″E, 3826 m.

Type material. Holotype ♂ (MPEC, abdominal segments lost): 'China, Yunnan [province] / Haba Shan [Haba Xue Shan Mt.], N27°21′20″ / E100°06′36″ / 19.vi.2012, 3826 m / sift25, V. Grebennikov [leg.] [p]'. Paratypes: same data as holotype, 3 ♀♀ (JRUC, MPEC); Paratypes: 3 ♀♀ (MPEC, RMNH – voucher specimen to DNA isolates No. RMNH.INS.63350): same data as holotype; 1 ♀ (JRUC), same data, but 'N27°20′58″ / E100°05′20″ / 18.VI.2012, 4133 m / sift22, [p]'; 2 ♀♀ (JRUC, MPEC), same data, but 'N27°20′58″ / E100°05′58″ / 19.vi.2012, 4114 m / sift24, [p]'; 1 ♀ (MPEC), same data, but 'N27°20′58″ / E100°05′57″ / 27.vi.2012, 4120 m / sift33, [p]'; 4 ♀♀ (MPEC, RMNH – voucher specimen to DNA isolates No. RMNH.INS.63349), same data, but 'N27°21′01″ / E100°05′44″ / 28.vi.2012, 4072 m / sift45, [p]'; 2 ♀♀ (MPEC, RMNH – voucher specimen to DNA isolates No. RMNH.INS.63351), same data, but 'N27°22′05″ / E100°06′25″ / 28.vi.2012, 3272 m / sift 37, [p]'.

Description. ***Measurements***: Total body length 3.05 mm in male HT and 2.45–3.05 mm in females, maximum body width 1.32 mm in male HT and 1.16–1.31 mm in females. Pronotum 1.70 × as wide as long in male HT, 1.52–1.67 × in females. Pronotum 2.04 × as wide as head in male HT, 1.92–2.02 × in females. Elytra 1.42 × as long as wide and 1.10 × as wide as pronotum in male HT; 1.13–1.39 × as long as wide and 1.07–1.12 × as wide as pronotum in females. ***External morphology***: Pronotum and elytra with short, recumbent, yellow setation. Head and pronotum glabrous (Figs. 84, 93), elytra with fine, transverse microsculpture (Fig. 94). Eye minute, with flat or even concave arrangement of < 10 facets, which are hard to distinguish (Fig. 84). Antenna short, with antennomere 8 transverse to subquadrate, ca. 0.8–1.0 × as long as wide. Pronotum cordate, regularly convex, widest at the mid-length (Fig. 2). Elytra with humeral region only slightly expanded laterally, more rounded in dorsolateral view (Fig. 2). Elytral epipleuron narrow in lateral view. ***Male terminalia***: Abdominal segment 8 in the single male specimen lost, shape of posterior margin of tergite 8 and medial part of ventrite 8 unknown. Tergum 9 of genital segment with apex regularly rounded (Fig. 48). Pleurite 9 with subtruncate apex in ventral view (Fig. 48). Aedeagus. Length of median lobe 0.20 mm, length of median lobe with parameres 0.21 mm (both in HT). Ratio of apical/basal part of median lobe 1.65. Ratio of length/width of basal part of median lobe 1.47. Median lobe robust, compact in dorsal view (Fig. 36), apex prolonged into short, rectangular tip in dorsal view (but narrower than in *A. smetanai*) (Fig. 36). Endophallus with two baso-medial parallel rows of strong teeth, not differentiated into two parts (Fig. 36). Paramere wide basally and around midlength, narrowed only in apical half of its length (Fig. 36); with a clear subapical constriction in dorsal view; sinuate in lateral view (Figs. 36–37); apex nearly straight, slightly convergent inwards at the apex, not thickened, the apical setae pointed inwards in orthogonal position; with four or five setae, outer seta is missing (Figs. 38–39). ***Female terminalia***: Ventrite 8 with spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite), with anterior emargination (Fig. 56). Ventrite 8 with posterior margin truncate (Fig. 56). Tergite 10 regularly rounded posteriorly, with setae of fairly uniform size regularly dispersed along posterior margin (Figs. 66, 109). Coxite with one basal and three subapical setae in ventral view (Fig. 66). Genital annulus diameter approximately 0.8× width of tergite 10 (Fig. 66).

Differential diagnosis. *Anemadus haba* sp.n. is very similar to *A. smetanai* (Fig. 120), both species are characterized in males by the robust, compact median lobe of aedeagus (Figs. 28, 36), with a short apex, distinctly curved dorsally in lateral view (Figs. 29, 37); the endophallus is simple, with two baso-medial parallel rows of strong teeth, not differentiated into two parts (Figs. 28, 36); the paramere has the clear subapical constriction in dorsal view and is sinuate in lateral view (Figs. 28–29, 36–37). In females of both species, ventrite 8 has posterior margin truncate (Figs. 56, 60), and its spiculum ventrale has moderately deep anterior emargination (Figs. 56, 60). Both species differ in reduction of eyes: flat to concave arrangement of facets, which is hard to distinguish (Fig. 84) in *A. haba* sp.n., but with hemispherical arrangement of distinct facets (Fig. 85) in *A. smetanai*. In males, the apex of aedeagus in dorsal view is prolonged into narrower tip in dorsal view (Fig. 36) in *A. haba* sp.n. but is slightly wider (Fig. 28) in *A. smetanai*. In females, ventrite 8 has spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite) (Fig. 56) in *A. haba* sp.n., but with divergent sides, wide (ca. 1/2 of width of ventrite) (Fig. 60) in *A. smetanai*.

Etymology. Named after Haba Xue Shan Mt., the type locality of this species, noun in apposition.

Collecting circumstances. In Haba Xue Shan Mts. collected by sieving in pure *Rhododendron* forest, or from upper edge of mixed forest with *Rhododendron* (Fig. 118). The only exception was sample #37 (Fig. 119), which was mixed forest with markedly lower altitude than other Haba samples (V.V. Grebennikov pers. comm.).

Distribution. Presently known only from Haba Xue Shan Mts. in north-western part of Yunnan province (Fig. 122).

Anemadus hajeki **sp.n.**
(Figs. 3, 9, 15, 20, 21, 26, 27, 49, 57, 67, 73–75, 82, 83, 90, 95–99, 111, 113, 122)

Type locality. China: Yunnan province, 32 km N Lijiang, Yulong Xue Shan mountain range, Maoniuping (Yak meadows), 27°09.9′N 100°14.5′E, 3540 m.

Type material. Holotype ♂ (NMPC): '**CHINA:** Yunnan province, / 32 km N Lijiang, 16.–21.VI.2007, / Maoniuping (Yak meadows), / 27°09.9′N 100°14.5′E, 3540 m, / J. Hájek & J. Růžička leg. (Ch41) // baited pitfall traps (fish meat) / steep slope, wet mixed forest (with *Pinus*, *Abies*, / *Rhododendron*) [p]'. Paratypes: 6 ♂♂ (and additional 2 ♂♂ specimens with head and pronotum missing, not paratypes), 8 ♀♀ (BMNH, JRUC, MPEC, NMPC): same data as holotype; 2 ♂♂, 1 ♀ (JRUC): same data, but '16.VI. 2007 ... (Ch28) // sifted detritus, leaves and moss; [p]'; 1 ♂, 3 ♀♀ (JRUC, MSCC, MPEC):'CHINA: Yunnan [province], Dali Bai Aut. Pref. / Diancang Shan, pass 43 km NW Dali / 25°59′33.5″N, 99°52′12.5″E / 3104 m, pasture & shrubs, litter, / moss and mushrooms sifted, 23.VIII. / 2009, leg. M. Schülke (CH09-01)'; 5 ♂♂, 2 ♀♀ (JRUC, MPEC, RMNH – voucher specimen to DNA isolates No. RMNH. INS.63347): 'P.R. CHINA, Yunnan [province], E / slope Cangshan at Dali / N25°39′54.7″ E100°06′ / 04.5″, 19.v.2010, 3815m, / sifting 19, V. Grebennikov [leg.] [p]'; 2 ♀♀ (JRUC): same data, but 'N25°40′14.7″ E100°06′ / 12.0″, 17.v.2010, 3827m, / sifting 16 [p]'; 1 ♀ (JRUC): same data, but 'N25°40′01.9″ E100°05′ / 45.5″, 15.v.2010, 4063m, / sifting 13 [p]'.

Description. ***Measurements***: Total body length 2.47–2.72 mm in males (2.72 mm in HT) and 2.61–2.79 mm in females, maximum body width 1.06–1.19 mm in males (1.16 mm in HT) and 1.10–1.12 mm in females. Pronotum 1.59–1.60× as wide as long in males (1.60× in HT), 1.49–1.56× in females. Pronotum 1.94–2.06× as wide as head in males (2.06× in HT), 1.90–2.05× in females. Elytra 1.23–1.33× as long as wide (1.30× in HT) and 1.00–1.04× as wide as pronotum (1.04× in HT) in males; 1.33–1.38× as long as wide and 1.02–1.04× as wide as pronotum in females. ***External morphology***: Pronotum and elytra with short, recumbent, yellow setation (Fig. 113). Head and pronotum glabrous or with distinct transverse microsculpture (Figs. 82, 95 vs. 83, 97), elytra with fine or only extremely fine, transverse microsculpture (Figs. 96, 98–99, 113) (see variability below). Eye minute, with flat or even concave arrangement of <10 facets, which are hard to distinguish (Figs. 82, 83). Antenna short, with antennomere 8 slightly transverse, ca. 0.8× as long as wide (Fig. 15). Pronotum cordate, regularly convex, widest behind the mid-length (Fig. 3). Elytra with humeral region only slightly expanded laterally, more rounded in dorso-lateral view (Figs. 3, 113). Elytral epipleuron narrow in lateral view (Fig. 9). ***Male terminalia***: Posterior margin of tergite 8 regularly rounded in dorsal view (Fig. 75). Ventrite 8 medially narrowed, regularly arched on both anterior and posterior margin in ventral view (Fig. 74). Tergum 9 of genital segment with apex regularly rounded (Fig. 49). Pleurite 9 with subtruncate apex in ventral view (Fig. 49). Aedeagus. Length of median lobe 0.12 mm, length of median lobe with parameres 0.15 mm (both in PT). Ratio of apical/basal part of median lobe 1.80. Ratio of length/width of basal part of median lobe 1.46. Median lobe robust, compact in dorsal view (but more slender than in *A. grebennikovi* sp.n.) (Fig. 20), apex with obtuse, narrow point in dorsal view (Fig. 20), slender in lateral view (Fig. 21). Endophallus with two medio-apical rows of moderately developed teeth, basally joined with larger, oval teeth (Fig. 20). Paramere wide basally, narrowed near the base (before 1/4 of its length) (Fig. 20); without subapical constriction in dorsal view; straight in lateral view (Figs. 20–21); apex nearly straight, slightly convergent inwards at the apex, thickened, the apical setae pointing inwards in oblique position; less distinctly sclerotized, less dorsally prominent than in *A. grebennikovi* sp.n. (Figs. 26–27); with two inner and two apical setae, outer seta is missing (Figs. 26, 27). ***Female terminalia*:** Ventrite 8 with spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite, but slightly more elongate than in *A. grebennikovi* sp.n.), with anterior emargination (Fig. 57). Ventrite 8 with posterior margin regularly rounded (Fig. 57). Tergite 10 regularly rounded posteriorly, with setae of fairly uniform size regularly dispersed along posterior margin (Fig. 67). Coxite only with 3 subapical setae in ventral view (Fig. 67). Genital annulus diameter approximately 0.4× width of tergite 10.

Variability. This species is the only member of "*smetanai* species group" with considerable geographical variability: head and pronotum of specimens from Maoniuping (type locality) are glabrous (Figs. 82, 95, 113), those from Diancang Shan and Cang Shan are with distinct transverse microsculpture (Figs. 83, 97). However, structure of male and female genitalia seems to be identical at all three localities. We consider this as only intraspecific variability, linked probably with the isolation of the Yulong Xue Shan and Cang Shan mountain ranges.

Differential diagnosis. *Anemadus hajeki* sp.n. is very similar to *A. grebennikovi* sp.n. (Fig. 120). For differentiation of both species from other species of the "*smetanai* species group" and differences between them see treatment of *A. grebennikovi* sp.n. above.

Etymology. Patronymic, named after Jiří Hájek (Praha, Czech Republic), an entomologist with a special interest in different water beetle families (Torridincolidae, Dytiscidae, Callirhipidae, Eulichadidae etc.), to acknowledge a long-time friendship with the senior author, and to remember a joint collecting trip in Yunnan.

Collecting circumstances. The new species was collected at Maoniuping using pitfall traps and also sifted from wet mixed forest with dominant *Pinus*, *Abies* and *Rhododendron*, on steep slope with sparse herbal undergrowth and abundant mosses and lichens (Fig. 117). The locality was close to the upper edge of forest and adjacent pastures with yaks (*Bos grunniens* Linnaeus, 1766). Samples at Cang Shan Mt. were taken in the upper part of the forest zone and in *Rhododendron* forest at the lower part of the alpine zone (Fig. 116). Most of the specimens were sifted, but one or two specimens were collected by hand, turning over large boulders deeply embedded in the soil (V.V. Grebennikov pers. comm.).

Distribution. Presently known from a single locality in Yulong Xue Shan mountain range, and from several localities in two regions along Cang Shan mountain range, all situated in north-western part of Yunnan province (Fig. 122).

***Anemadus imurai* sp.n.**
(Figs. 8, 14, 58, 68, 87, 100, 101, 110, 122)

Type locality. China: Sichuan province, Liangshan Yi Autonomous Prefecture, between Yanyuan and Muli, Mt. Mianya Shan [ca. 27°41′N 101°13′E], 3500 m.

Type material. Holotype ♀ (MNIC, will be deposited in NSMT): 'Mt. Mianya Shan [ca. 27°41′N 101°13′E] / (underground baited trap) / between Yanyuan and / Muli, ca. 3,500 m in alt. // Liong-shan-yi-zu / Zizhizhou [Liangshan Yi Autonomous Prefecture], South Sichuan / China, 1–XI–2010 / Y. Imura leg. [p]'.

Description. ***Measurements*:** Total body length 2.90 mm, maximum body width 1.10 mm. Pronotum 1.43× as wide as long. Pronotum 1.81× as wide as head. Elytra 1.45× as long as wide and 1.25× as wide as pronotum. ***External morphology*:** Pronotum and elytra with longer, semierect, yellow setation. Head, pronotum and elytra glabrous (Figs. 87, 100, 101). Eye absent, head laterally without any trace of facets (Fig. 87). Antenna short, with antennomere 8 distinctly transverse, ca. 0.4× as long as wide (Figs. 14, 111). Pronotum reduced, slightly narrower than elytra, trapezoidal, widest at mid-length (Fig. 8). Elytra with humeral region not expanded laterally, distinctly rounded in dorso-lateral view (Fig. 8). Elytral epipleuron narrow in lateral view. ***Male terminalia*:** Not known. ***Female terminalia*:** Ventrite 8 with spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite), without anterior emargination (Fig. 58). Ventrite 8 with posterior margin regularly rounded (Fig. 58). Tergite 10 regularly rounded posteriorly, with two pairs of large setae and several small setae regularly dispersed along posterior margin (Fig. 68). Coxite with one basal and three subapical setae in ventral view (Fig. 68). Genital annulus diameter approximately as wide as the tergite 10 (Fig. 68).

Differential diagnosis. *Anemadus imurai* sp.n. can be distinguished from other species of the "*smetanai* species group" by antennomere 8 distinctly transverse, only 0.4× as long as wide (Fig. 14) (antennomere 8 is elongate, twice as long as wide in *A. kabaki* (Fig. 17), and slightly transverse, 0.8–0.9× as long as wide in other *Anemadus* of this species group (as in Fig. 15)); head anophthalmous (Fig. 87) (same also in *A. kabaki* (Fig. 88), microphthalmous in other *Anemadus* of this species group (Figs. 81–86)); pronotum is trapezoidal, slightly narrower than elytra (Fig. 8) (subquadrate, distinctly narrower than elytra in *A. kabaki* (Fig. 7), slightly to distinctly cordate in most *Anemadus* of this species group (Figs. 1–5)); female ventrite 8 with spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite), without anterior emargination (Fig. 58) (spiculum ventrale differently shaped but always with shallow to deep anterior emargination in other *Anemadus* of this species group (Figs. 55–57, 59–61)); coxite with one basal and three subapical setae (Fig. 68) (as *A. kabaki* (Fig. 69), but in other *Anemadus* of this species group only three subapical setae present (Figs. 65–67, 70, 71)).

Etymology. Patronymic, named after Yuki Imura (Yokohama, Japan), excellent specialist of Carabidae, who collected the species.

Collecting circumstances. The holotype was collected using underground baited traps, similar to the design described in detail by Nishikawa et al. (2012). Traps were exposed for ca. six weeks, from the end of September to the beginning of November, baited with minced dry silk worms, and placed 40 – 60 cm deep in the soil (Fig. 121). Seven pitfall traps were placed on a slope, the only specimen was collected in the highest trap in a row. Habitat was coniferous mixture forest with large broad-leaved deciduous trees, with old trees particularly well-preserved at the highest point reached, at an altitude of ca. 3500 m (Fig. 120) (Y. Imura and M. Nishikawa pers. comm.).

Distribution. Presently known only from a single locality in Mt. Mianya Shan in southern part of Sichuan province (Fig. 122).

Anemadus kabaki Perreau, 2009

(Figs. 7, 10, 16, 17, 22, 23, 50, 59, 69, 88, 102, 103, 114, 122)

Anemadus kabaki Perreau, 2009: 9 (description).

Type locality. China: Sichuan province, E of Chiguguan, SSE of Shuajingsi [ca. 32°00′52″N 102°37′18″E], 3500 – 4400 m.

Type material. Holotype ♂ (JVAC): 'CH,Sichuan [province], 3500 – 4400m / SSE of Shuajingsi [ca. 32°00′52″N 102°37′18″E], E of / Chiguguan, 15.7.2000 / Belousov & Kabak leg. [p] // HOLOTYPE / Anemadus / kabaki / Perreau, 2008 [p, red label]'. Paratype: 1 ♀ (MPEC): 'CHINA, Sichuan prov. / Qunlaishan mt. ridge, / WSW of Lixian [ca. 31°26′36″N 103°10′45″E] / 2200-2700 m a.s.l. // W of mt. "5892", / 9.7.2000 / I.Belousov, I.Kabak & / G.E. Davidian leg. [p] // PARATYPE / Anemadus / kabaki / Perreau, 2008 [p, red label]'.

Redescription. ***Measurements***: Total body length 3.49 mm in male HT and 3.11 mm in female PT, maximum body width 1.38 mm in male HT and 1.32 mm in female PT. Pronotum 1.20 × as wide as long in male HT, 1.30 × in female PT. Pronotum 1.58 × as wide as head in male HT, 1.57 × in female PT. Elytra 1.42 × as long as wide and 1.45 × as wide as pronotum in male HT; 1.48 × as long as wide and 1.41 × as wide as pronotum in female PT. ***External morphology***: Pronotum and elytra with longer, semierect, yellow setation (Fig. 114). Head and pronotum glabrous (Figs. 88, 102, 114), elytra with very fine, transverse microsculpture (Figs. 103, 114). Eye absent, without any trace of facets (Fig. 88). Antenna elongate, with antennomere 8 ca. 2.0 × as long as wide (Figs. 16, 17). Pronotum reduced, distinctly narrower than elytra, subquadrate, widest at mid-length (Figs. 7, 114). Elytra with humeral region not expanded laterally, distinctly rounded in dorso-lateral view (Figs. 7, 114). Elytral epipleuron wide in lateral view (Fig. 10). ***Male terminalia***: Posterior margin of tergite 8 regularly rounded in dorsal view. Ventrite 8 medially wide, regularly arched on both anterior and posterior margin in ventral view. Tergum 9 of genital segment with apex regularly rounded (Fig. 50). Pleurite 9 with subtruncate apex in ventral view (Fig. 50). Aedeagus. Length of median lobe 0.14 mm, length of median lobe with parameres 0.19 mm. Ratio of apical/basal part of median lobe 1.93. Ratio of length/width of basal part of median lobe 1.56. Median lobe slender, elongate in dorsal view (Fig. 22), apex widely rounded in dorsal view (Fig. 22). Endophallus with uniformly dispersed, weak, undifferentiated spines (Fig. 22). Paramere wide basally, narrowed near the base (before 1/4 of its length) (Fig. 22); with indistinct subapical constriction in dorsal view; straight in lateral view (Figs. 22 – 23); apex nearly straight, slightly convergent inwards at the apex, thickened, the apical setae pointing inwards in oblique position; with two inner and two apical setae, outer seta is missing (Figs. 22, 23). ***Female terminalia***: Ventrite 8 with spiculum ventrale with short parallel sides, narrow (ca. 1/4 of width of ventrite), with shallow anterior emargination (Fig. 59). Ventrite 8 with posterior margin regularly rounded (Fig. 59). Tergite 10 truncate posteriorly, with one large pair of setae and several small setae only latero-posteriorly (Fig. 69). Coxite with one basal and three subapical setae in ventral view (Fig. 69). Genital annulus diameter approximately 0.6 × as wide as the tergite 10 (Fig. 69).

Differential diagnosis. *Anemadus kabaki* is a very characteristic species, it can be reliably distinguished from other species of the "*smetanai* species group" by very elongate hind legs (Fig. 7) (much shorter in other species (Figs. 1 – 5, 8)); head anophthalmous (Fig. 88) (eyes also completely absent in *A. imurai* sp.n. (Fig. 87), microphthalmous in other species (Figs. 81 – 86)); pronotum subquadrate, distinctly narrower than elytra (Fig. 7) (trapezoidal in *A. imurai* sp.n. (Fig. 8); slightly to distinctly cordate in other species (Figs. 1 – 5)); elongate antennomeres, with antennomere 8 ca. 2 × as long as wide (0.4 – 0.9 × as long as wide in other *Anemadus* of this species group); elytral epipleuron wide in lateral view (Fig. 10) (narrow in lateral view in other *Anemadus* of this species group (as on Fig. 9)); male ventrite 8 wide (narrow in other *Anemadus* of this species group); median lobe of aedeagus slender and elongate (Fig. 22) (robust and compact in most other *Anemadus* of this species group (Figs. 18, 20, 28, 36), similar elongation is present only in *A. tangi* sp.n. (Fig. 31); male is not known in *A. imurai* sp.n.); female ventrite 8 with spiculum ventrale short (Fig. 59) (more elongate and differently shaped in other *Anemadus* of this species group (Figs. 55 – 58, 60, 61)); female tergite 10 truncate posteriorly, with one large pair of setae and several small setae latero-posteriorly (Fig. 69) (regularly rounded posteriorly, with setae regularly dispersed along posterior margin in other *Anemadus* of this species group (Figs. 65 – 68, 70, 71)); coxite with one basal and three subapical setae (Fig. 69) (same in *A. imurai* sp.n. (Fig. 68), only three subapical setae present in other *Anemadus* of this species group (Figs. 65–67, 70, 71)).

Collecting circumstances. The holotype was collected probably by sifting, in the upper forest zone or on alpine meadows; the paratype was sifted in mixed forest (I.I. Kabak pers. comm.).

Distribution. Presently known only from two localities in northern part of Sichuan province (Fig. 122).

***Anemadus smetanai* Růžička, 1999**
(Figs. 4, 28, 29, 32, 33, 51, 60, 70, 85, 104, 105, 122)

Anemadus smetanai Růžička, 1999: 621 (description); Perreau (2000: 45, 2004: 134) (catalogue); Perreau (2009: 10) (additional distributional record).

Type locality. China: Yunnan province, Xue Shan Mts. near Zhongdian, 27°49′N 099°34′E, 3900 m.

Type material. Holotype ♂ (MHNG): 'CHINA N Yunnan [province] Xue / Shan [Mts.] nr. Zhongdian / 3900 m, 25.VI.1996 / 27°49[′]N 99°34[′]E C41 // A. Smetana, J. Farkač / and P. Kabátek [leg.] [p] // HOLOTYPUS / *Anemadus* ♂ / *smetanai* sp. n. / Jan Růžička det. 1997 [p, red label]'. Paratypes: 1 ♂, 3 ♀♀ (1 ♀ coated and used for SEM photographs) (JRUC): same locality data; 1 ♀ (MPEC): same locality data, but '4050 m, 24.vi.1996 / ... C39 [p]'.

Additional material examined. 1 ♂, 1 ♀ (OUMNH): 'CHINA (N-Yunnan), Zhongdian / Co., Xue Shan [Mts.], 10 km SW / Zhongdian, 3700–3800 m, 27°46.5′N, 99°36.5′E (primary / mixed forest, leaf litter sifted) / 20.VIII.2003 Wrase [leg.] (10A) [p] // OUMNH-2010-054 / J. Cooter colln. / Ox. Uni. Mus. of / Nat. Hist. (OUMNH) [p]'; 1 ♀ (MPEC): 'CHINA: N-Yunnan, [C2005-05b] / Diqing Tibet. Aut. Pref., / Zhongdiang Co., Xue Shan near / lake 23 km S Zhongdian, 3895 m, // 27°37.1′N 99°38.5′E, devast. / mixed forest, meadows, lake / border, leaf litter, dead wood, / sifted, 15.vi.2005, / leg. M. Schülke [C2005-05B] [p]'.

Redescription. ***Measurements*:** Total body length 2.45–3.01 mm in males (2.70 mm in HT) and 2.73–3.05 mm in females, maximum body width 1.20–1.25 mm in males (1.25 mm in HT) and 1.15–1.35 mm in females. Pronotum 1.60–1.68× as wide as long in males (1.60× in HT), 1.61–1.80× in females. Pronotum 1.95–2.00× as wide as head in males (1.95× in HT), 1.87–2.08× in females. Elytra 1.37–1.49× as long as wide (1.49× in HT) and 1.07–1.10× as wide as pronotum (1.07× in HT) in males; 1.29–1.51× as long as wide and 1.08–1.12× as wide as pronotum in females. ***External morphology*:** Pronotum and elytra with short, recumbent, yellow setation. Head glabrous (Fig. 85), pronotum and elytra with fine, transverse microsculpture, more dense on elytra (Figs. 104, 105). Eye reduced, minute, with hemispherical arrangement of 10 distinct facets (Fig. 85). Antenna short, with antennomere 8 slightly transverse, ca. 0.9× as long as wide. Pronotum slightly cordate, regularly convex, widest behind the mid-length (Fig. 4). Elytra with humeral region only slightly expanded laterally, more rounded in dorso-lateral view (Fig. 4). Elytral epipleuron narrow in lateral view. ***Male terminalia*:** Posterior margin of tergite 8 regularly rounded in dorsal view. Ventrite 8 medially narrowed, regularly arched on both anterior and posterior margin in ventral view. Tergum 9 of genital segment with apex regularly rounded (Fig. 51). Pleurite 9 with subtruncate apex in ventral view (Fig. 51). Aedeagus. Length of median lobe 0.16 mm, length of median lobe with parameres 0.17 mm. Ratio of apical/basal part of median lobe 1.69. Ratio of length/width of basal part of median lobe 1.51. Median lobe robust, compact in dorsal view (Fig. 28), apex prolonged into short, rectangular tip in dorsal view (but slightly narrower than in *A. haba* sp.n.) (Fig. 28). Endophallus with two baso-medial parallel rows of strong teeth, not differentiated into two parts (Růžička 1999: 625, fig. 6; Fig. 28). Paramere wide basally and along midlength, narrowed only in apical half of its length (Fig. 28); with a clear subapical constriction in dorsal view; sinuate in lateral view (Figs. 28–29); apex nearly straight, slightly convergent inwards at the apex, not thickened, the apical setae pointed inwards in orthogonal position (Růžička 1999: 625, figs. 6, 7; Fig. 28); with four inner setae, outer seta is missing (Figs. 32, 33). ***Female terminalia*:** Ventrite 8 with spiculum ventrale with divergent sides, wide (ca. 1/2 of width of ventrite), with anterior emargination (Fig. 60). Ventrite 8 with posterior margin truncate (Fig. 60). Tergite 10 regularly rounded posteriorly, with setae of fairly uniform size regularly dispersed along posterior margin (Fig. 70). Coxite only with 3 subapical setae in ventral view (Fig. 70). Genital annulus diameter approximately 1.1× as wide as the tergite 10 (Fig. 70).

Differential diagnosis. *Anemadus smetanai* is very similar to *A. haba* sp.n. (Fig. 120). For differentiation of both species from other species of the "*smetanai* species group" and differences between them, see treatment of *A. haba* sp.n. above.

Collecting circumstances. Most of the specimens from the type series were collected from deep layers of rotten leaves and detritus in montane primary forest (with dominant *Abies*, *Betula*, *Carpinus* and *Rhododendron*), a single specimen collected at 4050 m was sifted from layers of moss, rotting bark and humus under a huge fallen *Abies* in a primary high montane forest with dominant *Abies* and tree-like *Rhododendron* (A. Smetana pers. comm.). Additional specimens were sifted from litter in primary montane forest (D.W. Wrase pers. comm.), but also sifted from leaf litter and dead wood in devastated mixed forest and meadows near a lake margin (M. Schülke pers. comm.).

Distribution. Presently known only from several localities in Xue Shan Mts. in northern part of Yunnan province (Fig. 122).

Anemadus tangi **sp.n.**
(Figs. 5, 12, 30, 31, 34, 35, 52, 61, 71, 76, 77, 86, 106, 107, 122)

Type locality. China: Xizang autonomous region (= Tibet), Linzhi county, West Sejila (ca. 29°39.8′N 094°16.5′E), 3300 m.

Type material. Holotype ♂ (SHNU): 'West Sejila [ca. 29°39.8′N 094°16.5′E] / Linzhi Coun.[ty] / Xizang A. R. / alt. 3300m / 2-VIII-2005 / Tang Liang leg. [p]'. Paratypes: 5 ♀♀ (JRUC, MPEC, SHNU): same data as holotype; 2 ♂♂, 2 ♀♀ (JRUC, MPEC, SHNU): 'Lulang [ca. 29°36′59″N 094°41′53″E] / Linzhi Coun.[ty] / Xizang A. R. / alt. 4100m / 2-VIII-2005 / Tang Liang leg. [p]'.

Description. ***Measurements*****:** Total body length 3.07–3.45 mm in males (3.45 mm in HT) and 2.92–3.33 mm in females, maximum body width 1.26–1.40 mm in males (1.40 mm in HT) and 1.32–1.34 mm in females. Pronotum 1.58–1.82× as wide as long in males (1.58× in HT), 1.65–1.70× in females. Pronotum 2.09–2.12× as wide as head in males (2.12× in HT), 1.88–2.05× in females. Elytra 1.41–1.46× as long as wide (1.46× in HT) and 1.03–1.09× as wide as pronotum (1.03× in HT) in males; 1.25–1.43× as long as wide and 1.02–1.04× as wide as pronotum in females. ***External morphology*****:** Pronotum and elytra with short, recumbent, yellow setation. Head glabrous (Fig. 86), pronotum and elytra with superficial, transverse microsculpture, very dense on elytra (Figs. 106, 107). Eye reduced, minute, with hemispherical arrangement of 15 distinct facets (Fig. 86). Antenna short, with antennomere 8 slightly transverse, ca. 0.8× as long as wide. Pronotum cordate, regularly convex, widest behind the mid-length (Fig. 5). Elytra with humeral region only slightly expanded laterally, more rounded in dorso-lateral view (Fig. 5). Elytral epipleuron narrow in lateral view. ***Male terminalia*****:** Posterior margin of tergite 8 truncate in dorsal view (Fig. 76). Ventrite 8 medially narrowed, regularly arched on both anterior and posterior margin in ventral view (Fig. 77). Tergum 9 of genital segment with apex truncate (Fig. 52). Pleurite 9 with apex narrow, sharply pointed in ventral view (Fig. 52). Aedeagus. Length of median lobe 0.18 mm, length of median lobe with parameres 0.19 mm. Ratio of apical/basal part of median lobe 2.10. Ratio of length/width of basal part of median lobe 1.62. Median lobe slender, elongate in dorsal view (Fig. 31), prolonged into rounded, slightly broadened tip (Fig. 31). Endophallus with baso-medial sclerotized structures divided into two parts, more or less overlapping: basal one, consisting of two parallel differentiated rows of strong teeth, and median one, consisting of two parallel phanerae of undifferentiated spines (Fig. 31). Paramere wide basally and around midlength, narrowed only in apical half of its length (Fig. 31); without subapical constriction in dorsal view; straight in lateral view (Figs. 30, 31); apex nearly straight, slightly convergent inwards at the apex, not thickened, the apical setae pointed inwards in orthogonal position; with four inner setae, outer seta is missing (Figs. 34, 35). ***Female terminalia*****:** Ventrite 8 with spiculum ventrale with divergent sides, wide (ca. 1/2 of width of ventrite), with very deep anterior emargination (Fig. 61). Ventrite 8 with posterior margin regularly rounded (Fig. 61). Tergite 10 regularly rounded posteriorly, with setae of fairly uniform size regularly dispersed along posterior margin (Fig. 71). Coxite only with 3 subapical setae in ventral view (Fig. 71). Genital annulus diameter approximately as wide as the tergite 10 (Fig. 71).

Differential diagnosis. *Anemadus tangi* sp.n. can be distinguished from other species of the "*smetanai* species group" by the following combination of characters: the cordate pronotum (Fig. 5) and the aedeagus with median lobe slender, elongate in both dorsal and ventral view (Figs. 30, 31) (similar shape of aedeagus only in *A. kabaki* (Fig. 22), which has very different, more elongated habitus, with subquadrate pronotum shape (Fig. 7)). Other species of the "*smetanai* species group" with the cordate pronotum, have the aedeagus differently shaped, but its median lobe is always robust and compact (Figs. 18, 20, 28, 36). In male of *A. tangi* sp.n., the endophallus of aedeagus is complex: baso-medial sclerotized structures are divided into two parts, more or less overlapping: the basal one, consisting of two parallel differentiated rows of strong teeth, and the median one, consisting of two parallel phanerae of undifferentiated spines (Fig. 31). Males of other members of the "*smetanai* species group" have the endophallus of aedeagus much simpler, with two baso-medial parallel rows of strong teeth, not differentiated into two parts (Figs. 28, 29, 36–37), with two medio-apical rows of moderately developed teeth, basally joined with larger, oval teeth (Figs. 18–21) or only with uniformly dispersed, weak, undifferentiated spines (Figs. 22, 23) (male of *A. imurai* sp.n. is not known). In *A. tangi* sp.n., the male tergum 9 of the genital segment has a truncate apex (Fig. 52), in other members of the "*smetanai* species group" apex is regularly rounded (Figs. 47–51) (situation is unknown in *A. imurai* sp.n.). Female of *A. tangi* sp.n. has ventrite 8 with posterior margin regularly rounded (Fig. 61), its spiculum ventrale is wide (ca. 1/2 of width of ventrite), with extremely deep anterior emargination (Fig. 61); this is similar only to *A. smetanai*, which also has the wide spiculum ventrale, but the posterior margin of ventrite 8 is truncate and the spiculum ventrale has much less emarginated anterior margin (Fig. 60). Other members of the "*smetanai* species group" have the spiculum ventrale with parallel sides and narrow (ca. 1/4 of width of ventrite) (Figs. 55–59).

Etymology. Patronymic, named after Liang Tang (Shanghai, China), an enthusiastic specialist of staphylinoid beetles (Staphylinidae: Steninae, Scaphidiinae and Omaliinae, Agyrtidae etc.), who collected this new species.

Collecting circumstances. At both localities, the series of specimens were sifted in forest near the road, at an altitude of 3300 and 4100 m (L. Tang pers. comm.).

Distribution. Presently known only from two localities in Linzhi County, in the south-eastern part of Xizang autonomous region (= Tibet) (Fig. 122).

5.3. Key to species of *Anemadus smetanai* species group

1 Pronotum trapezoidal or subquadrate, 1.20 – 1.43 × as wide as long (Figs. 7 – 8). Head anophthalmous (Figs. 87, 88). Distribution: Sichuan. **2**

1' Pronotum cordate, 1.49 – 1.82 × as wide as long (Figs. 1 – 5). Head microphthalmous, eyes reduced but present (Figs. 81 – 86). Distribution: Yunnan, Xizang (Tibet). **3**

2 Antenna elongate, antennomere 8 elongate, ca. 2.0 × as long as wide (Fig. 17). Pronotum subquadrate (Fig. 7). Female ventrite 8 with spiculum ventrale short, with very shallow anterior emargination (Fig. 59). Distribution: northern Sichuan. .... ***A. kabaki*** **Perreau**

2' Antenna short, antennomere 8 distinctly transverse, ca. 0.4 × as long as wide (Fig. 14). Pronotum rectangular (Fig. 8). Female ventrite 8 with spiculum ventrale more elongate, anterior margin without emargination (Fig. 58). Distribution: southern Sichuan. .... ***A. imurai*** **sp.n.**

3 Paramere distinctly longer than median lobe of aedeagus (Figs. 18, 20), apex thickened, the apical setae pointing inwards in oblique position (Figs. 24 – 27). Aedeagus with endophallus in dorsal view with two medio-apical rows of moderately developed teeth, basally joined with larger, oval teeth (Figs. 18, 20). Median lobe in lateral view with straight apex (Figs. 19, 21). Female ventrite 8 with posterior margin regularly rounded; spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite), with anterior emargination (Figs. 55, 57). Female genital annulus small, approximately 0.4 × width of tergite 10 (Figs. 65, 67). **4**

3' Paramere only slightly longer than median lobe of aedeagus (Figs. 28, 31, 36), apex not thickened, the apical setae pointed inwards in orthogonal position (Figs. 32, 34, 38). Aedeagus with endophallus in dorsal view with two baso-medial parallel rows of strong teeth, not differentiated into two parts, or baso-medial sclerotized structures divided into two parts, more or less overlapping: basal one, consisting of two parallel differentiated rows of weak or strong teeth, and median one, consisting of two parallel phanerae of undifferentiated spines (Figs. 28, 31, 36). Median lobe in lateral view with dorsally curved apex (Figs. 29, 30, 37). Female ventrite 8 with posterior margin truncate or regularly rounded (Figs. 66, 70, 71); if rounded, spiculum ventrale is wide (ca. 1/2 of width of ventrite), with apically divergent sides, and very deep anterior emargination (Fig. 61). Female genital annulus large, ca. 0.8 – 1.1 × as wide as tergite 10 (Figs. 66, 70, 71). **5**

4 Median lobe of aedeagus more robust both in dorsal and lateral views (Figs. 18 – 19). Apex of paramere more distinctly sclerotized and dorsally prominent (Figs. 24 – 25), with two inner and two apical setae and one smaller outer seta (Fig. 24). Female ventrite 8 with wider spiculum ventrale (Fig. 55). Distribution: Yunnan: Jizu Shan Mts. .... ***A. grebennikovi*** **sp.n.**

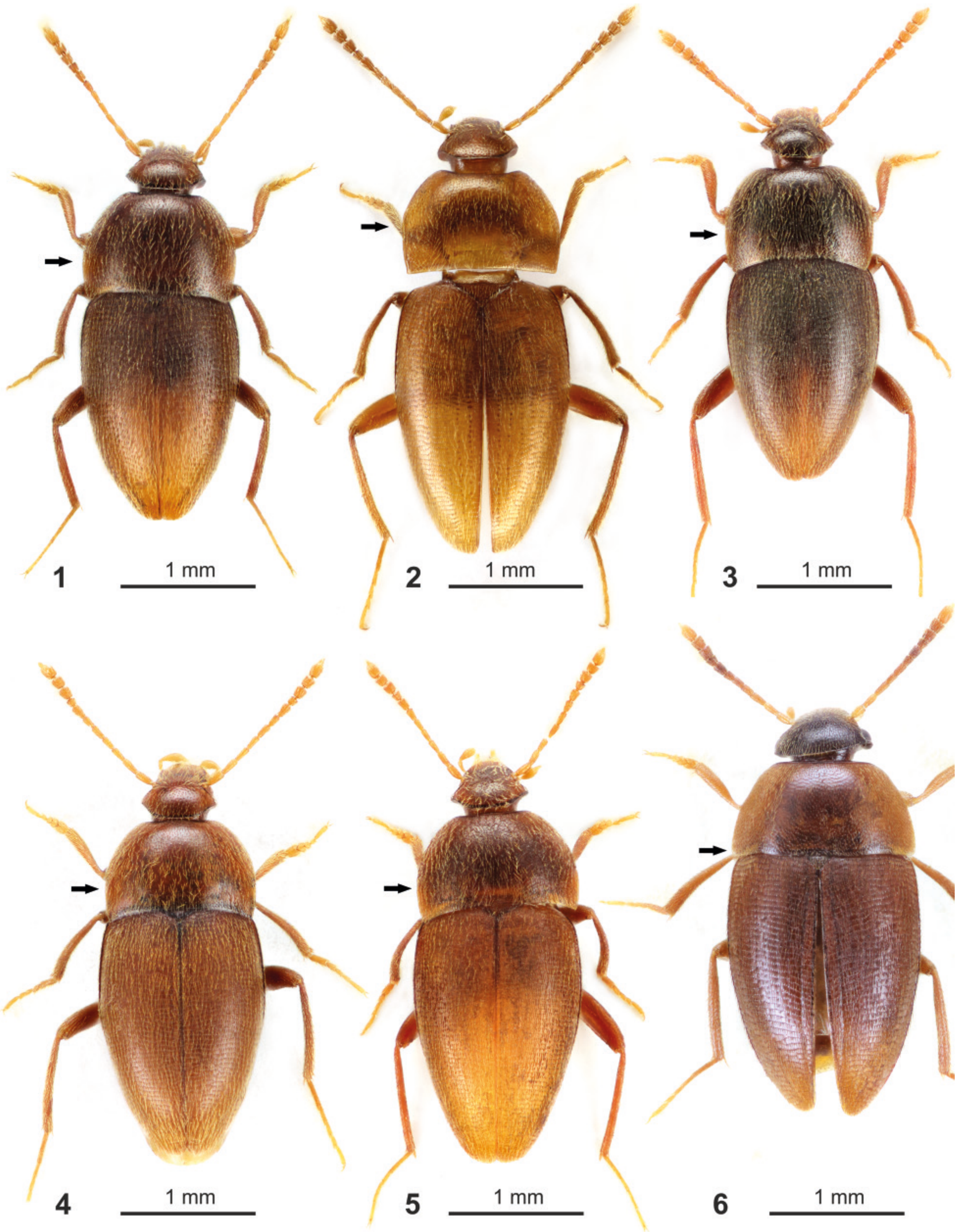
4' Median lobe of aedeagus more slender both in dorsal and lateral views (Figs. 20, 21). Apex of paramere less distinctly sclerotized, less dorsally prominent (Figs. 26, 27), only with two inner and two apical setae, outer seta is missing (Figs. 26, 27). Female ventrite 8 with narrower and more elongated spiculum ventrale (Fig. 57). Distribution: Yunnan: Yulong Xue Shan Mts., Cang Shan Mts. .... ***A. hajeki*** **sp.n.**

5 Aedeagus with median lobe slender, elongate in dorsal view (Fig. 31); endophallus with baso-medial sclerotized structures divided into two parts, more or less overlapping: basal one, consisting of two parallel differentiated rows of weak or strong teeth, and median one, consisting of two parallel phanerae of undifferentiated spines (Fig. 31). Apex of aedeagus in lateral view elongate, only slightly curved dorsally (Fig. 30). Paramere without subapical constriction in dorsal view; straight in lateral view (Figs. 30, 31). Tergum 9 of male genital segment with apex truncate (Fig. 52). Female ventrite 8 with posterior margin regularly rounded (Fig. 61), spiculum ventrale with extremely deep anterior emargination (Fig. 61). Distribution: Xizang (Tibet): Linzhi county. .... ***A. tangi*** **sp.n.**

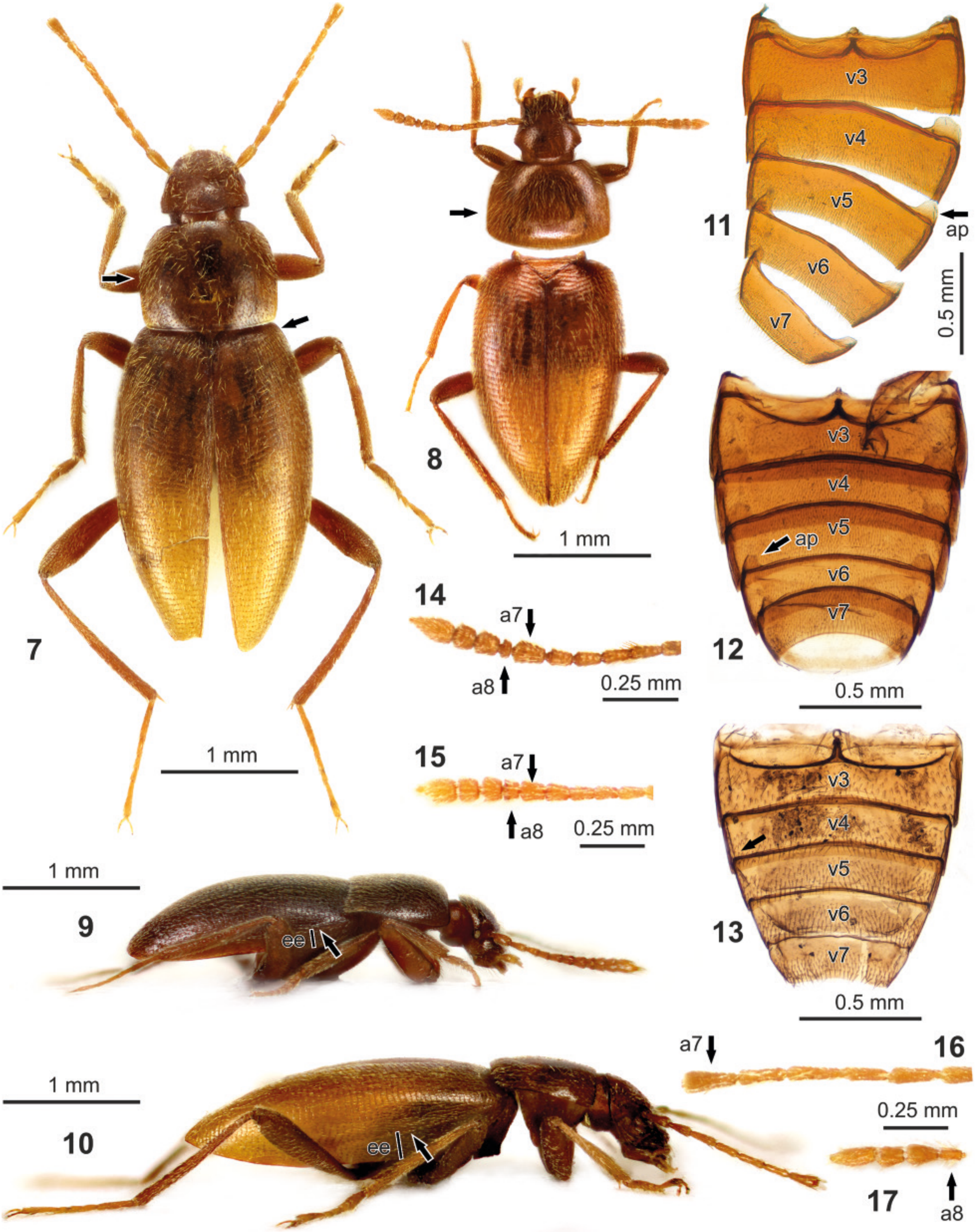
5' Aedeagus with median lobe robust, compact in dorsal view (Figs. 28, 36); endophallus simple, with two baso-medial parallel rows of strong teeth, not differentiated into two parts (Figs. 28, 36). Apex of aedeagus in lateral view short, distinctly curved dorsally (Figs. 29, 37). Paramere with a clear subapical constriction in dorsal view; sinuate in lateral view (Figs. 28, 29, 36, 37). Tergum 9 of male genital segment with apex regularly rounded (Figs. 48, 51). Female ventrite 8 with posterior margin truncate (Figs. 56, 60), spiculum ventrale with moderately deep anterior emargination (Figs. 56, 60). **6**

6 Eye with flat to concave arrangement of facets, which are hard to distinguish (Fig. 84). Apex of aedeagus prolonged into narrower, rectangular tip in dorsal view (Fig. 36). Pleurite 9 of male genital segment in ventral view with apex wide, emarginate on medial margin (Fig. 48). Female ventrite 8 with spiculum ventrale with parallel sides, narrow (ca. 1/4 of width of ventrite) (Fig. 56). Distribution: Yunnan: Haba Xue Shan Mt. .... ***A. haba*** **sp.n.**

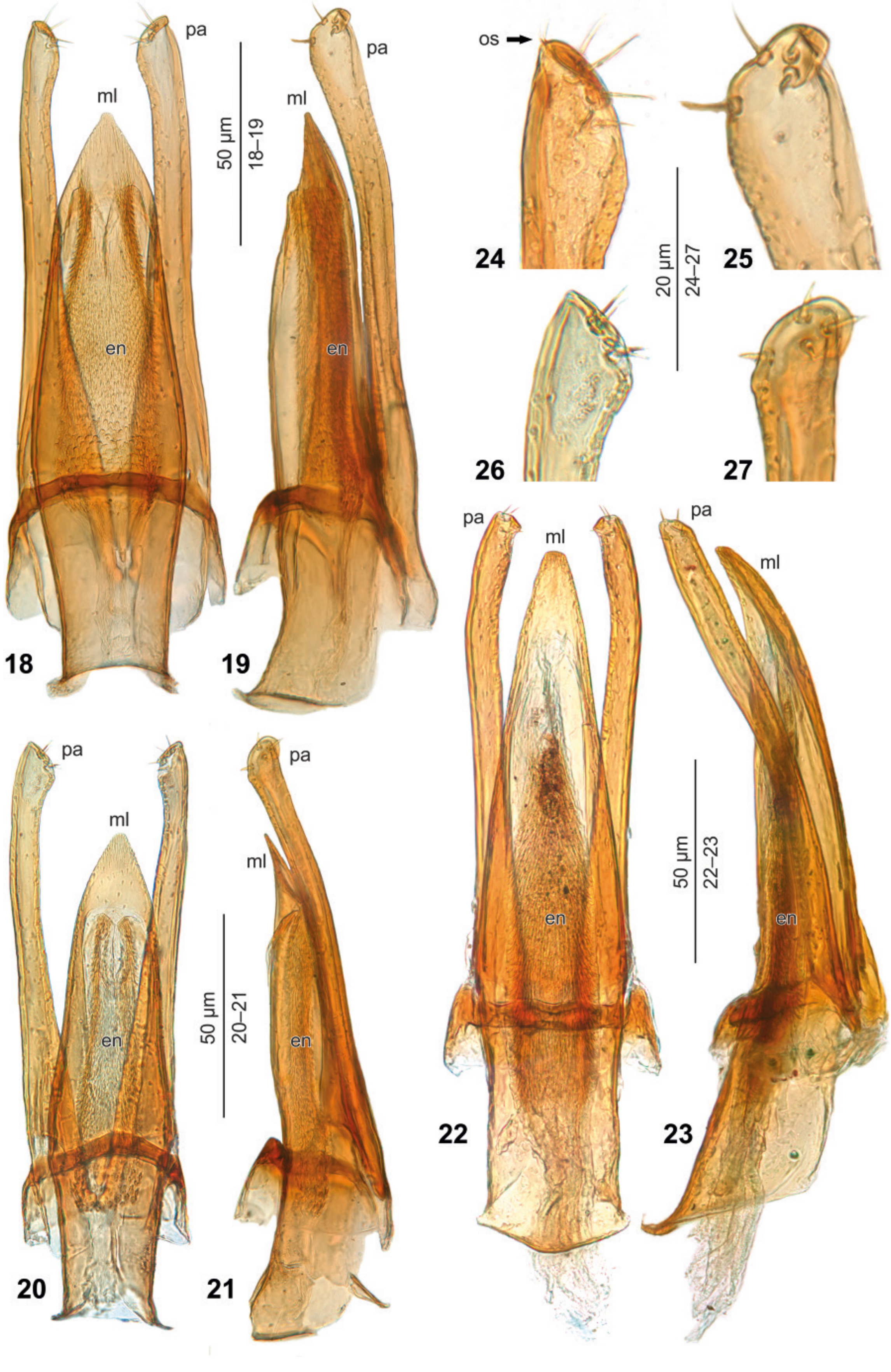
6' Eye with hemispherical arrangement of distinct facets (Fig. 85). Apex of aedeagus prolonged into slightly wider, rectangular tip in dorsal view (Fig. 28). Pleurite 9 of male genital segment in ventral view with apex subtruncate (Fig. 51). Female ventrite 8 with spiculum ventrale with divergent sides, wide (ca. 1/2 of width of ventrite) (Fig. 60). Distribution: Yunnan: Xue Shan Mts. near Zhongdien .... ***A. smetanai*** **Růžička**



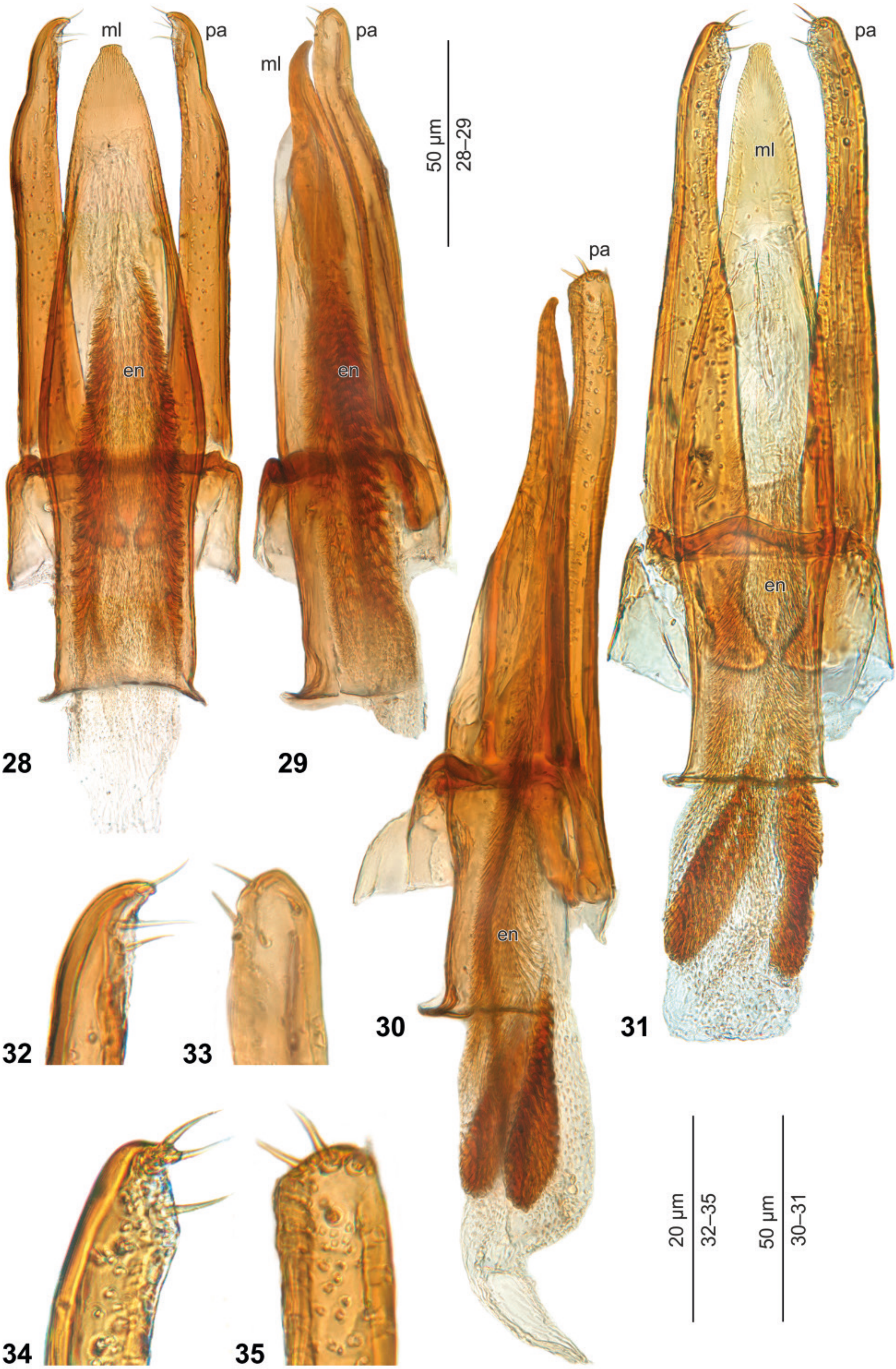
Figs. 1–6. Habitus of *Anemadus* in dorsal view. **1**: *A. grebennikovi*, PT male (JRUC). **2**: *A. haba*, HT female (MPEC). **3**: *A. hajeki*, HT male (NMPC). **4**: *A. smetanai*, male (10 km SW Zhongdian, OUMNH). **5**: *A. tangi*, PT male (Lulang, JRUC). **6**: *A. strigosus*, male (Czech Republic, Praha, Stromovka city park, JRUC). — ***Note***: elytra of *A. haba* were coalescent, separate elytra are an artefact of mounting and dissecting.



Figs. 7–17. Habitus of *Anemadus* in dorsal (7, 8) and lateral (9, 10) view. **7**, **10**: *A. kabaki*, HT male (JVAC). **8**: *A. imurai*, HT female (NSMT). **9**: *A. hajeki*, HT male (NMPC). — Abdomen in ventral view, showing lateral apodemes (ap) on ventrites. **11**: *A. haba*, PT female (MPEC). **12**: *A. tangi*, PT male (JRUC). **13**: *A. strigosus*, female (Czech Republic, Újezd u Průhonic, JRUC). — Antennae, dorsal view. **14**: *A. imurai*, HT female (NSMT), antennomeres 3–11. **15**: *A. hajeki*, HT male (NMPC), antennomeres 3–11. **16**: *A. kabaki*, HT male, antennomeres 2–7 (JVAC). **17**: *A. kabaki*, PT female, antennomeres 8–11 (MPEC). — ***Abbreviations***: a – antennomere, ap – apodemes, ee – elytral epipleuron, v3–v7 – ventrite 3 to 7. ***Note***: elytra of *A. kabaki* were coalescent, separate elytra are an artefact of mounting and dissecting.



Figs. 18–27. Aedeagus of *Anemadus* in dorsal (18, 20, 22) and lateral (19, 21, 23) view (only a single paramere is presented for clarity); apex of paramere in dorsal (24, 26) and lateral (25, 27) view. **18**, **19**, **24**, **25**: *A. grebennikovi*, HT male (MSCC). **20**, **21**, **26**, **27**: *A. hajeki*, PT male (JRUC). **22**, **23**: *A. kabaki*, HT male (JVAC). — ***Abbreviations***: en – endophallus, ml – median lobe, os – outer seta, pa – paramere.


ml
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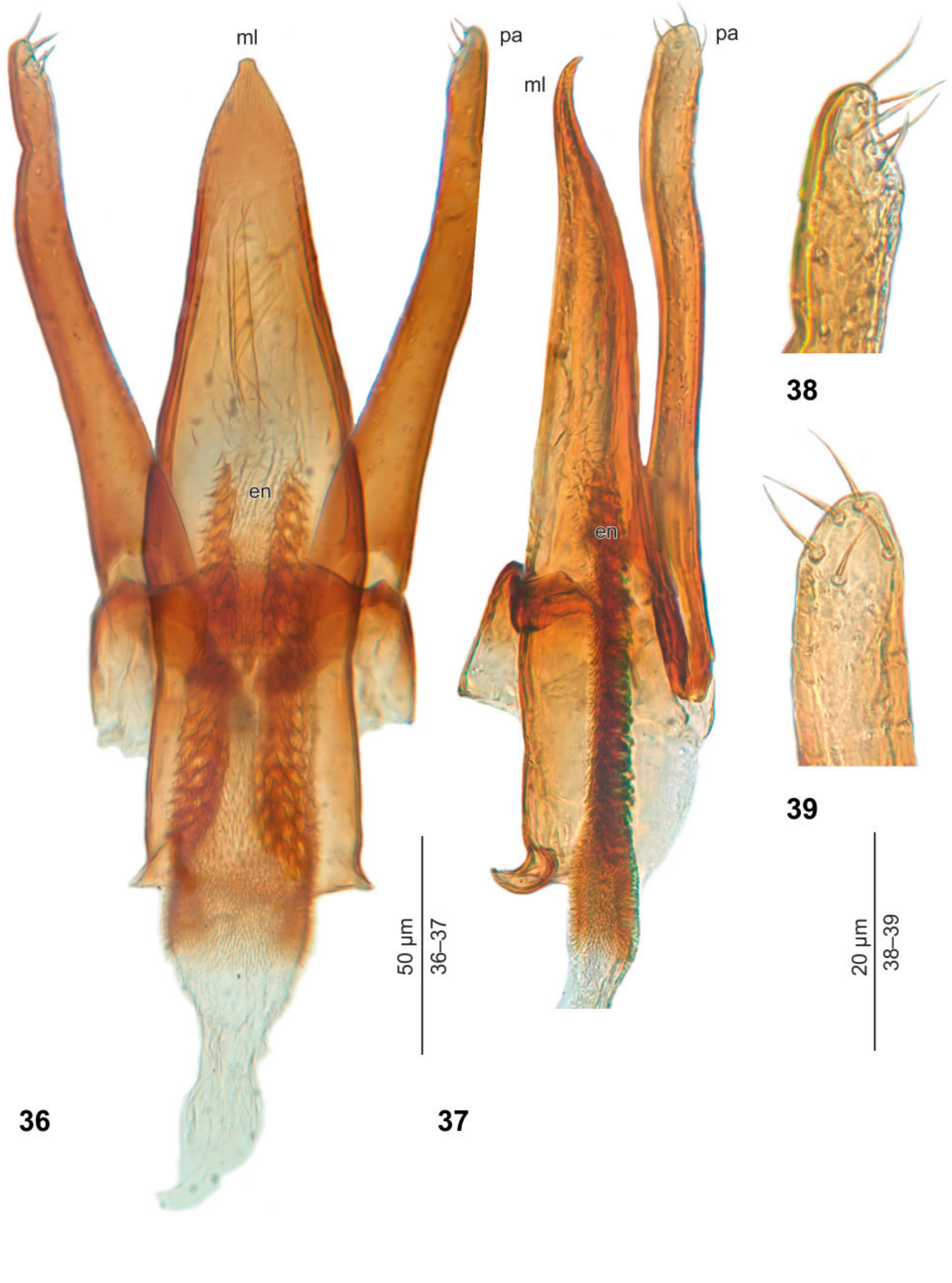
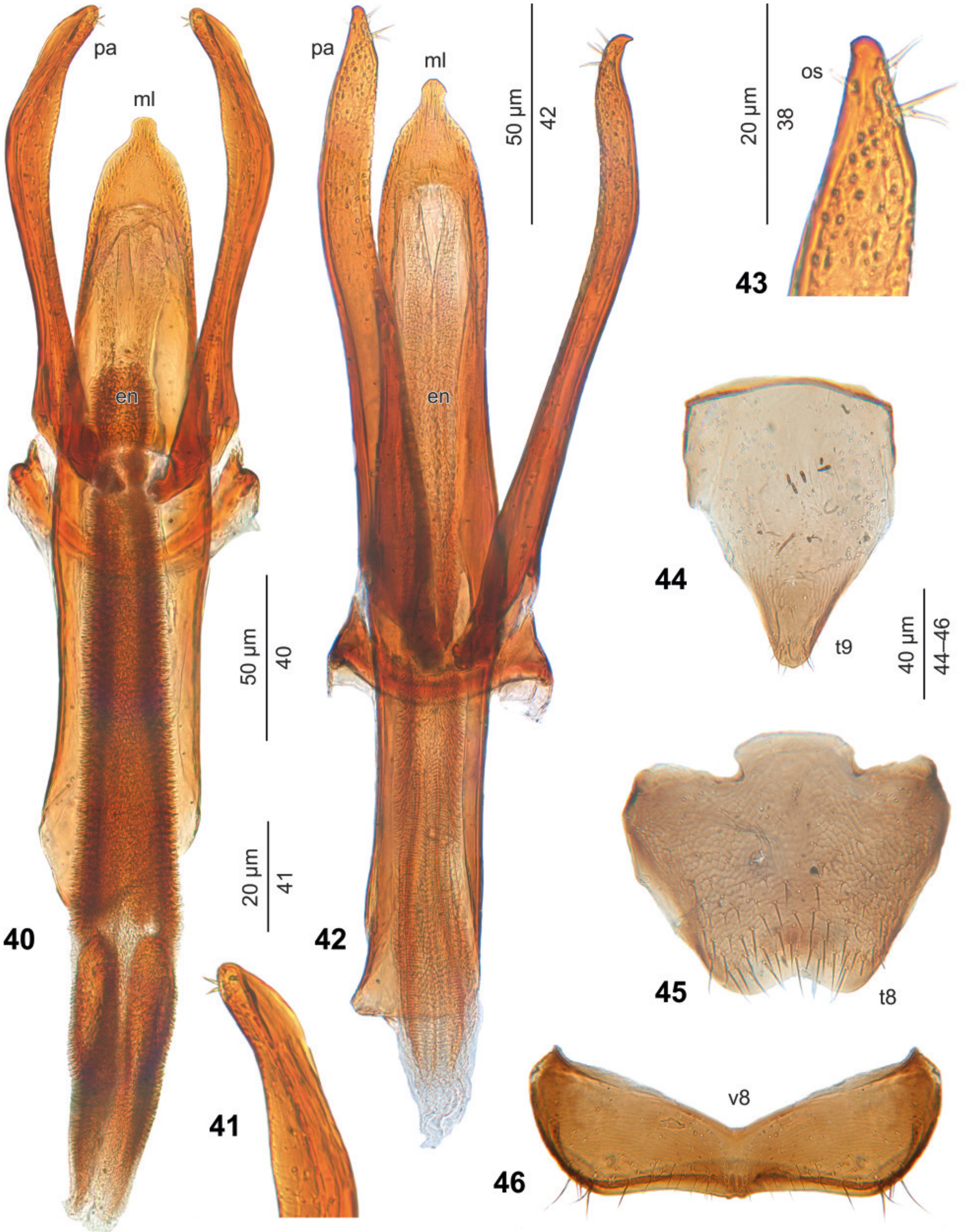
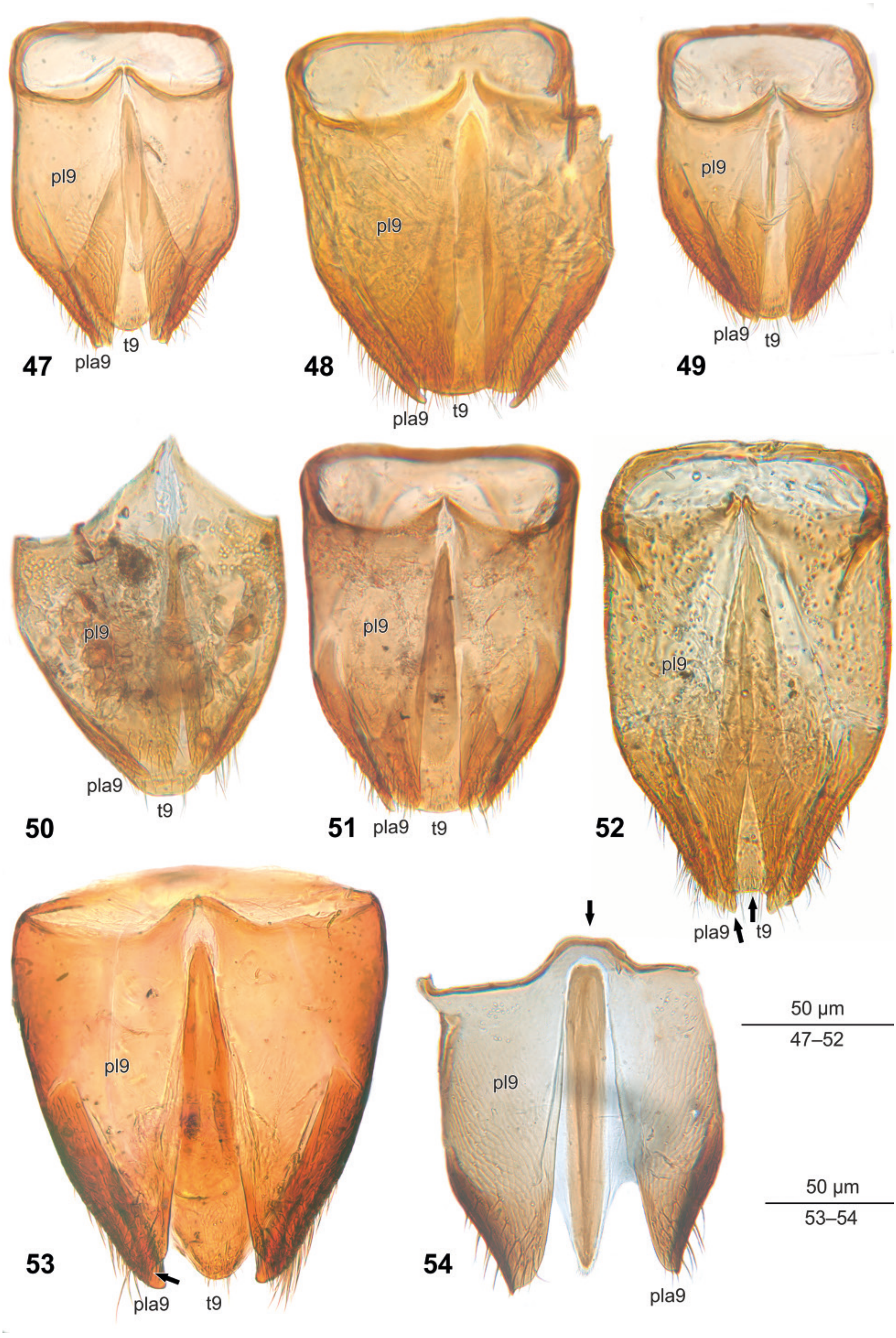


Figs. 28–39. Aedeagus of *Anemadus* in dorsal (28, 31, 36) and lateral (29, 30, 37) view (only a single paramere is presented for clarity); apex of paramere in dorsal (32, 34, 38) and lateral (33, 35, 39) view. **28**, **29**, **32**, **33**: *A. smetanai*, male (10 km SW Zhongdian, OUMNH). **30**, **31**, **34**, **35**: *A. tangi*, PT male (Lulang, JRUC). **36–39**: *A. haba*, HT male (MPEC). — ***Abbreviations***: en – endophallus, ml – median lobe, pa – paramere.



Figs. 40 – 46. Aedeagus of *Anemadus* in dorsal view (40, 42); apex of paramere in dorsal view (41, 43); male tergum 9 in dorsal view (44), male tergum 8 in dorsal view (45), male ventrite 8 in ventral view (46). **40**, **41**: *A. acicularis*, male (France, grotte près de Peille, MPEC). **42 – 46**: *A. strigosus*, male (42, 43: Greece, Peloponnesos, Kalentzi, MPEC; 44 – 46: Greece, Lake Prespa, MPEC). — ***Abbreviations***: en – endophallus, ml – median lobe, os – outer seta, pa – paramere, t9 – tergum 9, t8 – tergum 8, v8 – ventrite 8.

→ **Figs. 47 – 54.** Male genital segment of *Anemadus* in ventral view. **47**: *A. grebennikovi*, HT male (MSCC). **48**: *A. haba*, HT male (MPEC). **49**: *A. hajeki*, PT male (JRUC). **50**: *A. kabaki*, HT male (JVAC). **51**: *A. smetanai*, male (10 km SW Zhongdian, OUMNH). **52**: *A. tangi*, PT male (Lulang, JRUC). **53**: *A. acicularis*, male (France, grotte près de Peille, MPEC). **54**: *A. strigosus*, male (Greece, Lake Prespa, MPEC). — ***Abbreviations***: pl9 – pleurite 9, pla9 – apex of pleurite 9, t9 – tergite 9.


pl9
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pla9
t9
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48
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pla9
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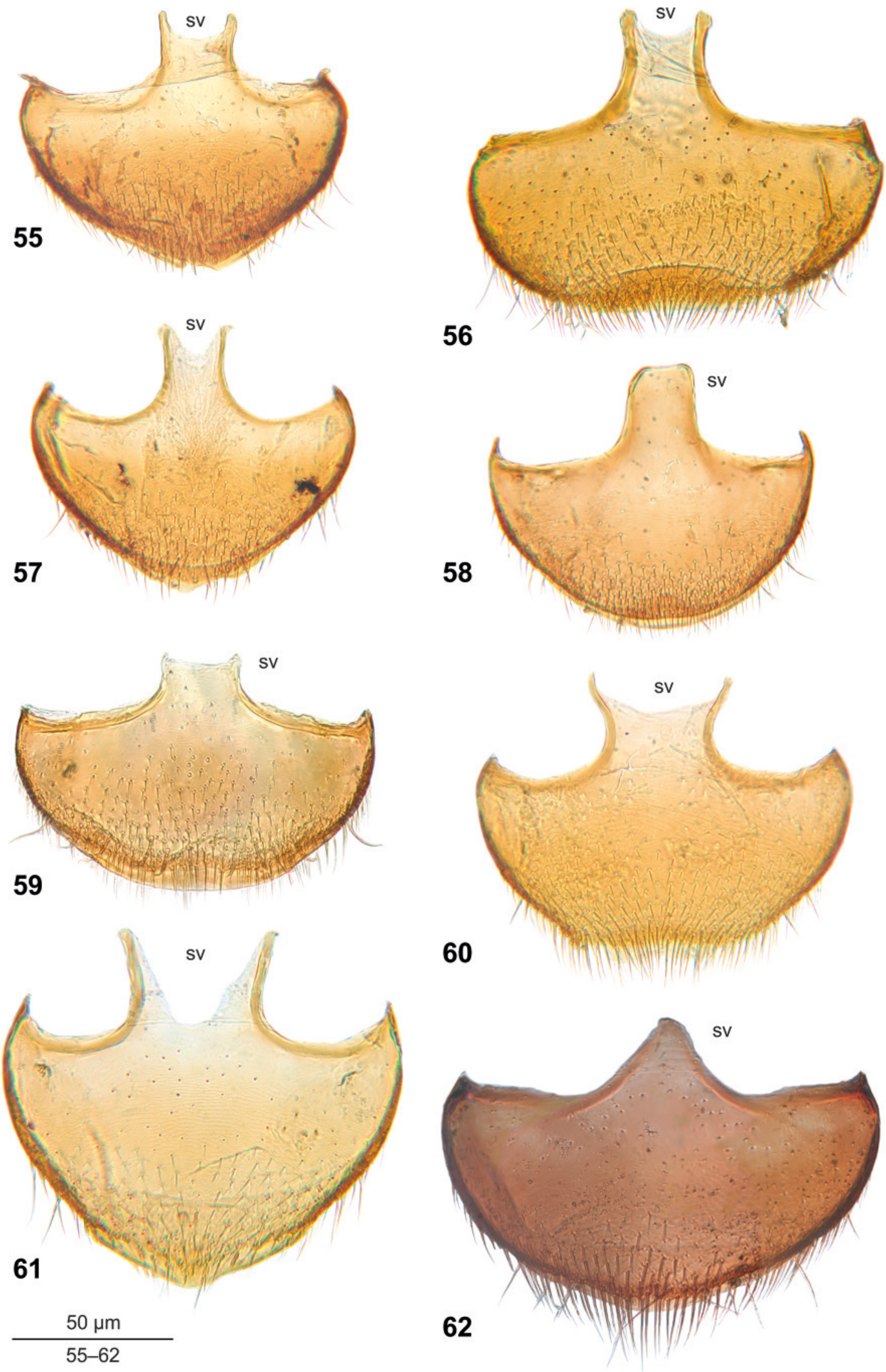
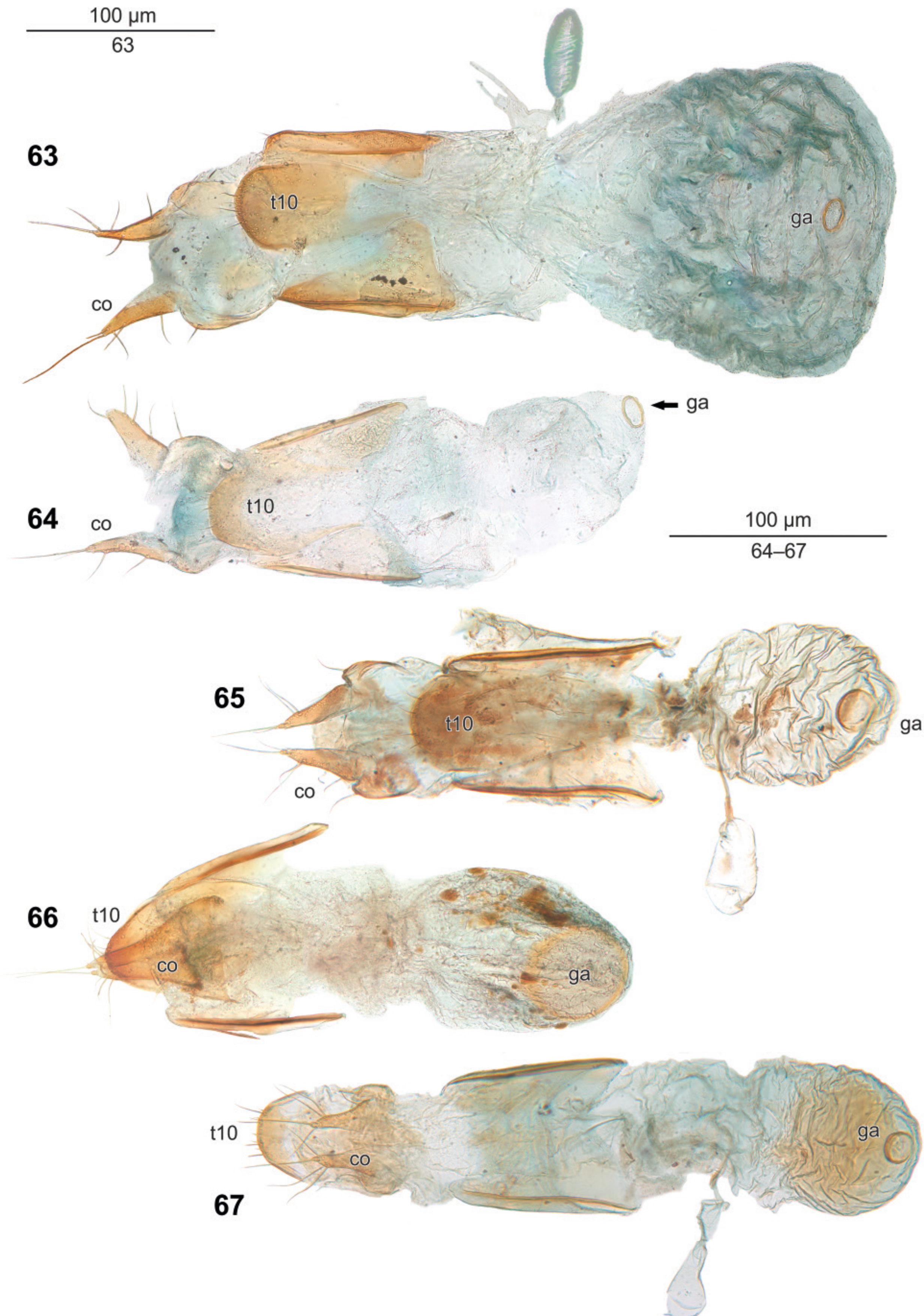
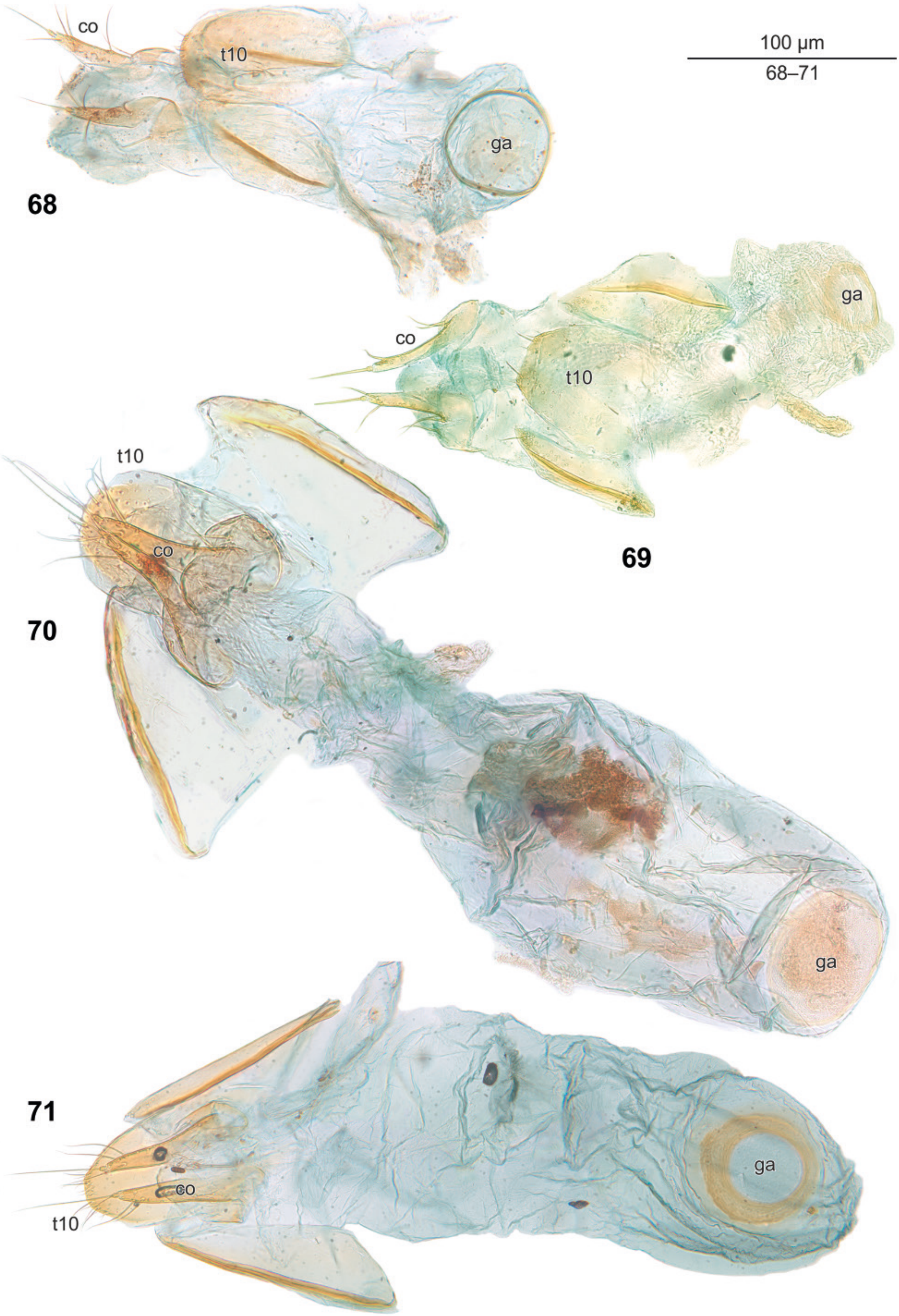
53–54



Figs. 55 – 62. Female ventrite 8 of *Anemadus* in dorsal view. **55**: *A. grebennikovi*, PT female (MPEC). **56**: *A. haba*, PT female (MPEC). **57**: *A. hajeki*, PT female (pass 43 km NW Dali, MPEC). **58**: *A. imurai*, HT female (NSMT). **59**: *A. kabaki*, PT female (MPEC). **60**: *A. smetanai*, female (10 km SW Zhongdian, OUMNH). **61**: *A. tangi*, PT female (West Sejila, MPEC). **62**: *A. acicularis*, female (France, grotte près de Peille, MPEC). — ***Abbreviations***: sv – spiculum ventrale.



Figs. 63–67. Female genitalia, dorsal view. **63**: *A. acicularis*, female (France, grotte près de Peille, MPEC). **64**: *A. strigosus*, female (Greece, Peloponnesos, Kalentzi, MPEC). **65**: *A. grebennikovi*, PT female (MPEC). **66**: *A. haba*, PT female (MPEC). — Female genitalia, ventral view. **67**: *A. hajeki*, PT female (pass 43 km NW Dali, MPEC). — ***Abbreviations***: co – coxite, ga – genital annulus, t10 – tergite 10.


100 µm
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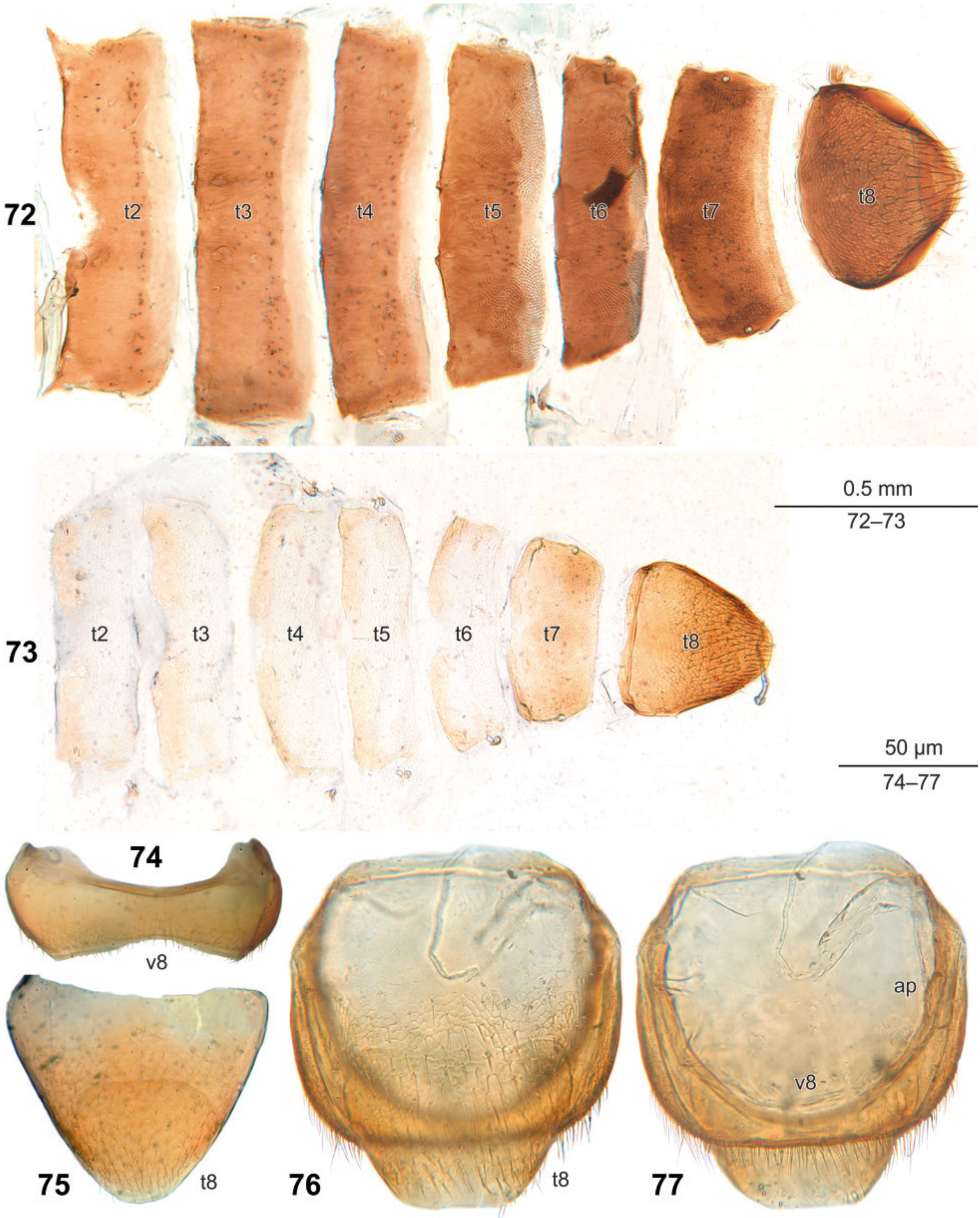
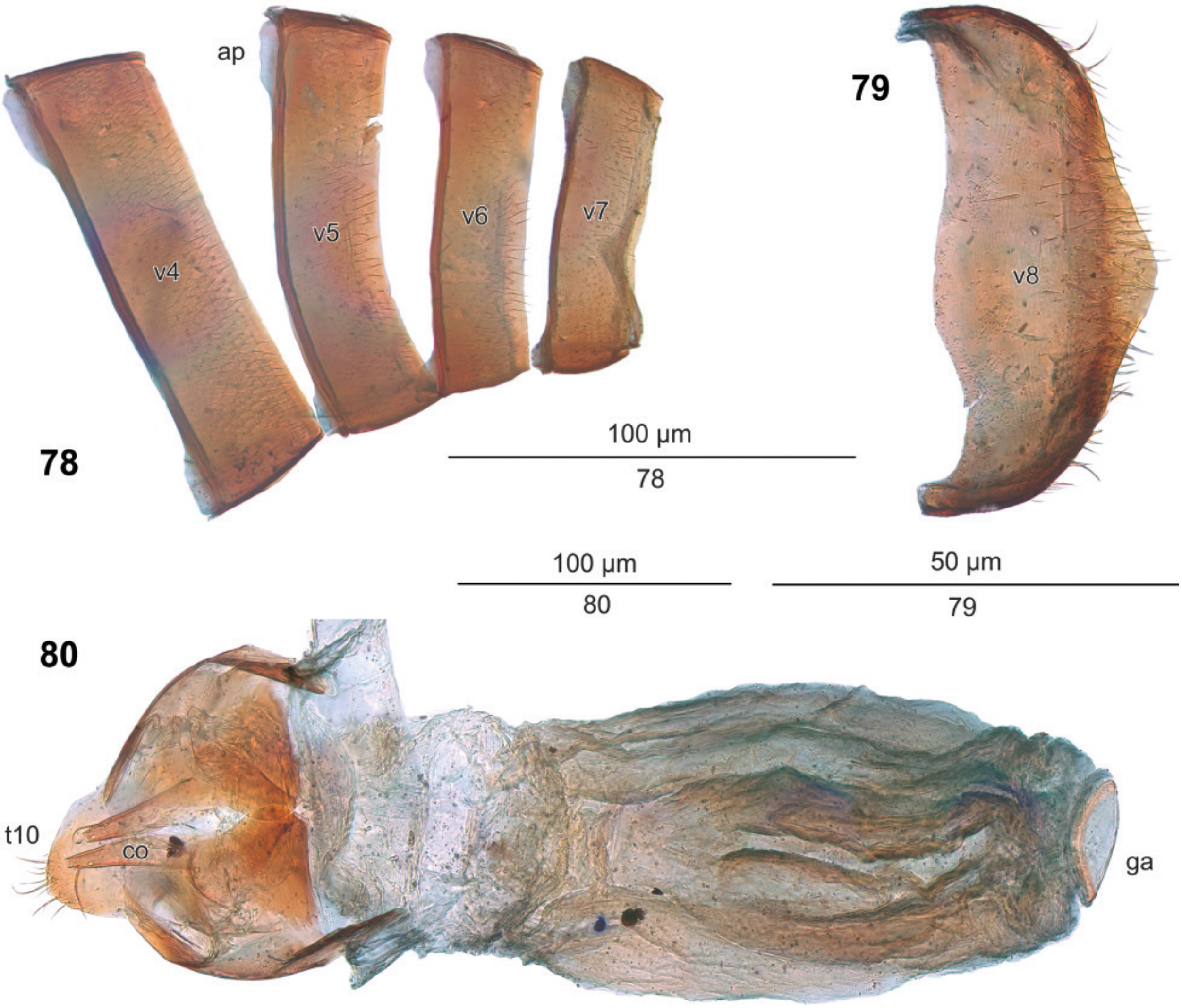


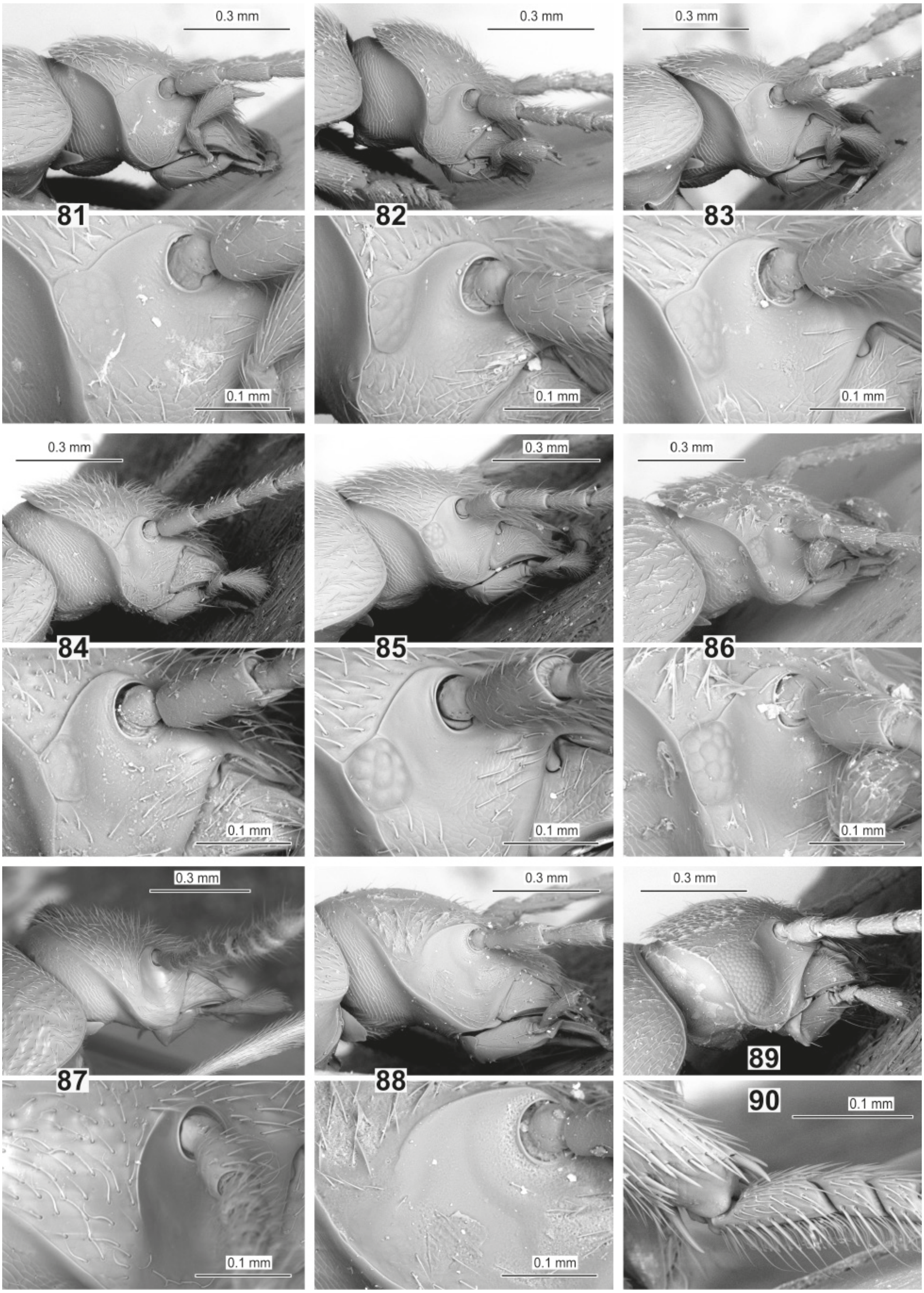
Figs. 72–77. 72, 73: abdominal tergites in dorsal view; 74, 77: ventrite 8 in ventral view; 75, 76: tergite 8 in ventral view. **72**: *A. acicularis*, female (France, grotte près de Peille, MPEC). **73–75**: *A. hajeki*, PT male (MPEC). **76–77**: *A. tangi*, PT male (JRUC). — ***Abbreviations***: t2–t8 – tergites 2 to 8, v8 – ventrite 8.

← **Figs. 68–71.** Female genitalia, dorsal view. **68**: *A. imurai*, HT female (NSMT). **69**: *A. kabaki*, PT female (MPEC). **70**: *A. smetanai*, female (23 km S Zhongdian, MPEC). **71**: *A. tangi*, PT female (West Sejila, MPEC). — ***Abbreviations***: co – coxite, ga – genital annulus, t10 – tergite 10.



Figs. 78–80. *Cholevodes tenuitarsis*, female (Japan, Mt. Takao near Hachioji, MNHN). **78**: ventrites 4–7 in ventral view. **79**: ventrite 8 in dorsal view. **80**: female genitalia in dorsal view. — ***Abbreviations***: ap – apodemes, co – coxites, ga – genital annulus, t10 – tergite 10, v4–v8 – ventrites 4 to 8.

→ **Figs. 81–90.** Head of *Anemadus*, lateral view (above) and detail of eye (below). **81**: *A. grebennikovi*, PT male (JRUC). **82**: *A. hajeki*, HT male (Maoniuping, NMPC). **83**: *A. hajeki*, PT male (Cangshan, JRUC). **84**: *A. haba*, PT female (JRUC). **85**: *A. smetanai*, male (10 km SW Zhongdian, OUMNH). **86**: *A. tangi*, PT male (Lulang, JRUC). **87**: *A. imurai*, HT female (NSMT). **88**: *A. kabaki*, HT male (JVAC). **89**: *A. strigosus*, male (Czech Republic, Praha, Stromovka city park, JRUC). — Apex of protibia and tarsus. **90**: *A. hajeki*, PT male (Cangshan, JRUC).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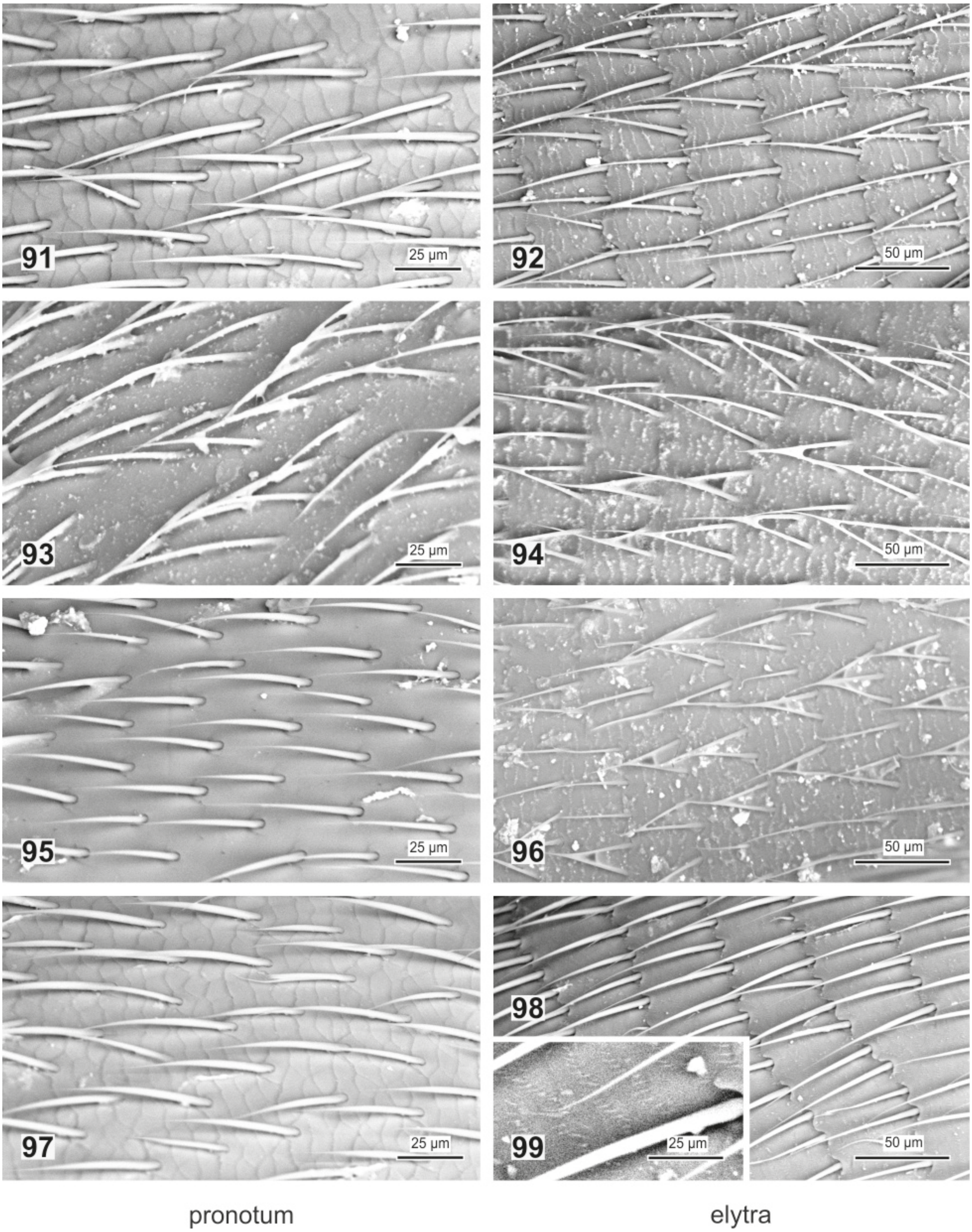
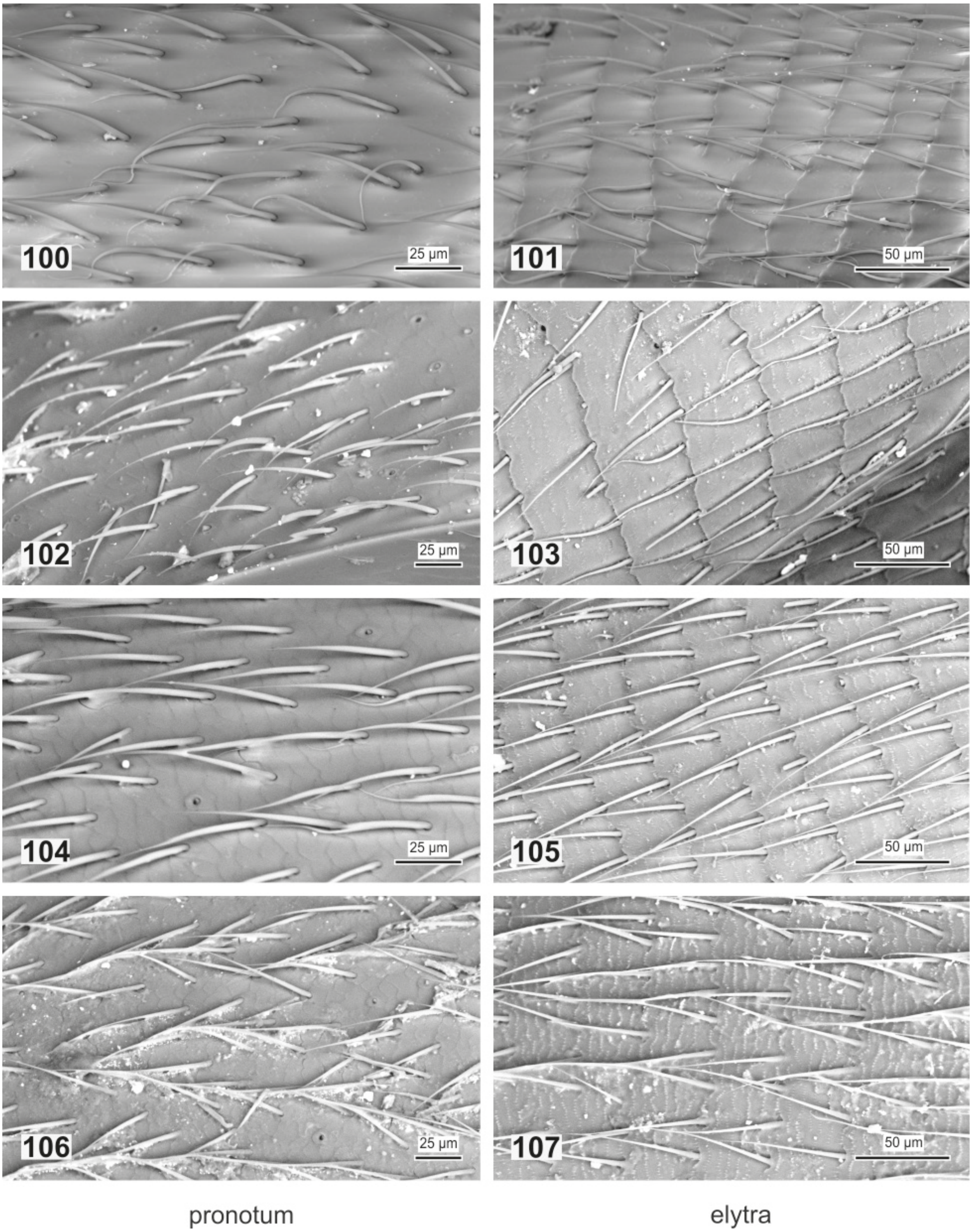
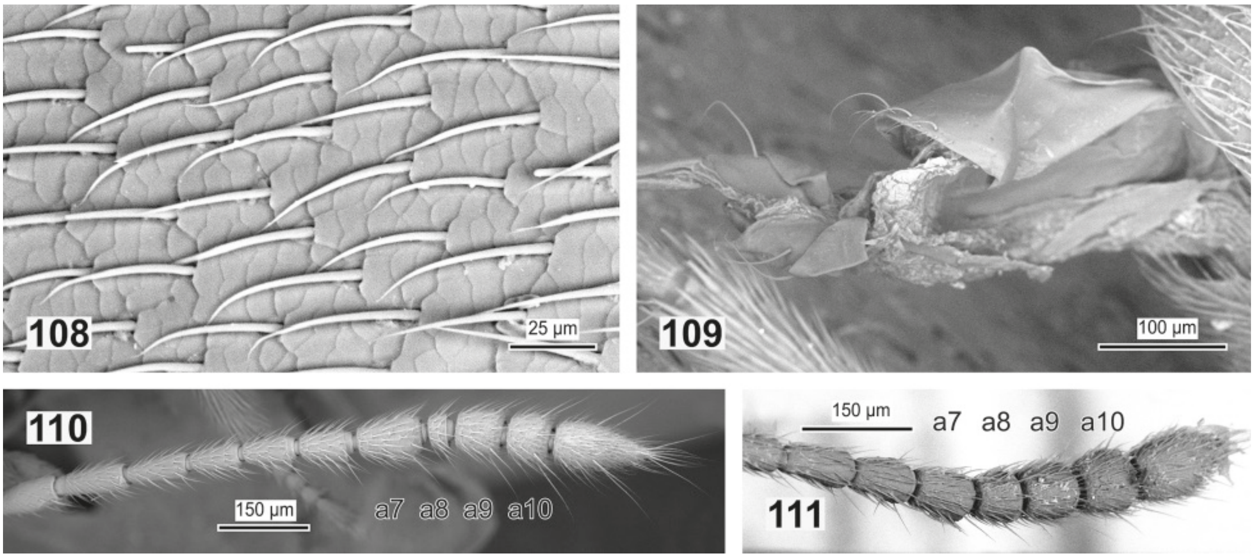


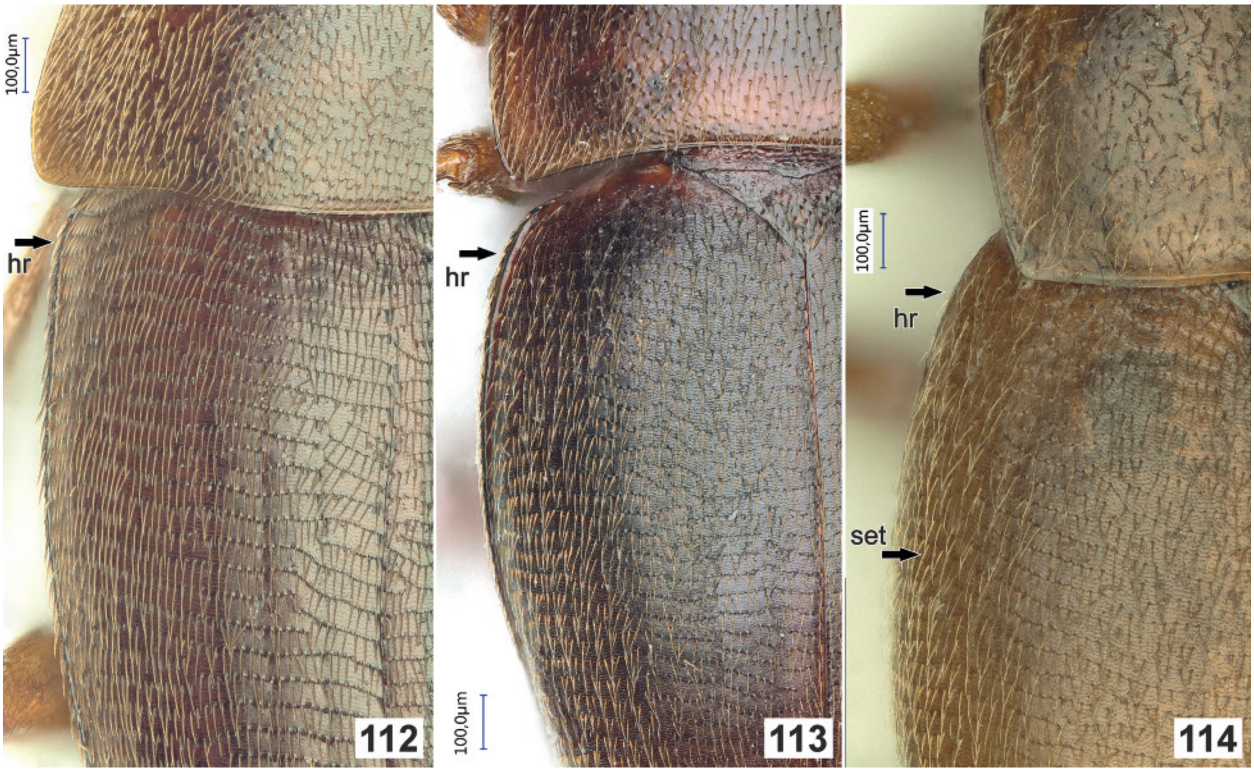
Figs. 91–99. Detail of surface microsculpture in *Anemadus*, pronotum (91, 93, 95, 97) and elytra (92, 94, 96, 98, 99). **91**, **92**: *A. grebennikovi*, PT male (JRUC). **93**, **94**: *A. haba*, PT female (JRUC). **95**, **96**: *A. hajeki*, HT male (Maoniuping, NMPC). **97–99**: *A. hajeki*, PT male (Cangshan, JRUC) (99: part of 98 in larger magnification).



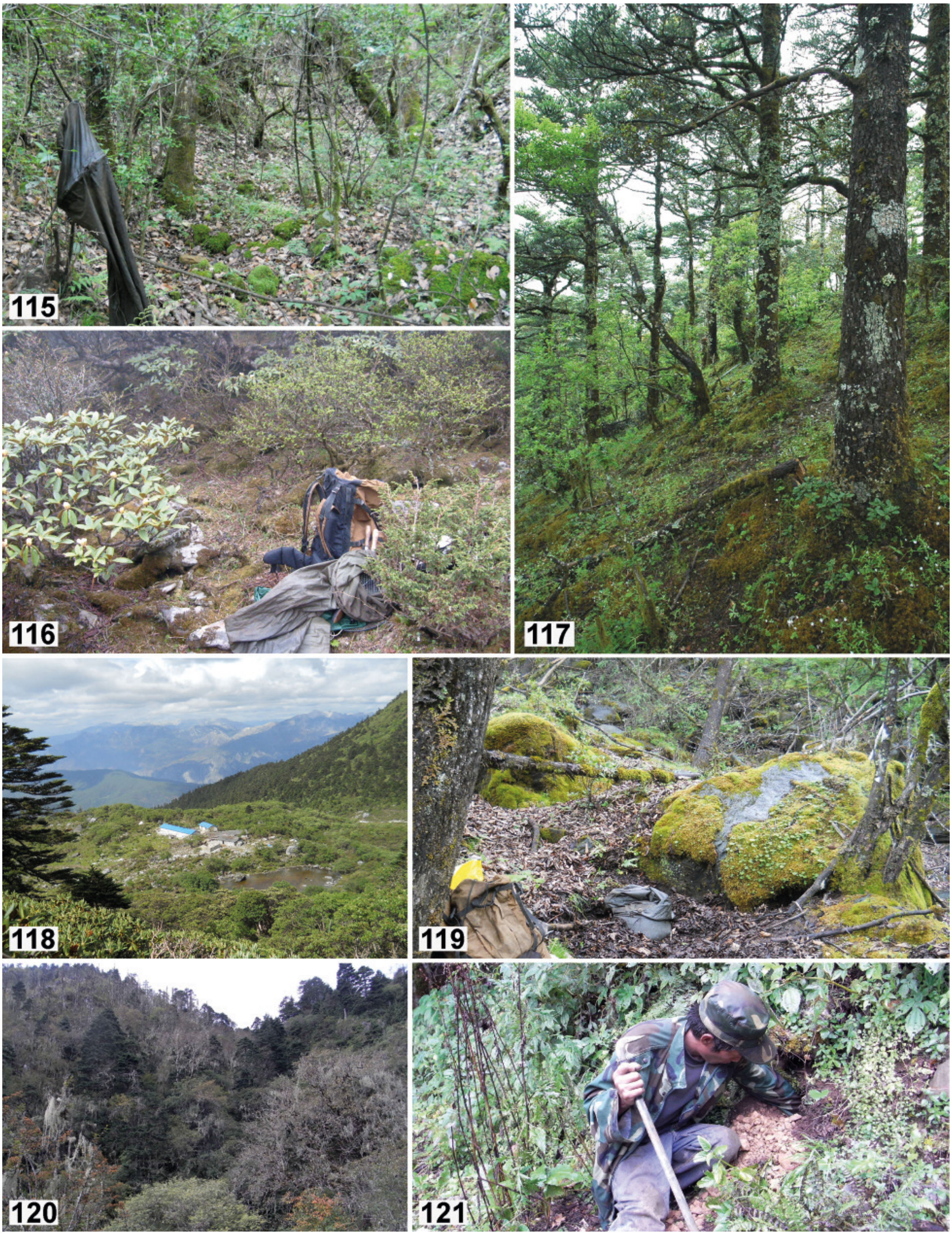
Figs. 100–107. Detail of surface microsculpture in *Anemadus*, pronotum (100, 102, 104, 106) and elytra (101, 103, 105, 107). **100**, **101**: *A. imurai*, HT female (NSMT). **102**, **103**: *A. kabaki*, HT male (JVAC). **104**, **105**: *A. smetanai*, male (10 km SW Zhongdian, OUMNH). **106**, **107**: *A. tangi*, PT male (Lulang, JRUC).



Figs. 108 – 111. Detail of structures in *Anemadus*. **108**: *A. strigosus*, surface of pronotum, male (Czech Republic, Praha, Stromovka city park, JRUC). **109**: *A haba*, female genitalia in lateral view, PT female (JRUC). **110**: *A. imurai*, antenna in lateral view, HT female (NSMT). **111**: *A. hajeki*, apex of antenna in lateral view, HT male (Maoniuping, NMPC). — ***Abbreviations***: a7 – a10 – antennomeres 7 to 10.



Figs. 112 – 114. Detail of pronotum and left elytron in *Anemadus*. **112**: *A. strigosus*, female (Libice nad Cidlinou env., Libický luh forest, JRUC). **113**: *A. hajeki*, PT male (Maoniuping, MPEC). **114**: *A. kabaki*, PT female (MPEC). — ***Abbreviations***: hr – humeral region of elytron, set – setation.



Figs. 115–121. Habitats of *Anemadus* in China. **115**: Jizu Shan Mt., deciduous forest (ca. 2700 m a.s.l.), ca. 500 m lower from the locality with *A. grebennikovi*. **116**: Cang Shan mountain range, *Rhododendron* forest at the lower part of alpine zone (4063 m a.s.l.), locality of *A. hajeki*. **117**: Maoniuping in Yulong Xue Shan mountain range, upper part of mixed forest (3540 m a.s.l.), type locality of *A. hajeki*. **118**: Haba Xue Shan Mt., *Rhododendron* forest (4072–4133 m a.s.l.), locality of *A. haba*. **119**: Haba Xue Shan Mt., upper edge of mixed forest with *Rhododendron* (3272 m a.s.l.), locality of *A. haba*. **120**: Mt. Mianya Shan, coniferous mixture forest with large broad-lived deciduous trees (3500 m a.s.l.), type locality of *A. imurai*. **121**: same locality, exposition of underground pitfall trap. — Photos by V. Grebennikov (115, 116, 118, 119), J. Růžička (117) and Y. Imura (120, 121).

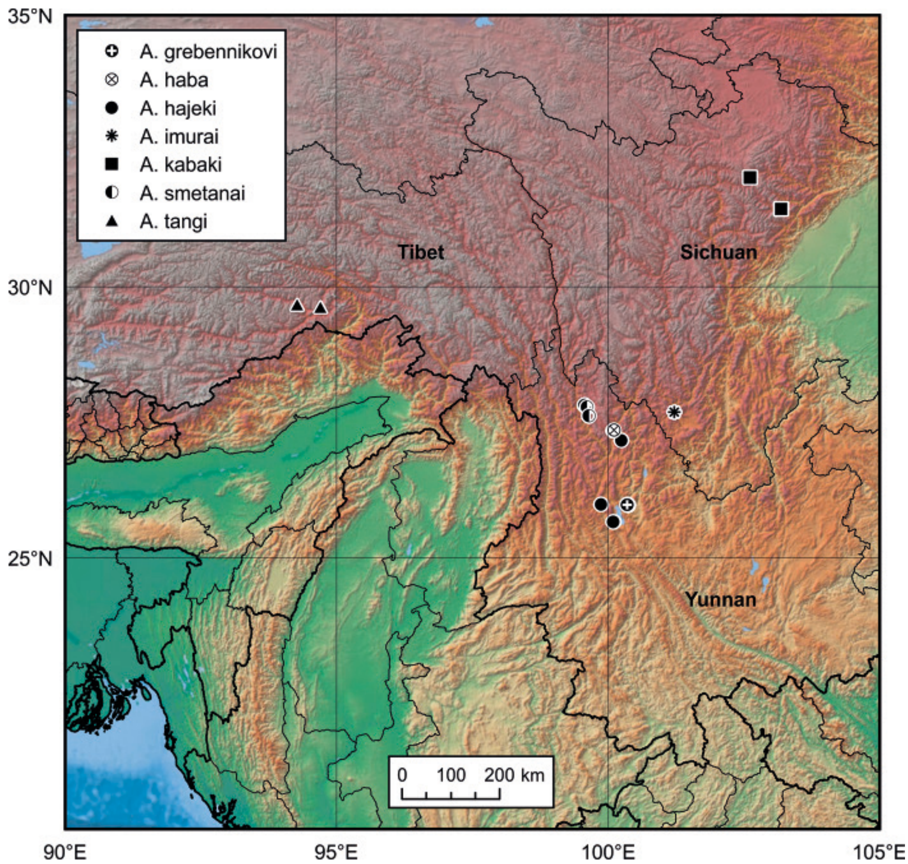


Fig. 122. Known distribution of *Anemadus smetanai* species group in China.

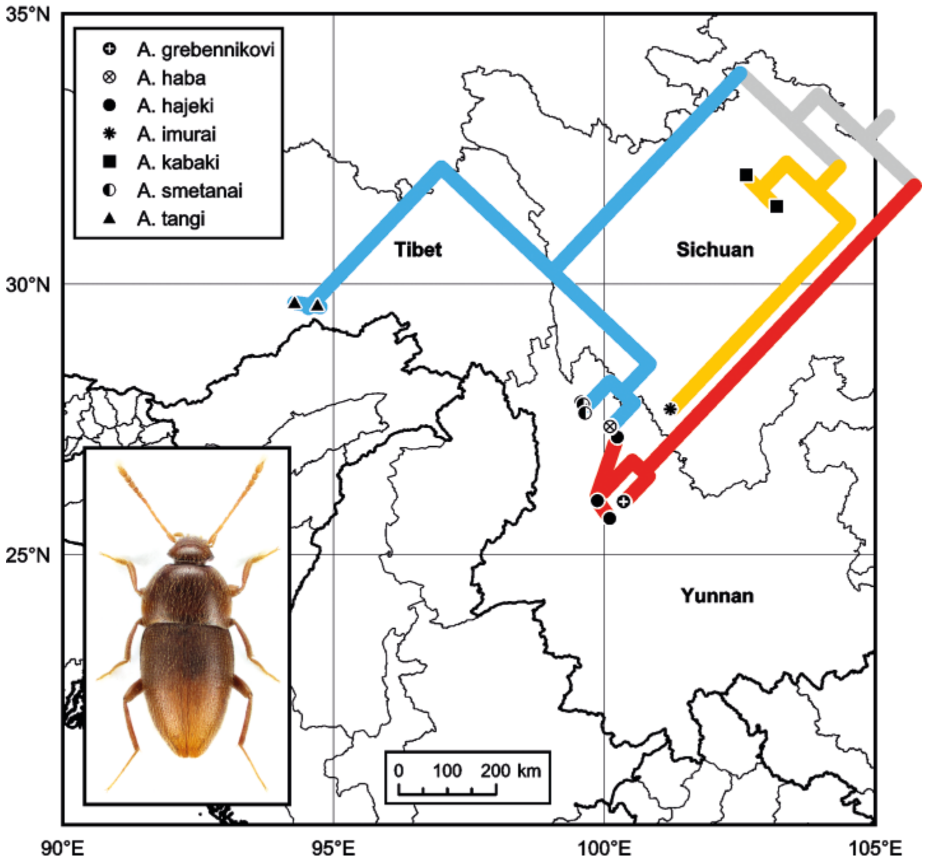


Fig. 123. Correlation of phylogenetic analysis of "*Anemadus smetanai* species group" with distribution of its members in China.

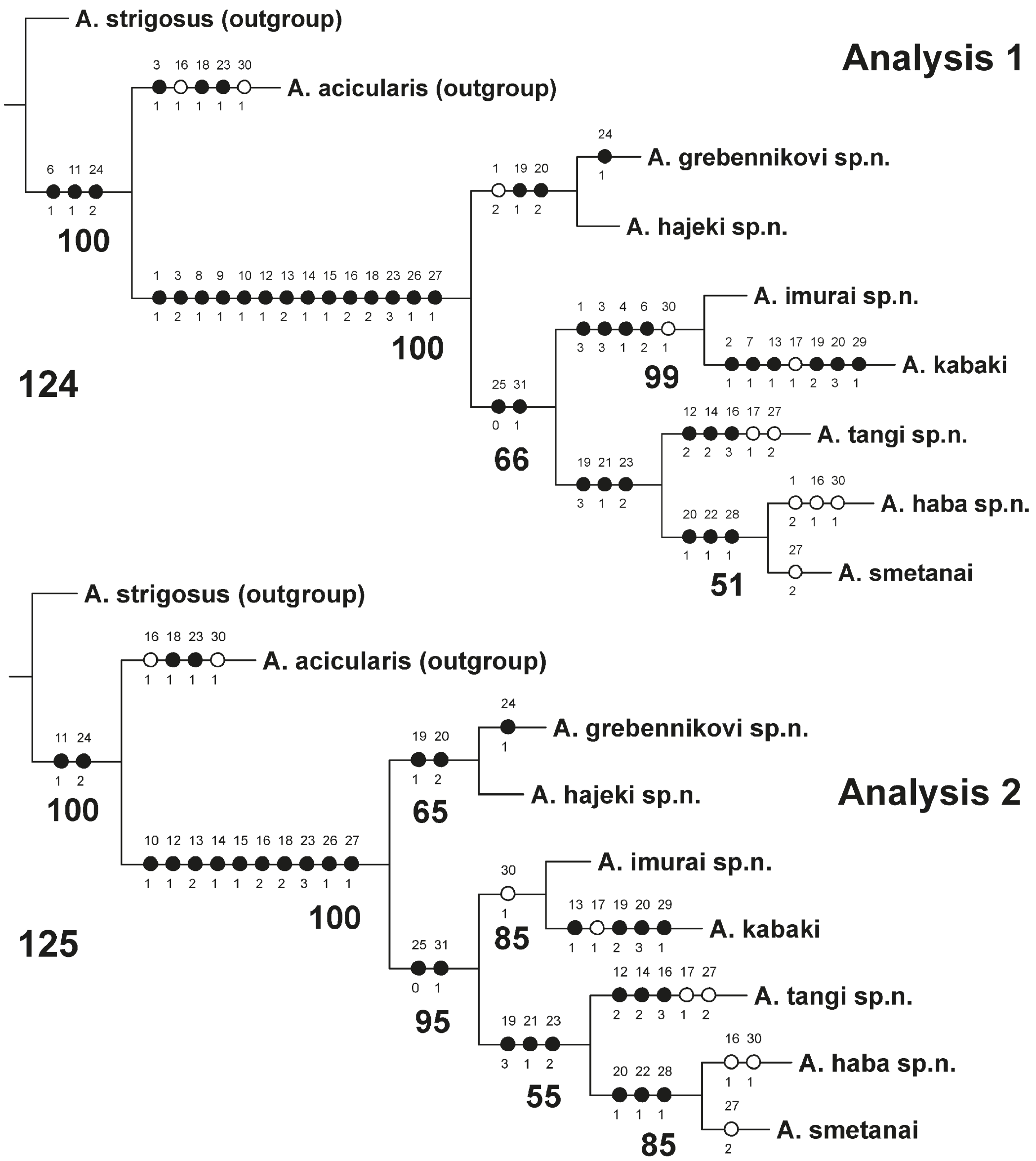


Fig. 124–125. Most parsimonious topologies from phylogenetic analyses of "*Anemadus smetanai* species group" based on morphological characters, obtained from implicit enumeration analyses. **124**: Analysis 1: character 1 ordered, character 5 inactive; single most parsimonious tree (length = 56, consistency index = 0.87, retention index = 0.82). **125**: Analysis 2: characters 1–9 inactive; single most parsimonious tree (length = 45, consistency index = 0.77, retention index = 0.75). Ambiguous characters are optimized with ACCTRAN (accelerated optimization in WinClada). Character numbers are given above, character states below. Solid circle indicates uncontroverted synapomorphy; empty circle indicates homoplasy or reversal apomorphy. Numbers below branches are bootstrap values (with 1000 replicates).

6. Discussion

6.1. Geographical distribution

Present knowledge on the distribution of Chinese *Anemadus* is limited, and new taxa from several species groups of the genus have been recently discovered (Perreau 2009, 2016; Wang & Zhou 2016). Based on current knowledge, the "*smetanai* species group" seems to be limited to the eastern part of Xizang (Tibet), Sichuan and north-western Yunnan (Figs. 122, 123). All species of the group have limited distribution and are local endemics, restricted to different "sky islands" in high mountains; the only known exception being *A. hajeki* sp.n., known from two adjacent mountain ridges (Yulong Xue Shan and Cang Shan, with distance between localities up to 160 km); but see comments on its geographical variability above. Similar pattern of allopatric lineages with rather limited distribution is known also in several groups of subterranean small carrion beetles, e.g. Neotropical *Proptomaphaginus* (Peck 1983) and south-east Nearctic *Ptomaphagus* (*Adelops*) and *Adelopsis* (Peck 1979, 1984).

The internal phylogeny of the group is congruent with the distribution of species (Fig. 123). Two species within the group (*A. imurai* sp.n. + *A. kabaki*) form a cluster distributed in Sichuan (Fig. 123, yellow branch). The remaining two supported clusters are from southern part of the north-western Yunnan (*A. grebennikovi* sp.n. + *A. hajeki* sp.n.) (Fig. 123, red branch) and from northern part of north-western Yunnan and Xizang (Tibet) (*A. haba* sp.n., *A. smetanai* + *A. tangi* sp.n.) (Fig. 123, blue branch, sister to the two species from Sichuan). Members of two of these clusters (*A. haba* sp.n. and *A. hajeki* sp.n.) seem to be found in closely situated localities (with distance between them only ca. 25 km); but Yulong Xue Shan and Haba Xue Shan Mts. are separated by the deep valley of the Jinsha River (a primary tributary of the upper Yangtze River), which probably completely isolates both upper forest and lower alpine species of these massifs. A similar pattern of distribution in two allopatric, closely related species is known also in the genus *Odontotrypes* Fairmaire, 1887 (Geotrupidae) with *O. haba* Král, Malý & Schneider, 2001 and *O. yulong* Král, Malý & Schneider, 2001 (Král et al. 2001).

6.2. Subterranean modifications

Members of the "*smetanai* species group" exhibit several morphological modifications, linked to a subterranean (in this case mostly endogean) habitat in a relatively constant, humid environment. Some can be considered as reductions, this probably applies to eye modifications (different extents of microphthalmy), absence of metathoracic wings, reduction of metendosternite and corresponding structures (Růžička 1999: 625, fig. 13), general depigmentation and weaker sclerotization of the body, especially of the abdominal tergites 2 – 6 (Fig. 73). In the clade *A. imurai* sp.n. + *A. kabaki*, these reductions are more prominent, with complete anophthalmy, general elongation of body, reduction of pronotum width and, in *A. kabaki*, elongation of appendages.

Other modifications are probably linked with improvement of the body rigidity to move in deep soil, here enhancing the interlocking devices of elytra and abdomen. Elytra are fused medially and elytral epipleuron is extended ventrolaterally, fixing tightly the abdomen. Other structures which can be related to rigidity of the abdomen is the presence of pairs of lateral apodemes, developed anteriorly on ventrites 4 – 7 (Figs. 11, 12).

Similar, but much smaller and weakly sclerotized apodemes (Fig. 78) are found also in the Japanese *Cholevodes tenuitarsis* Portevin, 1928, another genus of Anemadina, but are missing in other species groups of *Anemadus*. However, the homology of these structures remain questionable. The single species of *Cholevodes* Portevin, 1928 from Japan also has slightly reduced size of eyes, distinctly slender legs, but functional metathoracic wings (Nishikawa 1994). It is reported to occur in cavities of decayed trees and under bark of rotten logs (Nishikawa 1994).

Similar structures were reported also on ventrite 7 in several species of the "*Tachinus fimbriatus* species group" (Staphylinidae: Tachyporinae), such as *T. holzschuhi* Schülke, 2006 from Bhutan and *T. loebli* Schülke, 2006 and *T. paramalaisei* Li & Ohbayashi, 1996 from Nepal (Schülke 2006: 1704, fig. 6H, 1707, fig. 9A, 1712, fig. 14I).

6.3. Monophyly of Anemadini and Anemadina

Few apomorphic characters presently support the monophyly of Anemadina and even of the whole tribe Anemadini (Newton 1998; Perreau 2000). An unexpected consequence of the detailed investigation of the "*Anemadus smetanai* species group" is to bring to light a new female genital structure: the genital annulus, a sclerotized oval to round structure located at the bottom (so in the anterior part) of the invaginated vaginal ducts. This structure is abundantly illustrated in this paper (Figs. 63 – 71, 80). Its size is variable, either small (with its diameter less than 1/3 of maximum width of tergite 10, which seems to be the plesiomorphic state; Figs. 63 – 65, 67) or large (with its diameter 0.6 – 1.1 as wide as maximum width of tergite 10; Figs. 66, 68 – 71); with either a narrow (e.g., Figs. 67, 68) or broad rim (e.g., Fig. 71). It probably works as an attachment for muscles. The presence of this character has been checked in other species groups of *Anemadus*: *A. acicularis* (Fig. 63), *A. leonhardi*, *A. strigosus* (Fig. 64), and in the three other genera of Anemadina: *Anemadiola* (checked in *A. smetanai* Perreau, 1996), *Cholevodes tenuitarsis* (Fig. 80) and *Speonemadus* (checked in *S. subcostatus* (Reiche, 1864)). In Nemadina, we find presence of this structure in *Nemadus colonoides* (Kraatz, 1851), *N. japanus* Coiffait & Ueno, 1955 and *N. asagi* Nishikawa, 1986. The absence of a genital annulus has been checked in the three other subtribes of Anemadini: Paracatopina (in *Paracatops relatus* (Broun, 1893), which has nevertheless other kinds of differentiated structures in the vaginal ducts) and in Eocatopina (in *Eocatops ellipticus* Jeannel, 1936). The phylogenetic significance of this character, which has not yet been recorded in other groups of Leiodidae, necessitates an exhaustive inventory of species provided with these structures. Such an inventory is beyond the scope of this paper.

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8. References

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***Anemadus tangi* Růžička & Perreau, 2017:** http://zoobank.org/urn:lsid:zoobank.org:act:AE5998E8-2571-446E-953A-AD4472DE34E8

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