

New insight into the systematics of Heteromurini (Collembola: Entomobryidae: Heteromurinae) with special reference to *Alloscopus* and *Sinodicranocentrus* gen.n.

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Abstract. Classification of Heteromurini represented by *Heteromurus* and *Dicranocentrus* is currently under debate due to the presence of 5 or 6 antennal segments, respectively. Among the Heteromurini, *Alloscopus* is traditionally considered to be closely related to *Heteromurus* but its phylogenetic position is challenged by recent molecular evidence. A multilocus molecular phylogeny and topology tests conducted here indicate the closer relationship of *Alloscopus* and *Dicranocentrus*, and one non-*Dicranocentrus* basal group, *Sinodicranocentrus* gen.n. Two new species, *Alloscopus bannaensis* and *A. liuae*, are described from southern China. Intact tergal chaetotaxy including macrochaetae, microchaetae and S-chaetae is illustrated in *Alloscopus* for the first time. A new genus *Sinodicranocentrus* gen.n. is also erected based on the unique paired outer teeth on unguis and S-chaetotaxic pattern. Transformation among S-chaetae on the fifth abdominal tergite is presented to further illuminate the possible relationships among Heteromurini taxa. Main distinguishing characters used in the classification of Heteromurini and the phylogenetic position of supraspecific taxa are discussed. Comprehensive keys to the genera of Heteromurini and the species of *Alloscopus* are provided. This study provides the new insight into the relationships among Heteromurini genera and highlights the great systematic values of intact tergal chaetotaxy within the tribe.

Key words. Classification, *Dicranocentrus*, *Heteromurus*, *Heteromurtrella*, molecular phylogeny, *Sinodicranocentrus* gen.n., S-chaetae.

1. Introduction

Heteromurinae (*sensu* ZHANG & DEHARVENG 2015) represents all scaled members which were in the past inside Orchesellinae (MARI-MUTT 1980a; SOTO-ADAMES et al. 2008). Traditionally, Heteromurinae members were grouped within Orchesellinae in the light of the subdivision of the first and the second antennal segments and ratio of dorsal side of abdominal segments IV/III at midline < 2 (Table 1). ZHANG & DEHARVENG (2015) based on tergal sensillar pattern, validated the Heteromurinae, including taxa with five (e.g. *Heteromurus* Wankel, 1860) and six antennal segments (e.g. *Dicranocentrus* Schött, 1893). Heteromurinae comprises two tribes, Heteromurini, with apically rounded or truncate scales present on antennae

and legs, and Mastigocerini with apically pointed scales on body, but absent in antennae and legs (ZHANG & DEHARVENG 2015).

Within Heteromurini, CIPOLA et al. (2016b) provided a diagnostic review for six taxa, and stated that their relationships were uncertain. In addition, many important morphological details, particularly homology of dorsal tergal chaetae, are still lacking for Heteromurini (ZHANG & DEHARVENG 2015).

Heteromurini species with five antennal segments are divided into four groups (MARI-MUTT 1980a): *Heteromurus* s.str., *Verhoeffiella* Absolon, 1900, *Alloscopus* Börner, 1906, *Heteromurtrella* Mari-Mutt, 1979b. These taxa

Table 1. Different classifications of Heteromurinae. Ant., antennal segments; Abd., abdominal segments; Th., thorax segments; *, genera without body scales.

Year	Author	Taxa	Genera	Diagnosis
1906	BÖRNER	Orchesellini	Not specified (include body with or without scales)	Ant. I and II subdivided
1939	WOMERSLEY	Orchesellini	<i>Alloscopus</i> , <i>Dicranocentrus</i> , <i>Heteromurus</i> , <i>Mastigoceras</i> , <i>Orchesella</i> *, <i>Verhoeffiella</i>	Ant. I and II subdivided, if not then dorsal length ratio of Abd. IV/III at midline < 2
1942	ABSOLON & KSEMAN	Lepidocyrtinae Heteromurini	<i>Heteromurus</i>	Not specified
1961	YOSHII	Orchesellinae	<i>Alloscopus</i> , <i>Dicranocentrus</i> , <i>Heteromurus</i> , <i>Orchesella</i> *	Ant. I and II subdivided
1980a	MARI-MUTT	Orchesellinae Heteromurini	<i>Alloscopus</i> , <i>Heteromurus</i> , <i>Heteromurtrella</i> , <i>Verhoeffiella</i>	Ant. I subdivided, II not; body scales apically rounded or truncate, present on antennae, legs and furcula
2008	SOTO-ADAMES et al.	Orchesellinae Heteromurini	<i>Alloscopus</i> , <i>Australotomurus</i> *, <i>Heteromurus</i> , <i>Heteromurtrella</i> , <i>Orchesellides</i> *, <i>Verhoeffiella</i>	Ant. I subdivided, II not
2015	ZHANG & DEHARVENG	Heteromurinae	Not specified	Body scales present; tergal sens formula as 22 133-3(4)
2016b	CIPOLA et al.	Heteromurinae	<i>Alloscopus</i> , <i>Dicranocentrus</i> , <i>Heteromurus</i> , <i>Heteromurtrella</i> , <i>Pseudodicranocentrus</i> , <i>Verhoeffiella</i>	Follow ZHANG & DEHARVENG 2015
	This study	Heteromurinae	<i>Alloscopus</i> , <i>Dicranocentrus</i> , <i>Heteromurus</i> , <i>Heteromurtrella</i> , <i>Pseudodicranocentrus</i> , <i>Sinodicranocentrus</i> gen.n.	Follow ZHANG & DEHARVENG 2015

were treated differently as genera (THIBAUD & MASSOUD 1973; SOTO-ADAMES et al. 2008; CIPOLA et al. 2016b) or subgenera (MARI-MUTT 1977, 1980a; LUČIĆ et al. 2007, 2008; LUKIĆ et al. 2015). Actually, the current diagnostic characters used for the supraspecific separation are imperfect, such as annulation of Ant. III characteristic of *Verhoeffiella*. This segment is also annulated in most *Alloscopus* species (BÖRNER 1906: p. 177). *Alloscopus* was originally erected as a subgenus of *Heteromurus* based on the presence of dental spines and the annulated Ant. III and IV (BÖRNER 1906). MARI-MUTT (1977) distinguished *Alloscopus* from *Heteromurus* s. s. by the presence of dental spines and the absence of postoccipital macrochaetae on dorsal head. The postantennal organ (PAO) observed in several species of *Alloscopus* (MARI-MUTT 1982, 1985b), has been the main distinguishing character from other groups (YOSHII & SUHARDJONO 1989). The presence of dental spines often failed to distinguish *Alloscopus* from other 5-segmented groups because dental spines are also present in two *Heteromurtrella* species (CIPOLA et al. 2016b). However, a molecular phylogeny with limited sampling grouped *Alloscopus* sp. with *Dicranocentrus* rather than *Heteromurus*, distinctly contrary to the traditional views (ZHANG et al. 2015).

The remaining Heteromurini genera having six antennal segments are obviously closely related. Three Neotropical *Pseudodicranocentrus* species were placed there from *Dicranocentrus* based on having ciliate prelabral chaetae and macrochaetae A1 and Ps2 on dorsal head (MARI-MUTT 1980a, 1981). A recent published monotypic genus *Falcomurus* Mandal, 2018 differs from others by 1+1 modified ('falcate' type in his original description) chaetae on dental base; the status of this species is very doubtful because of its typical *Dicranocentrus*-like habitus and obvious incorrect descriptions of several characters.

To elucidate the phylogenetic position of *Alloscopus*, we conduct a multilocus phylogeny and a detailed morphological comparison among *Alloscopus*, *Heteromurus* and *Dicranocentrus*. Four species of *Dicranocentrus* are also included to assess their status, because they have unique characters (paired outer unguis teeth, 8–10 sens on Abd. V) differing from typical *Dicranocentrus* (ZHANG et al. 2018b). S-chaetotaxic patterns on the fifth abdominal tergite, as well as other important distinguishing characters, are presented and discussed to further illuminate the possible relationships among Heteromurini taxa. Two new species of *Alloscopus* from southern China are described. We also provide a key to the genera of Heteromurini and a key to the species of *Alloscopus*.

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2. Material and methods

2.1. Taxa sampling and sequencing

All materials were collected by aspirator or Tullgren-Berlese funnels, stored in 99% ethanol at –20°C, morphologically examined using Nikon SMZ1000 and ZEISS AXIO Scope.A1 microscopes, and deposited in the Department of Entomology, College of Plant Protection, Nanjing Agricultural University (NJAU), P. R. China. Twelve species were selected for molecular analyses: *Orchesella cincta* and *Orchesellides sinensis* as the outgroup, and two, two, and six species from *Alloscopus*, *Heteromurus* and *Dicranocentrus*, respectively for the ingroup. Species names, collection localities and GenBank accession numbers are provided in Table 2.

DNA was extracted by using an Ezup Column Animal Genomic DNA Purification Kit (Sangon Biotech, Shanghai, China) following the manufacturer's standard protocols. PCR amplification of the four fragments, mitochondrial COI and 16S rDNA (16S) and nuclear 18S rDNA (18S) and 28S rDNA D1–3 (28S), was performed following ZHANG et al. (2014a,b). All successful PCR products were purified and sequenced by GenScript (Nanjing, China) on an ABI 3730XL DNA Analyzer (Applied Biosystems). Sequences were assembled in Sequencher 4.5

Table 2. Sequenced species, collection localities and GenBank accession numbers. Asterisk marked are newly sequenced in the present study and others are extracted from ZHANG et al. (2015, 2018b).

Species	Region	18S	28S	COI	16S
<i>Orchesella cincta</i>	France, Paris	KC236250	KC236290	KM978365	KC236208
<i>Orchesellides sinensis</i>	China, Jiangxi	KC236251	KC236293	KM978363	KC236209
<i>Heteromurus major</i>	France, Paris	KC236241	KC236282	KM978355	KC236201
<i>Heteromurus nitidus</i>	France, Pyrénées	KC236242	KC236283	KM978356	KC291493
<i>Dicranocentrus wangi</i>	China, Guangdong	KC236232	KC236273	KM978348	KC236192
<i>Dicranocentrus hainanicus</i>	China, Hainan	MH605085*	MH600063*	MH605083*	MH602410*
<i>Dicranocentrus gaoligongensis</i>	China, Yunnan	MH605089*	MG807259	MG807184	MG807229
<i>Dicranocentrus similis</i>	China, Yunnan	MH605088*	MG807247	MG807195	MG807217
<i>Dicranocentrus pallidus</i>	China, Yunnan	MH605087*	MG807243	MG807174	MG807213
<i>Dicranocentrus varicolor</i>	China, Yunnan	MH605086*	MG807234	MG807189	MG807204
<i>Alloscopus bannaensis</i> sp.n.	China, Yunnan	MH605090*	MH600062*	MH605084*	MH602411*
<i>Alloscopus</i> sp.	China, Tibet	KM978398	KM978335	KM978344	KM978389

(Gene Codes Corporation, Ann Arbor, Michigan, USA), blasted in GenBank and checked for possible errors, and were finally deposited in GenBank (Table 2). The preliminary alignment was carried out by using MAFFT v7.310 by the Q-INS-I strategy for 16/18/28S and G-INS-I strategy for COI (KATO & STANDLEY 2013), and then were checked and corrected manually. Partial ambiguous sites of 16S were excluded from all the analyses. Final concatenated alignment included 658 bp, 546 bp, 1672 bp, and 1251 bp for COI, 16S, 18S, and 28S, respectively.

2.2. Phylogenetic inference

The partitioned dataset was analyzed using maximum likelihood (ML) and Bayesian inferences (BI). ML reconstructions were performed in IQ-TREE v1.6.1 (NGUYEN et al. 2015). Partitioning schemes and the substitution models automatically were estimated by ModelFinder (KALYANAMOORTHY et al. 2017) in IQ-TREE. Node supports were calculated using 10,000 ultrafast bootstrap (UFBoot, HOANG et al. 2018) and 10,000 SH-aLRT replicates (GUINDON et al. 2010). An unpartitioned model (General Heterogeneous evolution On a Single Topology, GHOST; CROTTY et al. 2017), addressing rate variation across sites and lineages (LOPEZ et al. 2002), was also performed to recover the topology which may offer unique biological insights. BI-analyses were conducted in MrBayes 3.2.6 (RONQUIST et al. 2012) with the model unlinked and the overall rate of the model allowed to be different across partitions. Partitioning schemes and the best-fitting substitution models were assessed under the BIC criterion in PartitionFinder v2.1.1 (LANFAR et al. 2016). The compound Dirichlet priors “brlenspr = unconstrained: gamadir (1, 1, 1, 1)” for branch lengths were incorporated to avoid the problem of branch-length overestimation (ZHANG et al. 2012). The MCMC search was run for ten million generations with a sampling frequency of 0.001 with a burn-in of 25%. The other parameters were set as default options. Burn-in sufficiency, convergence between runs and effective sample size were checked in Tracer 1.6 (RAMBAUT et al. 2014).

Four topology hypotheses on constraining monophyly were tested by evaluation of Bayes factors (BFs): A, best trees without any constraints; B, *Dicranocentrus*; C, (*Alloscopus* + *Heteromurus*); D, ((*Alloscopus* + *Heteromurus*) + *Dicranocentrus*). Marginal likelihood estimator by stepping-stone sampling (XIE et al. 2011) was calculated in MrBayes. Informed topology was strictly constrained in the prior because standard way of BF tests of monophyly can be misleading (BERGSTEN et al. 2013). Markov chain Monte Carlo (MCMC) processes were as above (ngen = 10,000,000 samplefreq = 1,000). A logarithm difference ($\log BF_1 - \log BF_0$) in the range of three to five is considered to give strong evidence against the null hypothesis, whereas a delta above five gives strong evidence the null hypothesis cannot be rejected (KASS & RAFTERY 1995).

2.3. Morphological descriptions and abbreviations

Specimens were mounted, after clearing in Nesbitt's fluid, under a coverslip in Hoyer's solution, and were studied using ZEISS AXIO Scope.A1 microscope. Dorsal body chaetae nomenclature follows SZEPTYCKI (1979) and ZHANG et al. (2018b), dorsal cephalic chaetae follow MARI-MUTT (1979a) and SOTO-ADAMES (2008), tergal S-chaetae follow ZHANG & DEHARVENG (2015), labial palp follows FJELLBERG (1999), and labial chaetae follow GISIN (1967). The dorsal chaetotaxy is given per half-tergite in the descriptions.

Abbreviations

PAO – postantennal organ; **PLQ** – postlabial quadrangle; **Th. I–III** – thoracic segment I–III; **Abd. I–VI** – abdominal segment I–VI; **Ant. I–IV** – antennal segment I–IV; **mac** – macrochaeta(-ae); **mes** – mesochaeta(-ae); **mic** – microchaeta(-ae); **pe** – postero-extern lamella of unguiculus; **ms** – S-microchaeta(-ae) (microsensillum); **sens** – ordinary S-chaeta(-ae) on terga.

Table 3. Comparison of tree topology hypotheses by Bayes factor tests. Monophyly constraints: A, best trees without any constraints; B, *Dicranocentrus*; C, (*Alloscopus* + *Heteromurus*); D, ((*Alloscopus* + *Heteromurus*) + *Dicranocentrus*). ** and * respectively represent very strong and strong evidence against an alternative hypothesis.

Hypotheses	Marginal likelihood	Logarithm difference
A	−13788.59	0
B	−13792.18	3.59*
C	−13793.16	4.57*
D	−13797.66	8.77**

3. Results

3.1. Phylogenetic relationships

Partitioned ML and BI and unpartitioned GHOST-ML analyses generated identical topologies, separating sampled species into four main clades with high node supports (SH-aLRT > 88, UFBoot > 85, BPP (Bayesian posterior probabilities) = 1): (*Dicranocentrus gaoligongensis*-complex + (*Heteromurus* + (*Alloscopus* + remaining *Dicranocentrus*))). *Dicranocentrus* did not form a monophyletic group and was divided into two clades (Fig. 1). The *gaoligongensis*-complex represents a new genus of Heteromurinae: *Sinodicranocentrus* gen.n. (Fig. 1C). Monophyly of (*Heteromurus* + sister taxa) was not well supported (UFBoot < 70, BPP = 0.53). Bayes factor tests strongly rejected three alternative hypotheses B, C and D, which are hypothesis of monophyly of *Dicranocentrus* and hypothesis of *Alloscopus* closer to *Heteromurus* (Table 3). The new classification proposal for Heteromurinae genera is as follows:

Family Entomobryidae Schäffer, 1896

Subfamily Heteromurinae Absolon & Kseneman, 1942 *sensu* Zhang & Deharveng, 2015

Tribe Heteromurini Absolon & Kseneman, 1942

3.2. Key to the genera of Heteromurini

(*Falcomurus* not included because of its doubtful status)

- 1 Ant. II subdivided in adults; Abd. III with 2+2 or more central mac 2
- 1' Ant. II not subdivided in adults; Abd. III with 1+1 central mac 4
- 2 Prelabral chaetae bifurcated; dorsal head with mac A1 and Ps2 *Pseudodicranocentrus*
- 2' Prelabral chaetae not bifurcated; dorsal head without mac A1 and Ps2 3
- 3 Unguis with paired outer teeth; Abd. V with 8–10 sens *Sinodicranocentrus* gen.n.
- 3' Unguis with a single outer tooth; Abd. V with 4 sens *Dicranocentrus*

- 4 Abd. I with mac; Abd. II with 1+1 central mac; sens as and acc.p3 on Abd. V not displaced anteriorly ... 5
- 4' Abd. I without mac; Abd. II with 2+2 central mac; sens as and acc.p3 on Abd. V displaced anteriorly *Heteromurus*, 6
- 5 PAO present; postoccipital mac on dorsal head absent; sens acc.p3 present and acc.p4 absent on Abd. V *Alloscopus*
- 5' PAO absent; postoccipital mac on dorsal head present; sens acc.p3 absent and acc.p4 present on Abd. V *Heteromurtrella*
- 6 Ant. III not annulated ... *Heteromurus* (*Heteromurus*)
- 6' Ant. III annulated *Heteromurus* (*Verhoeffiella*)

3.3. Genus *Sinodicranocentrus* Zhang gen.n.

Type species. *Dicranocentrus gaoligongensis* Zhang, 2018 (in ZHANG et al. 2018b).

Type locality. Gaoligong Mountain, Yunnan, China.

Diagnosis. Median to large size; scales apically rounded, truncate, or pointed with numerous short ciliations; scales present on Ant. I–II, Th. II to Abd. VI, legs, both sides of head, ventral tube and manubrium, and ventral side of dens; Ant. organ I–III well developed; Ant. III and IV annulated; Ant. IV without apical bulb and its apex with a pin chaeta and a bifurcate subapical organite; eyes 8+8; labral papillae pointed; prelabral and labral chaetae 4/5, 5, 4, all smooth; dorsal cephalic chaetotaxy with S0 as mac or mic, S2 absent, S4 present or not, and 5 anterior (A), 3 median (M), 1 posterocular (Pa5) and 12 postoccipital (P) mac; maxillary outer lobe with 4 smooth sublobal hairs; hypostomal and labial papillae with 2, 0, 5, 0, 4, 5 guard chaetae, respectively; lateral process of papilla E thin, with tip not reaching apex of labial papilla; labial chaeta L₁ ciliate and e and L₂ smooth; tibiotarsi without smooth chaetae; unguis with 3–4 inner, 2 outer and 2 lateral teeth; tenaculum with 4+4 teeth and its corpus with 1 ciliate chaeta; manubrium without smooth chaetae; dental base interno-basally with 1+1 large, ciliate chaetae; dens without spines; mucro bidentate with a basal spine; all tergal mic, mes and mac clearly ciliate under light microscope; Abd. I with 3+3 or 4+4 (m2i–4) central mac; Abd. II with 3+3 (m3–3e) central and 1+1 (m5) lateral mac; Abd. III with 2+2 (a3, m3) central and 3+3 (am6, pm6, p6) lateral mac; Abd. VI without smooth chaetae; tergal ms as 1, 0|1, 0, 1, 0, 0; tergal sens as 2, 2|1, 3, 3, 5–7 (elongated ones excluded), 8–10; sens acc.p3 on Abd. V present or absent.

Remarks. Four new *Dicranocentrus* species described in ZHANG et al. (2018b) belong to the new genus erected here. *Sinodicranocentrus* gen.n. differs from other Heteromurini genera by 2 paired outer teeth on unguis (1 in other genera) and abundant sens on Abd. V (4 or less in other genera) (Fig. 2). Great number (8–10) of sens on Abd. V resembles those in Orchesellinae (see ZHANG &

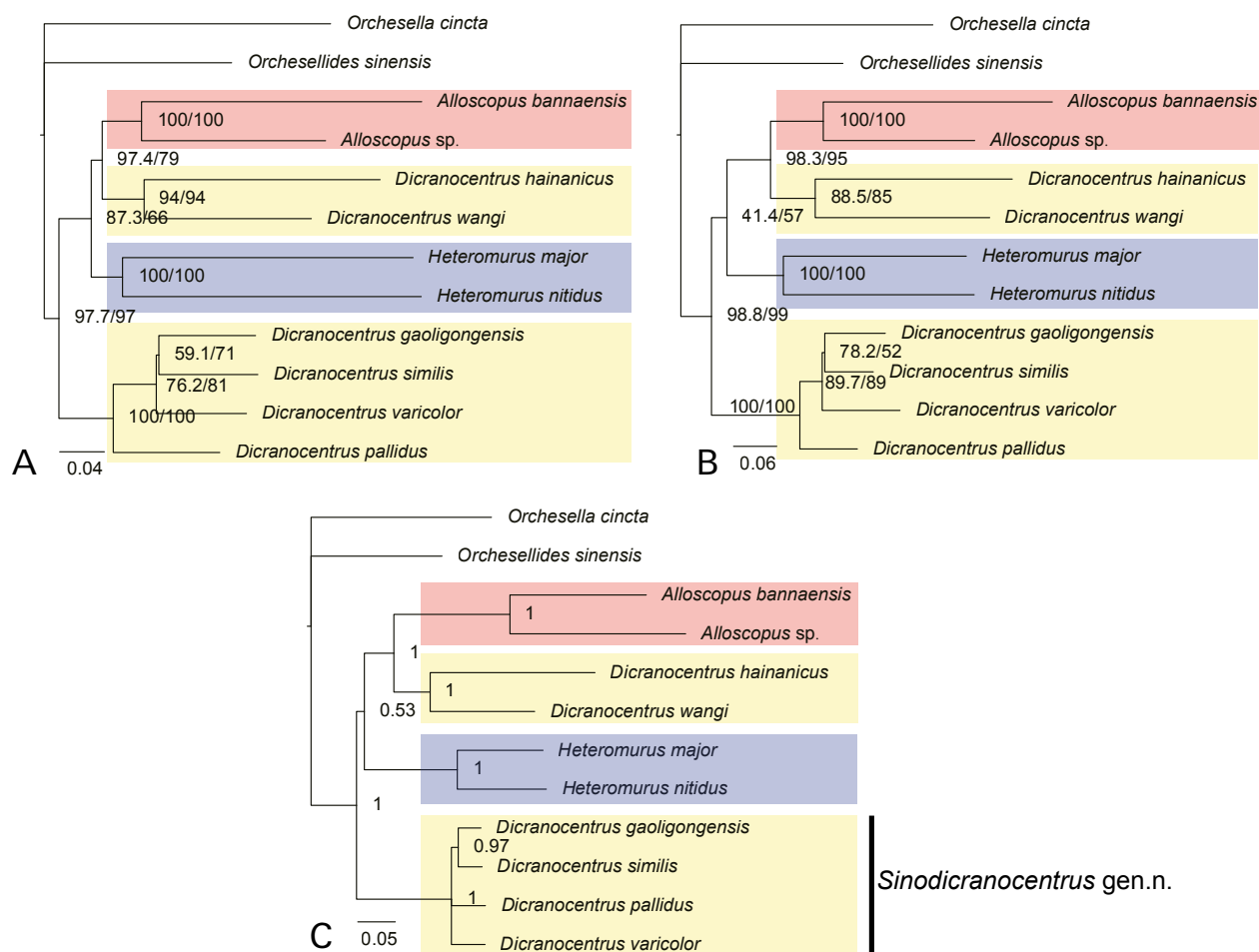


Fig. 1. Molecular phylogenies based on concatenated dataset. **A:** ML tree on partitioned analyses; **B:** ML tree on heterotachous GHOST model; **C:** Bayesian consensus tree. — Node values represent SH-aLRT and UFBoot supports for ML trees and posterior probabilities for Bayesian tree. Red, yellow and cyan colors indicate taxa of *Alloscopus*, *Dicranocentrus* and *Heteromurus*, respectively.

DEHARVENG 2015), the most basal group within Entomobryidae/Entomobryoidea. Molecular phylogeny further indicates *Sinodicranocentrus* gen.n. is the sister-group of the other Heteromurini lineages.

Some Asian species as *D. indicus* Bonet, 1930, from India and *D. janetscheki* Yosii, 1971 from Nepal, resembles *Falcomurus* and *Sinodicranocentrus* gen.n. by basal dens devoid of spines, but with one inner chaeta (MARI-MUTT 1979a: p. 40, fig. 51), and for this reason these species need to be reviewed. However, these species differ from both genera by head with S2 mac (absent in *Sinodicranocentrus* gen.n. and *Falcomurus*, S2 is S0 in MANDAL 2018), Abd. I with 3+3 or 4+4 central mac (absent in *Falcomurus*), tibiotarsi devoid of smooth chaetae (present in *Falcomurus*) and unguis with a single outer tooth (paired in *Sinodicranocentrus* gen.n.). This last feature also does not fit *Dicranocentrus fraternus* Mari-Mutt & Bhattacharjee, 1980 also from India in *Sinodicranocentrus* gen.n., although this species has other general similarities including the macrochaetotaxy pattern. However, these species of *Dicranocentrus*, as well as *Falcomurus chilikaensis* Mandal, 2018, the S-chaetae pattern is unknown, so they need to be revised to elucidate according to the current taxonomy.

Etymology. It is named after the type locality of the genus collected.

Distribution. Yunnan, China.

***Sinodicranocentrus gaoligongensis* (Zhang, 2018) comb.n.**

Dicranocentrus gaoligongensis Zhang, 2018 (in ZHANG et al. 2018b)

***Sinodicranocentrus similis* (Zhang, 2018) comb.n.**

Dicranocentrus similis Zhang, 2018 (in ZHANG et al. 2018b)

***Sinodicranocentrus pallidus* (Zhang, 2018) comb.n.**

Dicranocentrus pallidus Zhang, 2018 (in ZHANG et al. 2018b)

***Sinodicranocentrus varicolor* (Zhang, 2018) comb.n.**

Dicranocentrus varicolor Zhang, 2018 (in ZHANG et al. 2018b)

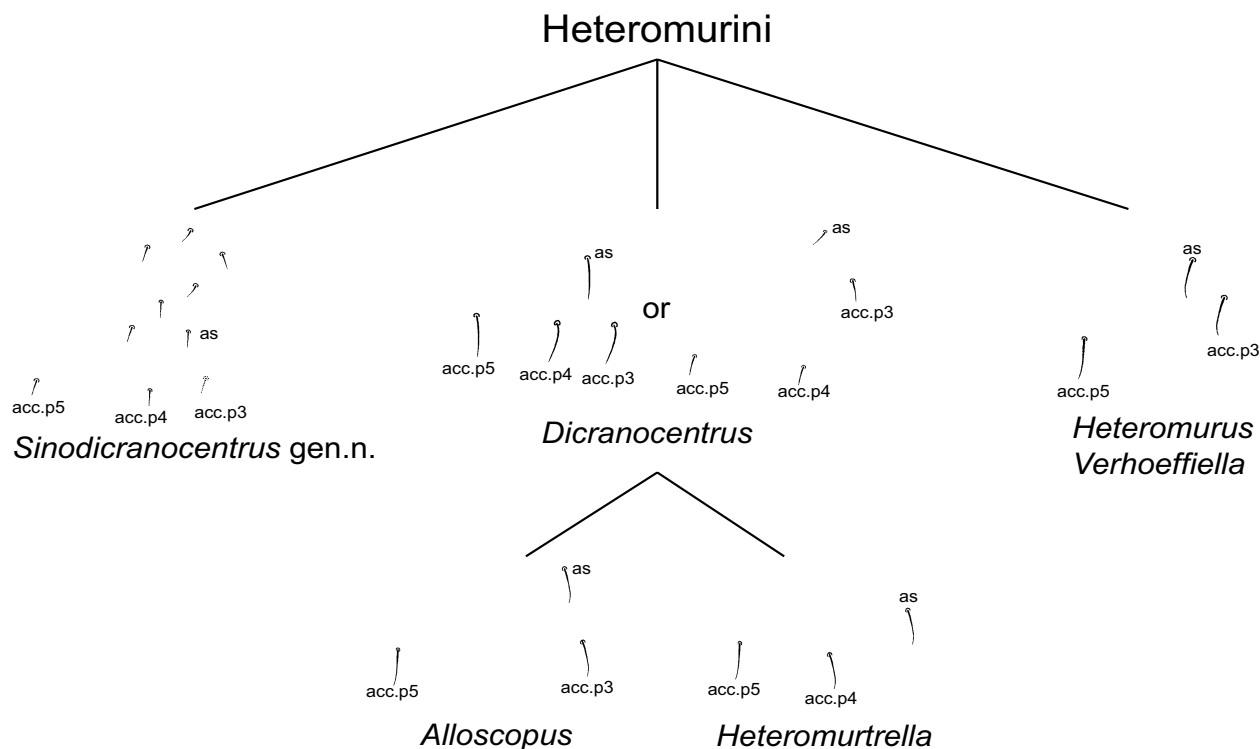


Fig. 2. Possible transformation among S-chaetotaxic patterns on Abd. V (left side) in Heteromurini. Information sources: *Sinodicranocentrus* from ZHANG et al. (2018b), *Dicranocentrus* from ZHANG & DEHARVENG (2015) and REN et al. (2018), *Alloscopus* from this study, *Heteromurtrella* from CIPOLA et al. (2016b), *Heteromurus* & *Verhoeffiella* from ZHANG & DEHARVENG (2015) and LUKIC et al. (2015).

3.4. Genus *Alloscopus* Börner, 1906

Syn. *Indoscopus* Prabhoo, 1971

Type species. *Heteromurus (Alloscopus) tenuicornis* Börner, 1906.

Type locality. Cibodas, West Java, Indonesia.

Diagnosis. Ant. I subdivided. Ant. III often and Ant. IV always annulated. Ratio of antennae to head less than three. Prelabral chaetae not bifurcated (Fig. 6B). Inner pair of labral papillae conical (Fig. 4E). Eyes 0–3 on each side. PAO small. Dorsal head with 7 (S0 present, S2 absent) sutural mac and without postsutural and postoccipital mac (except Pa5) (Fig. 4F). Abd. I with 2–3 (m2–4) mac. Abd. II with one (m3) central and 0–1 (m5) lateral mac. Abd. III with one (m3) central and 1–2 (pm6, p6) lateral mac. Abd. IV with 2 (A6, B5) central mac. Tergal ms as 1, 0|1, 0, 1, 0, 0; sens as 2, 2|1, 3, 3 (3+elongated ones), 3; on Abd. V sens acc.p3 present and acc.p4 absent (Figs. 5C, 7). Tenent hairs acuminate. Unguiculus outer edge with a large tooth or smooth edge (Fig. 4K). Anterior face of ventral tube without scales. Corpus of tenaculum with a chaeta. Manubrium and dens dorsally with smooth chaetae. Dental spines present and arranged in single (rarely two) rows (Fig. 7D). Mucronal spine mostly absent (Fig. 4N).

Remarks. PAO is the only character separating *Alloscopus* from other Heteromurini groups. Besides PAO, spe-

cies of *Alloscopus* differs from other *Heteromurus* s.lat. by postoccipital mac absent (except Pa5) on dorsal head, Abd. I–II with 2–3 and 1 (m3e absent) mac, respectively, and sens acc.p3 present on Abd. V but not displacing anteriorly (Figs. 5C, 7) and from *Dicranocentrus* s.str. by Ant. II not subdivided, eyes 0–3, 1+1 central mac on Abd. II and sens acc.p4 absent on Abd. V. Molecular phylogeny indicates its closer relationship with one clade of *Dicranocentrus* rather than *Heteromurus*. Its main geographical distribution in tropical Asia and Oceania does not fit the Holarctic distribution of *Heteromurus*. Therefore, following YOSHII & SUHARDJONO (1989), *Alloscopus* is treated here as a genus rather than subgenus.

It is noteworthy that type species *A. tenuicornis* described by different authors possibly represent a species complex. The forms described by MARI-MUTT (1977, 1982, 1985b) and YOSHII & SUHARDJONO (1989) share unique two (M3 absent) mac on dorsal head, but differ in posterior mac on Th. II–III. In addition, the number of dental spines is variable among those forms, 11–12 in BÖRNER (1906), ca. 20 in HANDSCHIN (1925), 6–10 (Java) or ≤ 7 (Micronesia) in MARI-MUTT (1977, 1982), > 10 in YOSHII & SUHARDJONO (1989). MARI-MUTT (1985b) reported variations in labial chaetae, postlabial chaetae, manubrial smooth chaetae, and 0–2 unpaired inner teeth on unguis based on materials from many islands of Philippines and Papua New Guinea. *Alloscopus fallax* Yoshii & Suhardjono, 1992 exactly coincides with the description of Mari-Mutt's *tenuicornis*. In this study, we tentatively accept Yoshii & Suhardjono's concepts on *tenuicornis* and *fallax*.

The following characters are shared by the two new *Alloscopus* species and are not repeated in the descriptions: ground color pale; scales apically rounded, truncate, or pointed with numerous short ciliations; scales present on Ant. I–II, body, legs, posterior side of ventral tube, lateral and ventral sides of manubrium, and ventral side of dens; Ant. III organ with 2 internal swollen and 3 guard S-chaetae (Fig. 4C); Ant. IV without apical bulb but its apex with a pin chaeta and a knobbed subapical organite (Figs. 4D, 6A); eyes absent but often with small patches; prelabral and labral chaetae 4/5, 5, 4, all smooth (Fig. 6B); clypeal chaetae with 3 prefrontal smooth chaetae but others not clearly seen; dorsal cephalic mac with 5 anterior (A), 3 median (M), 7 sutural (S) and 1 (Pa5) post-occipital mac (Figs. 4F, 6C); mandibles with 4+5 apical teeth; maxillary outer lobe with 4 smooth sublobal hairs (Fig. 4G); labial papillae A–E with 0, 5, 0, 4, 5 guard chaetae, respectively; lateral process of papilla E apically rounded and as thick as normal chaetae (Fig. 4H); labium with 5 smooth proximal chaetae; mentum with 5 smooth chaetae; PLQ with 2+2 smooth chaetae (Fig. 4I); pretarsus with a small chaeta on both sides; unguis with one outer and 2 lateral teeth; unguiculus lanceolate with an outer tooth (pe lamella); tenent hairs acuminate (Fig. 4K); tenaculum with 4+4 teeth and its corpus with one ciliate chaeta; manubrial plaque with 2 pseudopores (Fig. 4L); distal manubrium ventrally with 1+1 ciliate chaeta (Fig. 4M); dental lobe not seen; mucro bidentate without a basal spine (Fig. 4N); most tergal mic smooth under light microscope; Th. II with 2 (m1, m2) medio-medial, 3 (m4, m4i, m4p) medio-sublateral and 6 (p1–3, p1p, p2e, p5) posterior mac and chaetae m5, p1p2, p4 and p6 as mic; an additional mic antero-internal to acc.p6 but of unclear homology on Th. II–III; Th. III with p1–3, p1a and a4–6 as mac and a2, m1, m4–5, m7, p2a and p4–6 as mic (Figs. 5B, 6D); Abd. I with 3 (m2–4) mac and without p5 chaeta; Abd. II with 1 (m3) mac and without p5; Abd. III with 1 (m3) central mac; Abd. IV with 2 (A6, B5) central mac; Abd. V with 6 (m2, m3, m5, a6, p1, ap6) mac (Figs. 5C, 7E); tergal ms as 1, 0|1, 0, 1, 0, 0 and sens as 2, 2|1, 3, 3, 3 (elongated sens not included), 3.

Distribution. Mostly in tropical regions of Asia (southern China, India, Thailand, Malaysia, Indonesia, Philippines, Singapore) and Oceania (Papua New Guinea, Micronesia, Australia, Hawaii) and one species in South America (Peru, Ecuador).

3.5. *Alloscopus bannaensis* Zhang sp.n.

Figs. 3–5, Table 4

Description. Body length up to 3.02 mm (holotype). Orange pigment scattered on body, base of legs and manubrium (Fig. 3). Antenna 2.20–2.51 × (2.2 × in holotype) as long as cephalic diagonal. Antennal segment ratio as Ia : Ib : II : III : IV = 1 : 3.08–3.92 : 4.54–5.85 : 6.44–8.54 : 8.00–8.92 (1 : 3.36 : 4.64 : 7.36 : 8 in holotype). Ant.



Fig. 3. Habitus of *Alloscopus bannaensis* sp.n.

III and IV annulated. Smooth spiny mic at base of antennae: 6(5) dorsal, 4 ventral on Ant. Ia (Fig. 4A), 2 internal, 2 external and 1 ventral on Ant. II. Distal pseudopores 1, 2, 2 ventrally on Ant. Ib, II (Fig. 4B) and III, respectively. Distal short, slightly curved, thick S-chaetae 2, 3–4, 5(4) laterally on Ant. Ib, II (Fig. 4B) and III (Fig. 4C), respectively. Ant. II organ with 2–3 swollen S-chaetae (Fig. 4B). PAO overlapping. Labral papillae 4, outer ones rounded with smaller cone-like projections (Fig. 4E). Dorsal head with 8+8 antennal (An) mac (Fig. 4F). Tip of lateral process of labial papilla nearly reaching apex of labial papilla (Fig. 4H). Submentum with 2 small scales, an additional smooth chaeta present between a1 and m2 in one side of one specimen; chaeta e smooth or ciliate. Postlabium with 9 smooth chaetae and 2 chaetae posterior to PLQ ciliate (Fig. 4I). Trochanteral organ with 19–32 smooth spine-like chaetae; 12–18 in L-shaped arms and 7–14 between them (Fig. 4J). Tibiotarsi without smooth chaetae and with two rows of inner differentiated chaetae. Unguis inner edge with 2 paired teeth with unpaired ones absent (Fig. 4K). Abd. IV 1.03–1.23 × as long as Abd. III along dorsal midline. Ventral tube anteriorly with 8–11 ciliate chaetae; posteriorly with many chaetae and few scales, only apical 3 smooth chaetae clearly seen; each lateral flap with 13–16 smooth chaetae (Fig. 5A). Smooth, straight chaetae 3+3 and 1+1 present on manubrium dorsa-laterally and dens basally, respectively. Manubrial plaque with 3–4 ciliate chaetae on each side (Fig. 4L). Distal manubrium ventrally with 7–8 scales (Fig. 4M). Dens with 5–6 inner spines in a row. Smooth distal part of dens 1.79–1.94 × as long as mucro (Fig. 4N). Th. III with m6 as mac (Fig. 5B). Abd. III with 2 (pm6, p6) lateral mac. Abd. IV with 4 (E3 and F1–3) lateral mac; E4 as a mes with large socket. Abd. VI without smooth chaetae. Abd. IV with at least 11 elongated sens and 1 normal sens (ps) (Fig. 5C).

Etymology. Named after the type locality where the new species was collected.

Remarks. *Alloscopus bannaensis* sp.n. is the third blind species described in the genus although a pair of small

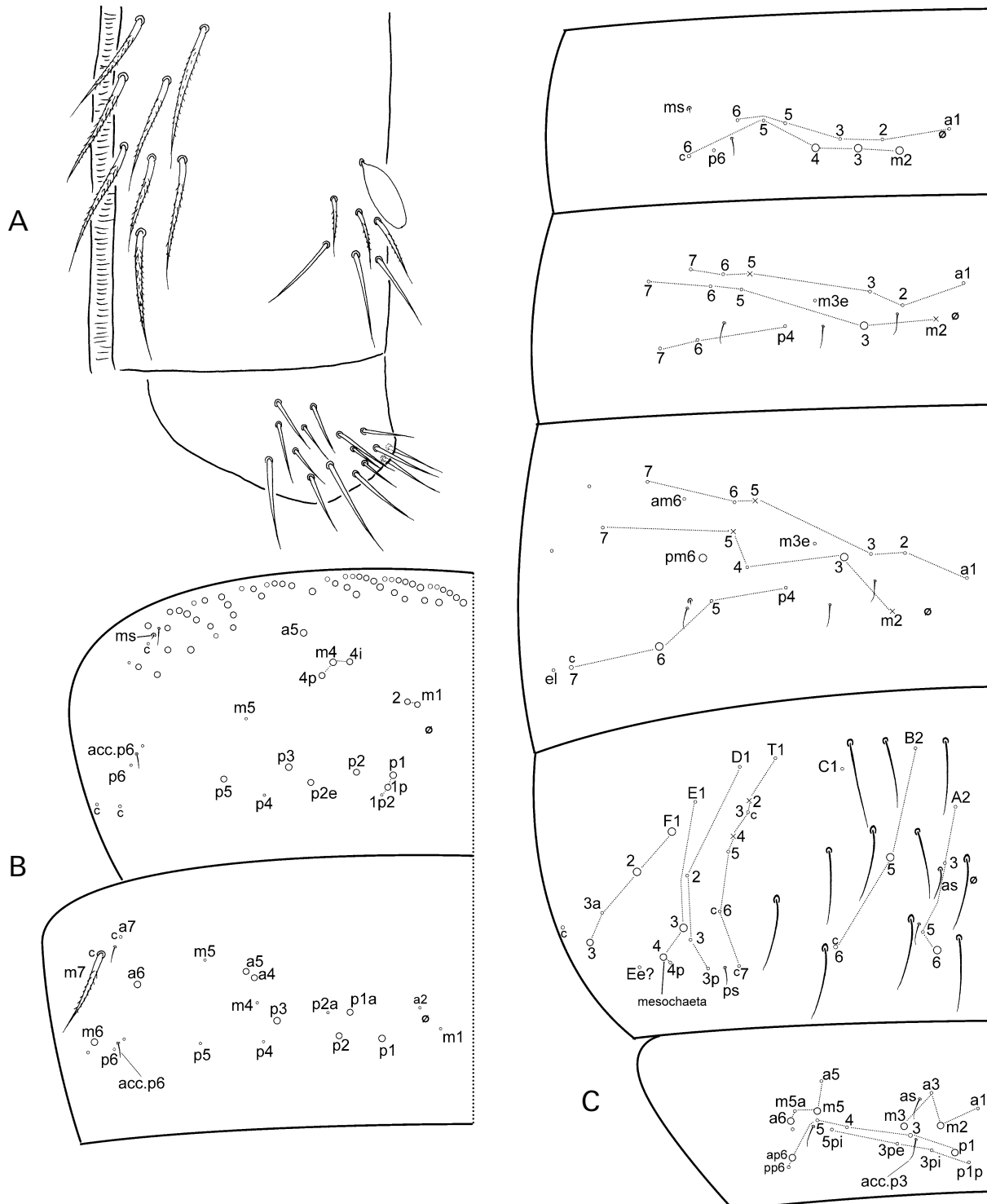
Table 4. Morphological comparison among four blind *Alloscopus* species. Reference: ⁽¹⁾MARI-MUTT (1985b).

Characters	<i>A. bannaensis</i> sp.n.	<i>A. liuae</i> sp.n.	<i>A. deharvengi</i> ⁽¹⁾	<i>A. thailandensis</i> ⁽¹⁾
Maximum body length [mm]	3.0	1.6	1.4	1.7
Cephalic mac An	8	8(7)	5	3
Chaetae on trochanteral organ	19–32	13–18	17	15
Tibiotarsal smooth chaetae	absent	present	present	absent
Unpaired inner teeth on unguis	0	1	0	1–2
Smooth chaetae on manubrium	3+3	4+4	4+4	4+4
Dental spines	5–6	3–5	3–5	3–6
Lateral mac on Abd. III	2 (pm6, p6)	1 (pm6)	2 (pm6, p6)	2 (pm6, p6)



← **Fig. 4.** *Alloscopus bannaensis* sp.n. **A:** right Ant. Ia; **B:** right Ant. II organ; **C:** right Ant. III organ; **D:** right Ant. IV apically; **E:** labral papillae; **F:** dorsal cephalic chaetotaxy (left side); **G:** maxillary outer lobe (right side); **H:** labial palp (left side); **I:** labial and postlabial chaetae (left side); **J:** trochanteral organ; **K:** hind claw; **L:** manubrial plaque; **M:** distal part of manubrium ventrally; **N:** mucro. — Symbols representing chaetal elements used in the figures are as follows: circle, chaeta; cross, bothriotrichum; circle with a slash, pseudopore; “v”-shape, scale.

↓ **Fig. 5.** *Alloscopus bannaensis* sp.n. **A:** ventral tube (lateral view); **B:** thoracic chaetotaxy (ciliate chaeta marked using letter c) (left side); **C:** abdominal chaetotaxy (left side).



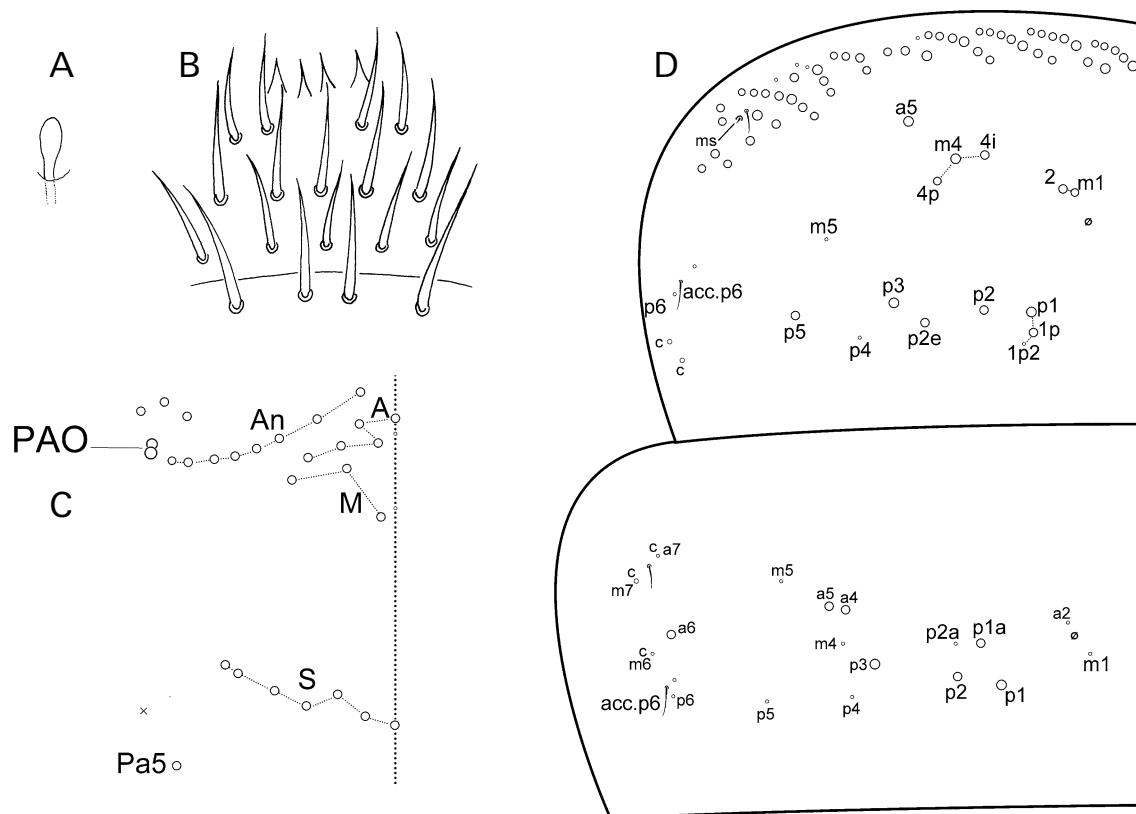


Fig. 6. *Alloscopus liuae* sp.n. **A:** Ant. IV subapical organite; **B:** labrum; **C:** dorsal cephalic chaetotaxy (left side); **D:** thoracic chaetotaxy (left side).

eye patches can be observed before mounting. It is most similar to *Alloscopus thailandensis* (Mari-Mutt, 1985) in most features but differs from the latter in having larger body size, 8 antennal mac, 19–32 chaetae on trochanteral organ, unpaired inner teeth absent on unguis, 3+3 dorsa-lateral smooth chaetae on manubrium (Table 4).

Habitat. In litter or on leaves of forest floor.

Type material. Holotype ♀ on slide, ‘CHINA, Yunn. [an], Mengla county | Menglun town | Xishuangbanna Tropical Botanical Garden | 21.919°N, 101.2709°E | 754 m | 27.xi.2017 | F. Zhang & D. Yu leg.’ – Paratypes 2 ♀ on slides and 4 in alcohol, same data as holotype (#17BN3).

3.6. *Alloscopus liuae* Zhang sp.n.

Figs. 6, 7, Table 4

Description. Body length up to 1.60 mm (1.55 in holotype). Pigment absent or light pigment sometimes restricted to small eye patches. Antenna 1.39–1.71 × (1.65 × in holotype) as long as cephalic diagonal. Antennal segment ratio as Ia: Ib: II: III: IV= 1 : 2.32–2.63 : 4.31–4.63 : 5.26–6.25 : 7.26–8.13 (1 : 2.63 : 4.63 : 6.25 : 8.13 in holotype). Ant. IV annulated. Smooth spiny mic at base of antennae: 4(3) dorsal, 3 ventral on Ant. Ia, one internal, one external and one ventral on Ant. II. PAO semidivided. Labral margin with 4 conical papillae (Fig. 6B). Dorsal

head with 8(7)+8(7) antennal (An) and 3 additional mac between An and antennae (Fig. 6C). Tip of lateral process of labial papilla not reaching apex of labial papilla. Submentum with 4 smooth and 1 ciliate chaetae and 2(1, 3) small scales; chaeta e smooth. PLQ with 2 posterior smooth chaetae. Trochanteral organ with 13–18 smooth spine-like chaetae; 9–12 in L-shaped arms and 4–6 between them (Fig. 7A). Tibiotarsi with two rows of smooth inner differentiated chaetae. Unguis inner edge with 2 paired and one unpaired median tooth (Fig. 7B). Abd. IV 1.13–1.47 × as long as Abd. III along dorsal midline. Ventral tube anteriorly with 6–9 weakly ciliate chaetae; posteriorly with 11–17 smooth chaetae and few scales; each lateral flap with 9–15 smooth chaetae (Fig. 7C). Smooth, straight chaetae 4+4 and 1+1 present on manubrium dorsa-laterally and dens basally, respectively (Fig. 7D). Manubrial plaque with 4 ciliate chaetae. Distal manubrium ventrally with 7–9 scales. Dens with 3–5 inner spines in a row. Smooth distal part of dens 4.42–5.61 × as long as mucro. Th. III with m6 as mic (Fig. 6D). Abd. III with one (pm6) lateral mac. Abd. IV with 3 (E3, F1, F3) lateral mac; E4, F3a and Ee as mes (Fig. 7E). Abd. VI with 1 smooth chaeta on each anal valve.

Etymology. Named after Ms Liu, who provided great help in the early study of this species.

Remarks. *Alloscopus liuae* sp.n. is the fourth blind species described in the genus. It is most similar to *Allosco-*

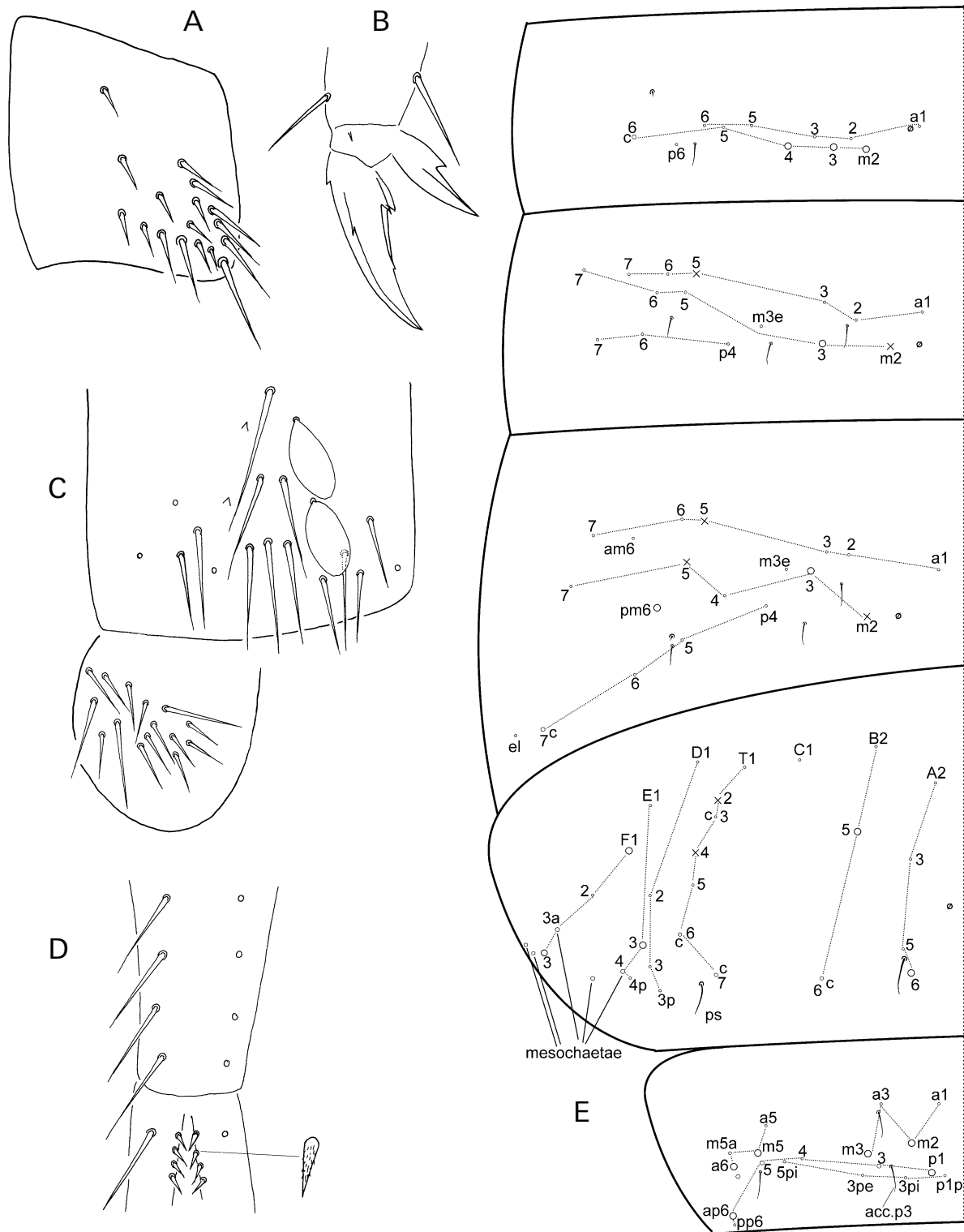


Fig. 7. *Alloscopus liuae* sp.n. **A:** trochanteral organ; **B:** hind claw; **C:** posterior face and lateral flap of ventral tube; **D:** furcula; **E:** abdominal chaetotaxy (left side).

pus deharvengi (Mari-Mutt, 1985) and differs from the latter in having 8(7) antennal mac, labial mentum with chaeta e smooth, unpaired median inner tooth present on unguis, and 1 + 1 lateral mac on Abd. III (Table 4).

Habitat. In litter.

Type material. Holotype ♀ on slide, 'CHINA, Guangdong, Guangzhou | Heshan Hilly Land Interdisciplinary Experimental Sta. [tion], 15.ix.2006, J.-X. Chen, F. Zhang & J.-G. Jiang leg. (#C9526)². Paratypes 12 ♀ and 1 ♂ on slides, same data as holotype.

3.7. Key to the species of *Alloscopus*

- 1 Mucro with a basal spine 2
- 1' Mucro without a basal spine 3
- 2 Eyes 2+2; Abd. I with 2+2 mac
..... *A. spinosus* (Prabhoo)
- 2' Eyes 3+3; Abd. I with 3+3 mac
..... *A. strebeli* Winter
- 3 Eyes 2+2; unguiculus without an outer tooth; Abd.
I with 2+2 mac *A. aspinosus* (Prabhoo)
- 3' Eyes 1+1 or absent; unguiculus with an outer tooth;
Abd. I with 3+3 mac 4
- 4 Eyes absent 5
- 4' Eyes 1+1 8
- 5 Tibiotarsi with rows of smooth inner chaetae 6
- 5' Tibiotarsi without rows of smooth inner chaetae ... 7
- 6 Abd. III with 1+1 lateral mac; unguis with an un-
paired median inner tooth *A. liuae* Zhang sp.n.
- 6' Abd. III with 2+2 lateral mac; unguis without un-
paired inner teeth *A. deharvengi* (Mari-Mutt)
- 7 Unguis without unpaired inner teeth; manubrium
with 3+3 smooth chaetae
..... *A. bannaensis* Zhang sp.n.
- 7' Unguis with 1–2 unpaired inner teeth (median and
apical); manubrium with 4+4 smooth chaetae
..... *A. thailandensis* (Mari-Mutt)
- 8 Tibiotarsi with rows of smooth inner chaetae
..... *A. tetracanthus* (Börner)
- 8' Tibiotarsi without rows of smooth inner chaetae ... 9
- 9 Th. II with 6+6 postero-medial (PM) mac
..... *A. fallax* Yoshii & Suhardjono
- 9' Th. II with less than 6+6 postero-medial (PM) mac
..... 10
- 10 Abd. II with 1+1 lateral mac
..... *A. tenuicornis* (Börner)
- 10' Abd. II without lateral mac 11
- 11 Th. II with 6+6(5+5) posterior (PM) mac; dens
with 27–55 spines in two rows
..... *A. multispinatus* (Mari-Mutt)
- 11' Th. II with 5+5(4+4) posterior(PM) mac; dens with
6–10 spines in one row ... *A. yosiius* (Mari-Mutt)

4. Discussion

4.1. Distinguishing characters used in Heteromurini

Morphological characters (Table 5) used in the taxonomy of Heteromurini generally include annulation of antennal segments, PAO, dental spines, chaetotaxy of head and Abd. I (see MARI-MUTT 1980a; CIPOLA et al. 2016b). However, the use of partial characters often brings confusion in practice. Annulation of Ant. III have been considered to be the only character distinguishing *Verhoeffiella* from three other *Heteromurus* s.lat. groups (MARI-MUTT 1980a,b). It also occurs in seven of 12 *Alloscopus* spe-

cies: *A. bannaensis* sp.n., *A. fallax*, *A. multispinatus*, *A. spinosus*, *A. strebeli*, *A. tenuicornis* and *A. tetracanthus*. Most authors overlooked the original definition of *Alloscopus*, in which BÖRNER (1906: p. 177) clearly stated the annulation of Ant. III–IV. PAO in *Alloscopus* is very small and slightly larger than sockets of mac and thus is often overlooked in early studies (MARI-MUTT 1977, 1982). Dental spines are present in *Dicranocentrus*, *Alloscopus* and *Heteromurtrella* and thus cannot be used as the main character separating *Alloscopus* from *Heteromurtrella*, or even some species in the same genus, due to interspecific overlap (e.g. Table 4).

Several recent studies in Heteromurini (CIPOLA et al. 2016b; SOTO-ADAMES & ANDERSON 2017; REN et al. 2018; LUKIĆ et al. 2018; ZHANG et al. 2018b), as well as this study, highlight the great significance of intact cephalic and tergal chaetotaxy at both generic and species levels, and consequently for modern taxonomy of Entomobryoidea. Heteromurini species show homogeneous chaetotaxy (MARI-MUTT 1979a,b, 1980b; CIPOLA et al. 2016b; LUKIĆ et al. 2018; ZHANG et al. 2018b). However, some groups of setae have unstable patterns and therefore cannot be defined as diagnostic characters. Example is the presence of postoccipital mac in head of all genera, except *Alloscopus* and some species of *Dicranocentrus* (*marias* group), therefore the loss of these mac happened more than once in Heteromurini (one in *Alloscopus* and other in *Dicranocentrus* part) or these taxa are related (from lineages of Neotropical *Dicranocentrus*). *Alloscopus* is mainly distributed in Tropical Asia and Oceania (Table 5). This latter hypothesis cannot be ruled out, since similar taxa with the same disjoint distribution (Asia South to Oceania with Neotropical) have already been observed in other Entomobryidae (CIPOLA et al. 2016a,b, 2017). In the same context, *Heteromurus*, *Verhoeffiella* and at least *Dicranocentrus litoreus* Mari-Mutt, 1985a from Philippine Islands, are devoid of mac on Abd. I. Therefore, this reduction is certainly an independently derived character state, since *Sinodicranocentrus* (basal group) has 3 central mac (Table 5). In addition, these data (Fig. 1) certainly indicate that the presence of at least 3 central mac (m2–4) on Abd. I is one characteristic conserved in most of Heteromurini taxa, while 5 or more central mac present in some *Dicranocentrus* species (and probably *Pseudodicranocentrus*) are derived additions (Table 5). Regardless of these hypotheses in the chaetal transformation series, it is evident that some elements of macrochaetotaxy are not robust enough to support some generic diagnoses, but that macrochaetotaxy can be used for interspecific determinations.

Species identification only relying on macrochaetotaxy has difficulty in many morphologically conserved genera or species complexes, such as *Pseudoparonella* (YOSHII 1989) and *Lepidocyrtus* (SOTO-ADAMES 2002), *Tomocerus* (YU et al. 2017), *Coecobrya* (ZHANG et al. 2018a), *gaoligonensis*-complex (ZHANG et al. 2018b). Consequently, tergal mic and S-chaetae could provide potential for separation of closely related species in Heteromurini as in *Sinodicranocentrus* (ZHANG et al. 2018b).

Table 5. Morphological comparison among the genera of Heteromurini. Symbol +, present; –, absent; status in brackets rarely present (*Falcomurus* is not included because of its doubtful status).

Characters	<i>Sinodicranocentrus</i> gen.n.	<i>Dicranocentrus</i>	<i>Pseudodicranocentrus</i>	<i>Alloscopus</i>	<i>Heteromurtrella</i>	<i>Heteromurus</i> (<i>Heteromurus</i>)	<i>Heteromurus</i> (<i>Verhoeffiella</i>)
Ant. II subdivided	+	+	+	–	–	–	–
Ant. IV annulated	+	+	+	+	+(–)	+	+
Ant. III annulated	+	+	+	+/–	–	–	+
Number of eyes	8	8	8	0–3	0/2/6	0/3/8	0
PAO	–	–	–	+	–	–	–
Bifurcate prelabral chaetae	–	–	+	–	–	–	–
Mac on dorsal head							
A1 and Ps2	–	–	+	–	–	–	–
S0	+/–	+	+	+	+/–	+/–	–
S2	–	+/–	–	–	–	–	–
postoccipital	+	+/–	+	–	+	+	+
Outer teeth on unguis	paired	single	single	single	single	single	single
Dental spines	–	+/–	–	+	–(+)	–	–
Mucronal spine	+	+	+	+/–	+/–	+/–	+
Mac on Abd. I	3/4	0/2–7	4/5	2/3	1–3	–	–
Central mac on Abd. II	3	2(3,4)	3	1	1	2	2
Central mac on Abd. III	2	2/3(4)	3/4	1	1	1	1
Sens on Abd. V							
Number	8–10	4	?	3	3	3	3
acc.p3	+/–	+	?	+	–	+	+
acc.p4	+	+	?	–	+	–	–
as and acc.p3 displaced anteriorly	–	+/–	?	–	–	+	+
Main geographical distribution	Southern China	Pantropical	Central America	Tropical Asia and Oceania	Pantropical	Holarctic	Europe

Caution is required because these elements are often lost during slide preparation or covered by scales. Tergal sens are often associated with primary chaetae (named as acc. in ZHANG & DEHARVENG 2015); sens associated with secondary mic in tandem were also observed in *Dicranocentrus* (REN et al. 2018), *Verhoeffiella* (LUKIĆ et al. 2018) and *Alloscopus* (this study). We recommend using intact chaetotaxy including mac, mic and S-chaetae as important descriptive components for the taxonomy of Heteromurini.

4.2. Classification of Heteromurini

This study provides new insights for the classification of Heteromurini by integrating morphological (Fig. 2, Table 5) and molecular evidence (Fig. 1, Table 3), although the phylogeny is not completely resolved. Possible transformation of S-chaetotaxic patterns across Heteromurini taxa are illustrated (Fig. 2) due to the great phylogenetic significance of tergal S-chaetae (ZHANG & DEHARVENG 2015; ZHANG et al. 2015). Heteromurini can be roughly divided into three clades (Fig. 2): *Sinodicranocentrus* gen.n., *Dicranocentrus*-group and *Heteromurus*-group.

Sinodicranocentrus gen.n. appears basal within Heteromurini (Fig. 1). It is distinguished morphologically by paired outer teeth on unguis (probably autapomorphic) and 8–10 S-chaetae on Abd. V. The latter character is likely plesiomorphic, since this number and pattern of sens is similar to *Orchesella* and *Orchesellides* (see ZHANG & DEHARVENG 2015). The reduction of sens on Abd. V correlates with reduced macrochaetotaxy (e.g. head and Abd. I part) in derived genera of Heteromurinae (*Heteromurus* + (*Alloscopus* + *Dicranocentrus*), and probably *Heteromurtrella* and *Verhoeffiella*, since *Orchesella* and *Orchesellides* have dense macrochaetotaxy. *Alloscopus* and *Heteromurtrella*, originally placed within *Heteromurus* s.lat., are closer to *Dicranocentrus* than to *Heteromurus* because of presence of mac on Abd. I, and similar S-chaetotaxic pattern on Abd. V derived from *Dicranocentrus*. Consequently, the number of three sens in Abd. V is not truly homologous, since acc.p3 was lost in *Heteromurtrella* and acc.p4 in *Alloscopus*, in addition the latter was also lost independently in *Heteromurus*. *Heteromurus* and *Verhoeffiella* are separated from others in the absence of mac on Abd. I (certainly one synapomorphy of *Heteromurus* + *Verhoeffiella*, see LUKIĆ et al. 2018) and acc.p4 on Abd. V, as and acc.p3 on Abd. V strongly displaced anteriorly, and non-tropical (northern)

Table 6. Morphological comparison between *Indoscopus* and *Alloscopus*.

Characters	<i>A. strebeli</i>	<i>I. spinosus</i>	<i>I. aspinosus</i>	Other <i>Alloscopus</i>
Eyes	3	2	2	0–1
Unguiculus outer tooth	1, large	0	0	1, large
Spine on dental lobe	1	0	0	0
Mucronal spine	present	present	absent	absent
Mac on Abd. I	3	2	2	3
Lateral mac on Abd. II	1	0	0	0(1)
Geographical distribution	South America	India	India	Southeast Asia and Oceania

distribution. They possibly originated from *Dicranocentrus*-like ancestor because anterior displacement of 2 inner sens also occurs in *Dicranocentrus* (*D. hainanicus*, Fig. 2). We expect another tropical genus *Pseudodicranocentrus* of unknown S- chaetotaxic pattern should be closely related to *Dicranocentrus* based on their morphological similarity (Table 5) and geographical distribution (MARI-MUTT 1980a, 1981). Final relationships among Heteromurini groups need more robust evidence.

Heteromurus (*Luoheteromurus*) *sinensis* Liu & Li, 1999 was described from China (Lushan Mountain, Jiangxi, China) and is probably a *Dicranocentrus* species, because its distribution and characteristics fully match those of *Dicranocentrus*, except for the number of antennal segments. It was incorrectly observed in original description resulting from regenerative antennal subdivision, a common condition in *Dicranocentrus* (MARI-MUTT 1979a: p. 27). In addition, we only discovered *Dicranocentrus* in the several expeditions of its type locality, therefore the presence of *Heteromurus* in this the region is doubtful.

The presence of PAO was previously considered the definitive character for *Indoscopus* Prabhoo, a genus later synonymized with *Alloscopus*. However, three species (*spinosus* (Prabhoo), *aspinosus* (Prabhoo), and *strebeli* (Winter)) originally placed in *Indoscopus* have some unique traits that differ from other *Alloscopus* members (Table 6). All three have more eyes, unguiculus outer tooth absent (*strebeli* (Winter) excluded), and different distributions. A mucronal spine is present in two of them but absolutely absent in other *Alloscopus* species. A strong spine on dental lobe and 1+1 lateral mac on Abd. II are present in *strebeli* but usually absent in others. Another *Alloscopus* species (*A. tenuicornis*) having 1+1 lateral mac is doubtful; YOSHII & SUHARDJONO (1989) synonymized their *A. tenuicornis* with *A. yosiius* (MARI-MUTT, 1985) but the latter does not have mac on Abd. II. Two instead of 3 mac on Abd. I are only present in two Indian species. The systematic status of *Indoscopus* requires reassessment considering the morphology of the above three species from India and South America.

Verhoeffiella is retained as a subgenus of *Heteromurus* for several reasons. First, the current evidence does not support the independent status of *Verhoeffiella* but indicates a close affinity to the *nitidus*-group of *Heteromurus*. They have almost identical dorsal macrochaetotaxy (MARI-MUTT 1980a; LUKIĆ et al. 2015) and S-chaetotaxic

pattern (Fig. 2). *Verhoeffiella* species are possibly derived from those taxa of *nitidus*-group adapted to cave life. It was tested by molecular analyses based on a wide sampling from European fauna (LUKIĆ et al. 2018). Second, the only character distinguishing *Verhoeffiella* from others, i.e. the annulation of Ant. III often occurs in *Alloscopus*. Other characteristic features of *Verhoeffiella*, e.g. elongation of antennae and unguis, likely represent gradients of troglomorphy, which are convergent features of adaption to cave dwelling (CHRISTIANSEN 1961).

The validation of *Falcomurus* Mandal, 2018 is very doubtful for several reasons. First, the species is more similar to *Dicranocentrus* than to *Heteromurus*-group in its appearance and tropical geographical distribution (MANDAL 2018: fig. 1). Second, modified chaetae or spines on dental base (1+1 ‘falcate’ chaetae in *Falcomurus*) are not rare in Heteromurinae, e.g., the large spines in *Alloscopus strebeli* Winter or compound spines in *Pseudodicranocentrus*. Third, original descriptions of several characters have obvious errors, such as ‘apical bulb’ (a thick sensillum), the number and position of bothriotricha on Abd. II–IV, homology assignment of tergal mac. In addition, some important characters (tergal sens, labium etc.) for current taxonomy of Entomobryoidea (e.g. ZHANG & DEHARVENG 2015) were not mentioned in the original description.

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Authors' contributions

F.Z. designed the study and led the writing of the manuscript. N.G.C. made general contributions in the manuscript, especially in chaetotaxic elements. F.Z., Z.-X.P. and Y.D. collected and analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.