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# Molecular phylogeny and trait evolution in an ancient terrestrial arthropod lineage: Systematic revision and implications for ecological divergence (Collembola, Tomocerinae)

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## ABSTRACT

Phylogenetic assessments of functional traits are important for mechanistically understanding the interactions between organisms and environments, but such practices are strongly limited by the availability of phylogenetic frameworks. The tomocerin springtails are an ancient, widespread and ecologically important group of terrestrial arthropods, whereas their phylogeny and trait evolution remained unaddressed. In the present study, we conducted the first comprehensive phylogenetic reconstruction of Tomocerinae, based on a multi-loci molecular dataset covering all major lineages within the subfamily, using Bayesian inference (BI), maximum-likelihood (ML) and maximum-parsimony (MP) approaches. Divergence time was estimated and ancestral character state reconstruction (ACSR) was performed to trace the evolutionary history of five ecomorphological traits correlated with sensory and locomotory functions. Our results support the monophyly of Tomocerinae, and indicate that current classification of Tomocerinae only partially reflects evolutionary relationships, notably the commonest and speciose genus *Tomocerus* is polyphyletic. The subfamily probably originated in Early Cretaceous and diversified in two Cretaceous and one Eocene radiation events. As indicated by the evolutionary patterns of functional traits, multiple ecological divergences took place during the diversification of Tomocerinae. The study suggests a potential underestimation of ecological divergence and functional diversity in terrestrial arthropods, calls for an update of present trait databases, and demonstrates the value of macroevolutionary knowledge for improving the trait-based ecology. In addition, *Tomocerus*, *Tomocerina* and *Tritomurus* are redefined, a new genus *Yoshiicerus* **gen. n.** and new subgenera *Coloratomurus* **subgen. n.**, *Ciliatomurus* **subgen. n.**, *Striatomurus* **subgen. n.** and *Ocreatomurus* **subgen. n.** are described in the appendix.

## 1. Introduction

During the past decade, trait-based techniques have been developed as fundamental and standard approaches to understand the interactions between organisms and environments (e.g. Pey et al., 2014; Moretti et al., 2017; Wong et al., 2018), based on the *a priori* hypothesis that functional traits as predictors of species fitness are filtered by

environmental factors (Keddy, 1992; Violle et al., 2007; Brousseau et al., 2018). Theoretically, organisms' trait syndromes are not only shaped by the ecological filter, but also strongly constrained by phylogenetic niche conservatism (Harvey and Pagel, 1991; Wiens and Graham, 2005) and trait trade-offs (Garland, 2014). While trade-offs can be assessed in a multidimensional trait-space framework (e.g. Céréghino et al., 2018; Ellers et al., 2018), evidence for phylogenetic conservatism is only

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implied in the macroevolutionary patterns of organisms. Therefore, illustrating the evolutionary patterns of traits in a robust phylogeny is essential for a comprehensive understanding of trait-based ecological phenomena.

Although phylogenetic inference has been well embedded in the methodological framework of trait-based ecology (e.g. Ovaskainen et al., 2017; Pearse et al., 2019), its application is strongly limited by the availability of existing phylogenetic frameworks (e.g. Ellers et al., 2018; Céréghino et al., 2018). For complex communities, when a robust phylogeny is absent, taxonomy is frequently used as a proxy to assess phylogenetic relatedness of traits (e.g. Ovaskainen et al., 2017; Céréghino et al., 2018). However, this substitution is still based on the assumption that current taxonomic systems of objective organisms have been robustly established on an evolutionary basis, which may not be true for the overwhelming majority of biota, notably the megadiverse terrestrial arthropods.

Springtails (Collembola) are a group of basal hexapods renowned for their ancient origin (ca. 400 million years ago, Mya), small body size (often <2 mm in length), winglessness and special abdominal apparatuses (i.e. ventral tube, tenaculum, furca). They are numerically dominant in various terrestrial environments, with most members dwelling in soil and playing essential roles in detrital food webs, and thus are key functional groups of soil fauna (Hopkin, 1997; Rusek, 1998; Potapov et al., 2016, 2018). Collembola have diverse ecomorphological traits determining their performance in various environmental conditions (e.g. Rusek, 2007; Salmon et al., 2014). Trait-based approaches have been widely applied to study the ecology of Collembola, notably their responses to anthropogenic environmental changes (e.g. Vandewalle et al., 2010; D'Annibale et al., 2017). However, although numerous attempts have been made (e.g. Xiong et al., 2008; Yu et al., 2016a,b; Leo et al., 2019; Sun et al., 2020), the phylogeny of Collembola and its lower taxa still remain largely unresolved, which hampers the mechanistic understanding of trait-based ecology of soil fauna.

To contribute a piece to the huge puzzle, in this study we focused on one of the commonest groups of Collembola, the Tomocerinae Schäffer, 1896. Amongst the earliest derived collembolan lineages (Sun et al., 2020; unpublished result), tomocerins have long (for Collembola) annulated antennae, dense layer of body scales, several pairs of thoracic bothriotricha, prominent spines on dens (mid segment of furca—the jumping organ) and elongated mucro (distal segment of furca), which allow them to colonise diverse habitats from upper soil to aboveground vegetation. Importantly, most tomocerins have distinctly larger body size (usually 3–8 mm in length) than other Collembola. Therefore, although usually not abundant, they can still constitute a large proportion of the community biomass (*sensu* Potapov et al., 2018). In the detrital food web, they are substantial grazers of microorganisms and non-vascular plants, and are considered to affect early-stage decomposition of litters by regulating fungal communities (Potapov et al., 2016, 2018).

Despite their broad range, wide habitat niche and ecological significance, tomocerins are amongst the most problematic groups of Collembola in terms of systematics and evolution (Yu et al., 2016b). Little substantial progress has been made since the last thorough review half-century ago (Yosii, 1967). This condition is a result of apparent morphological conservatism both through time and across taxa. The earliest definite fossil record of this subfamily is a Canadian amber dating back to the Campanian (79 Mya). Despite the missing body parts, the fossil tomocerin was strikingly identical with modern ones in morphology, while other coexisting Collembola all showed markedly differences from extant taxa (Christiansen and Pike, 2002). Compared to other groups, Tomocerinae has fewer taxonomic characters to use. Notably, the body chaetotaxy, which has been fundamental for both lower and higher-level classification of other groups (e.g. Yosii, 1960; Potapov, 2001; Zhang et al., 2019), is much less variable in this subfamily. As a result, the classification of Tomocerinae is for long controversial. On one side, the justification of all current generic

divisions used to be doubted (e.g. Christiansen, 1964; Massoud and Ellis, 1974; Ma et al., 2003; Lukić et al., 2010; Yu et al., 2014b, 2017b). On the other side, both molecular and morphological analyses have provided additional supports for several genera (e.g. Yosii, 1967; Felderhoff et al., 2010; Yu et al., 2014a; Yu and Deharveng, 2015), and even indicated further infra-generic division (e.g. Felderhoff et al., 2010; Zhang et al., 2014b; Yu et al., 2017a). Nevertheless, hypotheses of neither side have hitherto been rigorously tested under a comprehensive phylogenetic framework.

In several recent studies, detailed inspections have been conducted to find additional taxonomic characters and re-evaluate traditional ones. Several characters have been revealed of potential diagnostic value at supra-specific level (Fig. 1), including the number of mesothoracic bothriotricha (Yu et al., 2016a), the status of spine-like chaetae on the inner side of tibiotarsi (Felderhoff et al., 2010), the shape of dental spines (Zhang et al., 2014b) and the structures on mucro (Yu et al., 2014a). Besides the taxonomic value, these characters also represent functional traits of Collembola. Bothriotricha are considered to be sensitive to airflows (Hopkin, 1997), while the other structures are attached on the functional areas of legs and jumping organs. The sensory and locomotory functions determined by these traits are related to the habitat-niche of Collembola (Salmon et al., 2014). Therefore, evaluating these traits in a phylogenetic framework will not only help to resolve problems in systematics, but also improve our understanding of ecological divergences between lineages.

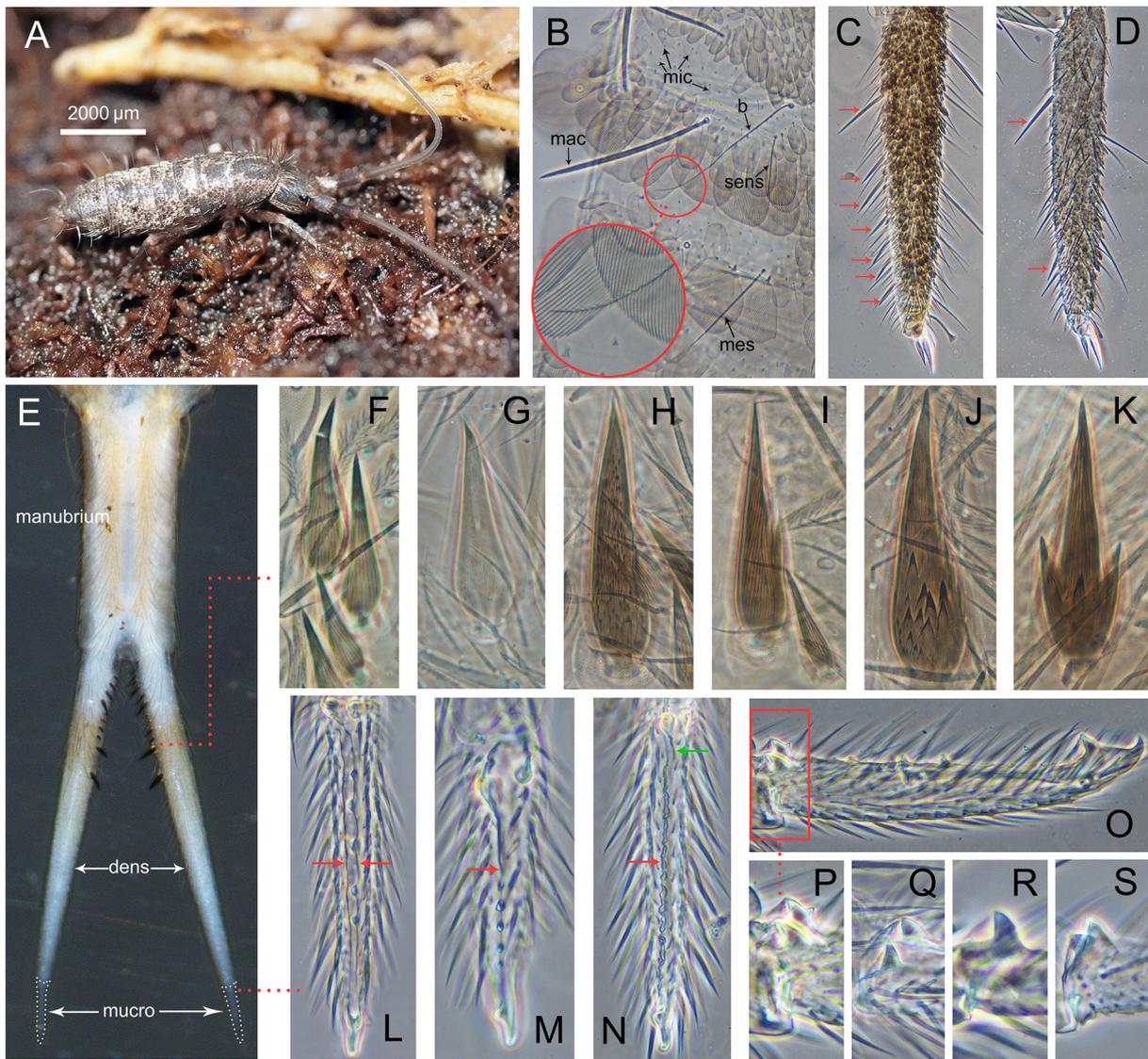
Recent applications of molecular phylogenetic approaches have begun to boost the evolutionary study on tomocerins. Several studies have shed light on the phylogenetic relationship between Tomocerinae and other Collembola (Yu et al., 2016b; Sun et al., 2020), and revealed extensive cryptic diversity within the subfamily (e.g. Felderhoff et al., 2010; Barjadze et al., 2016; Yu et al., 2018). However, existing phylogenetic analyses on Tomocerinae were based on very limited ingroups (e.g. Park and Lee, 1999; Fanciulli et al., 2000; Park, 2009; Yu et al., 2016b), thus they did not contribute much to the resolution of the confusing supra-specific relationships. Even the monophyly of the subfamily has not been rigorously tested by molecular phylogeny under a comprehensive sampling scheme.

In the present study, we conducted the first comprehensive phylogenetic reconstruction of Tomocerinae based on a multi-loci molecular dataset, covering most extant higher taxa and an extensive morphological diversity within the subfamily (e.g. long versus short antennae, presence versus absence of eyes, long versus short mucro). The dataset was analysed under both coalescent-based and concatenation-based frameworks, by using Bayesian inference (BI), maximum-likelihood (ML) and maximum-parsimony (MP) approaches. We estimated the divergence time between lineages, and traced the ancestral states and assessed the phylogenetic signals of several ecomorphological traits mediating sensory and locomotory functions. We hypothesised that (1) Tomocerinae as morphologically defined is monophyletic; (2) current classification of Tomocerinae only partially reflects its evolution, notably several problematic genera, e.g. *Tomocerus* Nicolet, 1842 and *Tomocerina* Yosii, 1955, may not represent natural groups, and (3) the supra-specific diversity of Tomocerinae can be attributed to ecological divergence, which can be reflected by the evolutionary patterns of traced ecomorphological traits. Moreover, this study also has implications for current trait-based ecology of soil invertebrates.

## 2. Material and methods

### 2.1. Taxon sampling and specimen examination

A total 53 species were sampled for the phylogenetic analyses, with closely related *Novacerus tasmanicus* (Womersley, 1937) of Lepidophorellinae Absolon, 1903 and *Harlomillsia oculata* (Mills, 1937) of Oncopoduridae Carl and Lebedinsky, 1905, and distantly related *Heteromurus major* (Moniez, 1889) of Orchesellidae (Börner, 1906) and



**Fig. 1.** Habitus and ecomorphological traits of Tomocerinae. **A**, habitus; **B**, dorso-lateral region of posterior thoracic segment (Th.) III, abdominal segment (Abd.) I and anterior Abd. II, showing main types of tergal chaetae, mac: macrochaeta, mes: mesochaeta, mic: microchaeta, b: bothriotrichum, sens: ordinary sensory chaeta; **C**, **D**, hind tibiotarsi, red arrows: blunt spine-like chaetae; **E**, dorsal side of furca; **F–K**, main types of dental spines; **L–M**, dorsal sides of right mucros, red arrows: complete dorsal lamellae, green arrow: rudimentary lamella; **O**, inner side of mucro; **P–S**, bases of mucros, showing basal teeth complex. Taxon affiliations: **A**, **E**, **J**, **L**, *Tomocerus (Ocreatomurus) subgen. n.*; **B**, **O**, **P**, *Yoshiicerus gen. n.*; **C**, **H**, *Tomocerus (Ciliatomurus) subgen. n.*; **D**, **F**, **M**, **Q**, *Pogonognathellus*; **G**, **S**, *Plutomurus*; **I**, *Tomocerus (Striatomurus) subgen. n.*; **K**, *Tomocerus (Coloratomurus) subgen. n.*; **N**, *Tritomurus*; **R**, *Monodontocerus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

*Folsomia quadrioculata* (Tullberg, 1871) of Isotomidae Schäffer, 1896 as outgroups. The ingroups consisted of six out of all nine extant genera and 49 species of Tomocerinae, including 35 *Tomocerus* (type genus), four *Pogonognathellus* (Börner, 1908), three *Monodontocerus* Yosii, 1955, three *Tritomurus* Frauenfeld, 1854, two *Tomocerina*, and two *Plutomurus* Yosii, 1956. Only two monotypic genera *Tomolonus* Mills, 1948 and *Aphaenomurus* Yosii, 1956, and an oligotypic and highly troglomorphic genus *Lethemurus* Yosii, 1970 (with two described species) were not included. Within the most speciose genus *Tomocerus*, species were sampled from as many species groups as possible, e.g. the *ocreatus*-group, the *nigrus*-group, the *kinoshitai*-group, as defined by previous studies (Zhang et al., 2014b; Yu et al., 2017a).

All species were collected at or near their type localities (Table B.1), including generic type species *Tomocerus minor* (Lubbock, 1862), *Pogonognathellus longicornis* (Müller, 1776), *Monodontocerus modificatus* Yosii, 1955 and *Tritomurus scutellatus* Frauenfeld, 1854. Specimens were captured by using aspirators or Tullgren-Berlese funnels and stored in

99% ethanol at  $-20^{\circ}\text{C}$ . Habitat preference and activity of species were observed and recorded on site. Where possible, living specimens were brought to laboratory to observe their locomotory performances. For morphological identification, specimens were thoroughly examined by using Nikon SMZ1000 (alcohol-preserved specimens) and Nikon Eclipse Ni microscopes (slide-mounted specimens), and compared with available type specimens, including those in the Yoshii's collection deposited in Muséum d'Histoire naturelle de Genève, Geneva, Switzerland (MHNG).

## 2.2. DNA extraction, amplification and sequencing

DNA was extracted by using an Ezup Column Animal Genomic DNA Purification Kit (Sangon Biotech, Shanghai, China) and following the manufacturer's standard protocols. Extractions were performed non-destructively for further morphological examination and identification of the specimens. Two mitochondrial gene fragments *COI* and *16S rDNA*,

and three nuclear gene fragments 18S rDNA, 28S rDNA D1–2 and D7–10 were amplified by using TC-5000 Thermal Cycler (TECHNE) in 25  $\mu$ L volumes containing 12.5  $\mu$ L of Premix Taq (TaKaRaTaq Version 2.0 plus dye), 1.25  $\mu$ L of each primer, 8  $\mu$ L of ddH<sub>2</sub>O and 2  $\mu$ L of template DNA. The primers, target fragment lengths, references and amplification programs are listed in Table B.2. All PCR products were checked on a 1% agarose gel. Successful products were purified and sequenced in both directions by Majorbio (Shanghai, China) on the ABI 3730XL DNA Analyser (Applied Biosystems). Raw sequences were assembled in Sequencher 4.5 (Gene Codes Corporation, Ann Arbor, USA), blasted in GenBank and checked for possible errors, and were then deposited in GenBank (Table B.1).

### 2.3. Phylogenetic reconstruction

Besides the newly generated 233 sequences, 27 additional sequences were extracted from the GenBank (Table B.1). For each gene fragment, sequences of all species were combined into a data matrix, and were preliminarily aligned by Muscle in Mega 7.0 (Kumar et al., 2016). The data alignments were checked by visual inspection, and then concatenated by Sequence Matrix 1.7.8 (Vaidya et al., 2011), generating a final 4680 bp alignment. Best-fitting substitution models for each fragments were assessed by using PartitionFinder2 (Lanfear et al., 2017) under the corrected Akaike Information Criterion (AICc), with GTR + I + G for 18S, 16S, 28S D7–10 and the first and second codon positions of COI, and TVM + I + G for 28S D1–2 and the third codon position of COI selected.

Phylogenetic reconstructions were conducted by using maximum-likelihood (ML), Bayesian inference (BI) and maximum-parsimony (MP) approaches. The ML analyses were conducted in the online CIPRES version of RAxML-HPC2 8.2.8 (Miller et al., 2010; Stamatakis, 2014). *H. major* and *F. quadrioculata* were selected as outgroups. Data were partitioned as five genes. GTRGAMMA model were selected. Bootstrap replicates were set to 1000.

The BI analyses were performed in the online CIPRES version of MrBayes 3.2.6 (Ronquist et al., 2012). *H. major* was selected as outgroup. Site model parameters were unlinked. To avoid the problem of branch-length overestimation, the compound Dirichlet priors 'brlenspr = unconstrained; gammadir (1, 1, 1, 1)' for branch lengths were incorporated (Zhang et al., 2012). Two runs were performed, with the number of generations set to 10<sup>8</sup> and the chain sampled every 10<sup>4</sup> generations. The initial 25% was set as burn-in, and other parameters were set as default. To confirm convergence, ASDSF (average standard deviation of split frequencies) and PSRF (potential scale reduction factor) values were visualised in MrBayes, and ESS (evaluating effective sample size) values were checked in Tracer v1.7.1 (Rambaut et al., 2018).

In the MP reconstruction, the concatenated data set was analysed in TNT v.1.5 (Goloboff and Catalano, 2016), by using either equal weighting or implied weighting for all characters, with all site states unordered. *H. major* was selected as outgroup. Trees were searched under traditional search, with 1000 random addition sequences, 100 trees saved per replication and tree bisection reconnection (TBR) swapping. Node support was measured by using symmetric resampling not influenced by uninformative characters, with 1000 pseudoreplicates, 100 addition sequences, and TBR branch swapping.

### 2.4. Divergence time estimation

Divergence time for major lineages was estimated by using \*BEAST in BEAST v.2.6.0 (Bouckaert et al., 2019), with parameters set as follows. Site models and clock models were unlinked for all gene fragments, whereas the gene trees were linked for COI + 16S and two 28S fragments, respectively, because of their genetic linkage. Uncorrelated lognormal relaxed clock and Yule process were applied. Because effective fossil calibrations for tomocerin Collembola were unavailable, and the mitochondrial substitution rate of Collembola was estimated to be

closest to that of Coleoptera (Cicconardi et al., 2010), we employed previous estimates of substitution rates by Papadopoulou et al. (2010): 3.36%, 1.08% and 0.12% pairwise divergence per Myr for COI, 16S and 28S, respectively, which represent some of the more rigorous estimates of evolutionary rates in hexapods (Ho and Lo, 2013). Monophyly of Tomocerinae was constrained to limit tree searching space. The MCMC chain was run twice, each with 10<sup>9</sup> generations, 10<sup>5</sup> sampling frequency, and the initial 10% were discarded as burn-in. The convergence was checked in Tracer v1.7.1 (Rambaut et al., 2018). Results from two independent runs were combined and summarised by using Log-Combiner and TreeAnnotator in the BEAST package.

### 2.5. Ancestral character state reconstruction

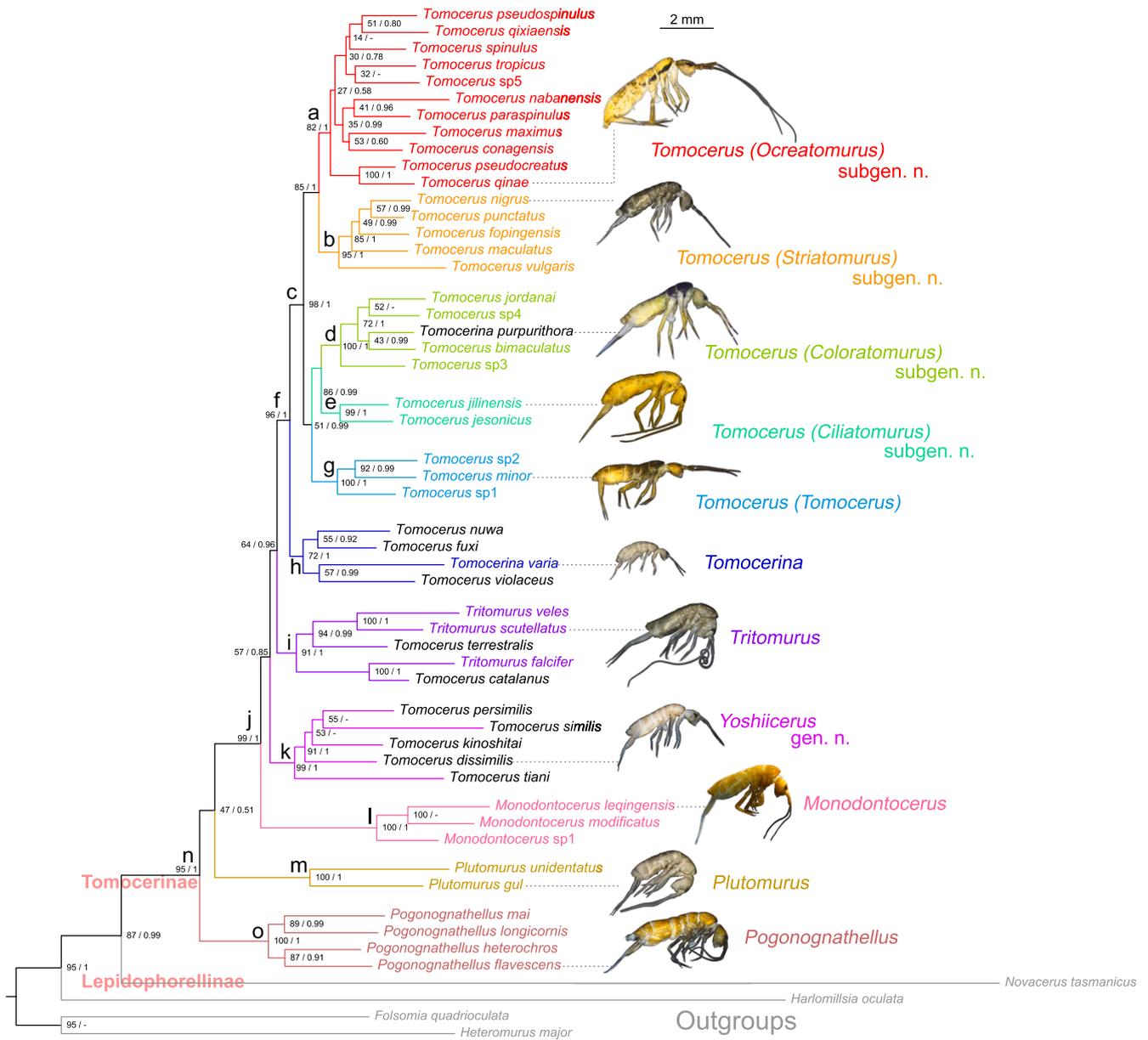
To trace the evolutionary history and estimate the taxonomic value of five ecomorphological traits on the airflow-sensory and locomotory organs, i.e. (1) number of mesothoracic bothriotricha; (2) status of tibiotarsal inner spine-like chaetae (Fig. 1C, D); (3) type of dental spines (Fig. 1F–K); (4) status of mucronal dorsal lamellae (Fig. 1L–N), and (5) status of mucronal basal teeth (Fig. 1P–S), ancestral character state reconstruction (ACSR) was performed in Mesquite v3.6.1 (Maddison and Maddison, 2018), which marks putative plesiomorphic states of characters on nodes of given trees. Detailed character states and coding are shown in Supplementary Table B.2. In addition to traditional classification of 'simple (Fig. 1F–I)', 'compound (Fig. 1J)' and 'multifurcate (Fig. 1K)' dental spines, the 'simple' spines are further classified into four types according to their sculptures, type A with discontinuous short striations and minute basal denticles (Fig. 1G), type B with discontinuous long striations (Fig. 1F), type C with continuous long striations, rarely bifurcate (Fig. 1I), and type D with evenly distributed fine cilia-tions (Fig. 1H). Because the results of ML and BI analyses shared similar topology and supports, results of the BI analysis were used for ACSR. Considering the uncertainty in the trees, ACSR was performed over 20,000 Bayesian posterior trees and summarised on the consensus tree. Both MP and ML analyses were conducted. ML reconstructions were performed under a single-rate Mk1 likelihood model (Lewis, 2001). The phylogenetic conservatism of morphological characters was assessed by employing the retention index (ri), with high ri values ( $\geq 0.85$ ) indicating low homoplasy and a demonstrable phylogenetic signal.

## 3. Results

### 3.1. Phylogenetic inference

All analytical approaches used for phylogenetic reconstruction in the present study (i.e. ML, BI using either concatenation-based (in MrBayes) or coalescent-based (in BEAST) methods, MP with either equal weighting/implied weighting) generated well resolved phylogeny of Tomocerinae (Figs. 2, 3, C.1, with highly congruent topology and robust support for most of the deep nodes (ML bootstrap (MLB)  $\geq 75$ , BI posterior probability (BPP)  $\geq 95$ , MP supporting (MPS)  $\geq 75$ ).

According to our results, the monophyly of Tomocerinae was supported by all analyses (clade n, MPS = 100 (implied weighting) /100 (equal weights), MLB = 95, BPP = 1). Three deeply divergent major branches were recovered within Tomocerinae, two of which were occupied by *Plutomurus* (clade m, MPS = 100 /100, MLB = 100, BPP = 1 (MrBayes) /0.99 (BEAST)) and *Pogonognathellus* (clade o, MPS = 100/100, MLB = 100, BPP = 1/1), respectively, and the third consisted of other groups (clade j, MPS = 100/98, MLB = 99, BPP = 1/0.99). Relationships between the three major branches have not been resolved given the inconsistent topology and fluctuated supports across analyses. Within the third and largest major branch, the genus *Monodontocerus* had a basal position (clade l, MPS = 100/100, MLB = 100, BPP = 1/1); species of the *kinoshitai*-group formed a monophyletic clade (clade k, MPS = 100/95, MLB = 99, BPP = 1/0.99), and were isolated from other species of *Tomocerus*; the genus *Tritomurus* as previously defined was



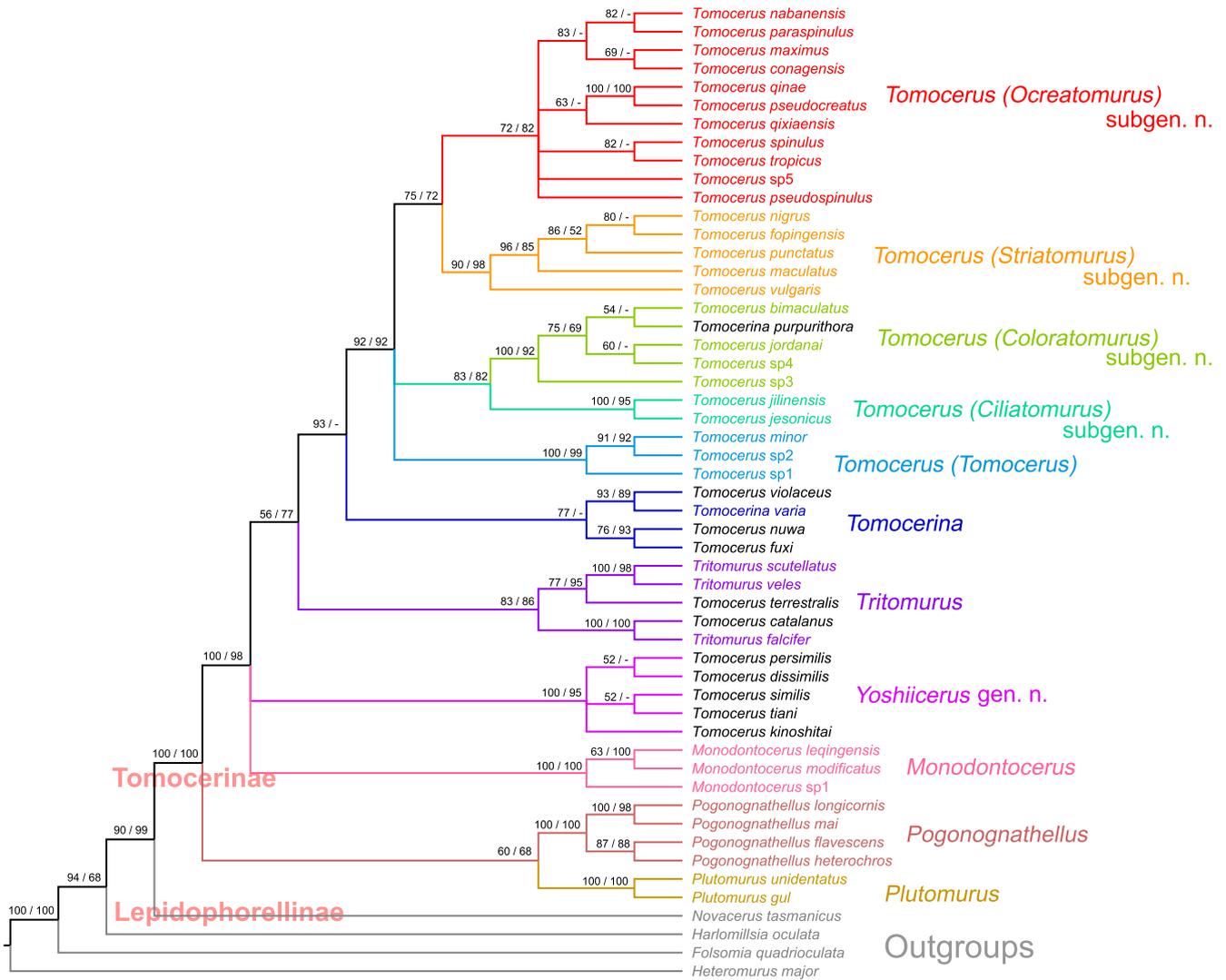
**Fig. 2.** Concatenation-based Maximum likelihood (ML) and Bayesian (BI) phylogeny of Tomocerinae based on COI, 16S, 18S, 28S D1–2 and 28S D7–10 sequences, summarised on a ML tree. Node labels represent bootstrap values/posterior probabilities. Tip labels represent specific names before taxonomic changes, while those in black represent species that underwent generic level replacement. Two subfamilies Tomocerinae and Lepidophorellinae are labelled at their basal nodes. All species are shown at the same scale.

revealed paraphyletic, clustering with *Tomocerus terrestris* Stach, 1922 and *Tomocerus catalanus* Denis, 1924 (clade i, MPS = 83/86, MLB = 91, BPP = 1/0.98); other species of the genera *Tomocerus* and *Tomocerina* clustered in a monophyletic clade in most analyses (clade f, MPS = 93/–, MLB = 96, BPP = 1/0.99), except that MP with equal weighting generated a polytomy as *Tritomurus* + (*Tomocerus nuwa* Yu, Pan and Shi, 2017 + *Tomocerus fuxi* Yu, Pan and Shi, 2017) + (*Tomocerina varia* (Folsom, 1899) + *Tomocerus violaceus* Yosii, 1956) + other species of *Tomocerus* and *Tomocerina* (MPS = 80); except in MP with equal weighting, *T. varia* clustered with *T. violaceus*, *T. nuwa* and *T. fuxi* in a monophyletic clade (clade h, MPS = 77/–, MLB = 72, BPP = 1/0.98); the other species, including the remaining *Tomocerus* and *Tomocerina purpurithora* Liu, Hou and Li, 1999, formed a monophyletic clade (clade c, MPS = 92/92, MLB = 98, BPP = 1/0.99).

Within clade c, five subclades were recovered corresponding to morphological groups: (1) the *minor*-clade consisting of European

species with multifurcate dental spines and without outer teeth on unguiculus, including the generic type of *Tomocerus*, *T. minor* (clade g, MPS = 100/99, MLB = 100, BPP = 1/0.98); (2) the *bimaculatus*-clade consisting of Asian species with multifurcate dental spines and with outer teeth on the unguiculus, including *T. purpurithora* previously assigned to *Tomocerina* (clade d, MPS = 100/92, MLB = 100, BPP = 1/0.99); (3) the *jilinensis*-clade consisting of two species with type D-simple dental spines (clade e, MPS = 100/95, MLB = 99, BPP = 1/0.99); (4) the *nigrus*-clade consisting of species with type C-simple dental spines, including the European species *Tomocerus vulgaris* Tullberg, 1871 (clade b, MPS = 90/98, MLB = 95, BPP = 1/0.97); (5) the *ocreatus*-clade consisting of Asian species with compound dental spines (clade a, MPS = 72/82, MLB = 82, BPP = 1/0.99).

Based on these results, we propose to establish a new genus *Yoshii-cer* gen. n. (urn:lsid:zoobank.org:act:921A4F37-99D5-4A98-86B1-627686DDE10A) for the *kinoshitai*-clade, new subgenera *Tomocerus*



**Fig. 3.** Maximum parsimony (MP) phylogeny of Tomocerinae based on COI, 16S, 18S, 28S D1–2 and 28S D7–10 sequences, summarised on a strict consensus tree using implied weighting for characters. Node labels represent support values calculated on trees generated using either implied weighting/equal weights. Tip labels represent specific names before taxonomic changes, while those in black represent species that underwent generic level replacement. Two subfamilies Tomocerinae and Lepidophorellinae are labelled at their basal nodes.

(*Coloratomurus*) **subgen. n.** (urn:lsid:zoobank.org:act:B94AD280-6695-447C-9FD2-73DF1DBFA853) for the *bimaculatus*-clade, *Tomocerus* (*Ciliatomurus*) **subgen. n.** (urn:lsid:zoobank.org:act:A16CFE4B-AF7D-4860-943D-9D7BF363AB04) for the *jilinensis*-clade, *Tomocerus* (*Ocreatomurus*) **subgen. n.** (urn:lsid:zoobank.org:act:930E9756-929B-44D3-9854-693ED0C351D0) for the *ocreatus*-clade, and *Tomocerus* (*Striatomurus*) **subgen. n.** (urn:lsid:zoobank.org:act:41183496-C66D-4C43-81A1-5F365013F708) for the *nigrus*-clade. For detailed descriptions and remarks of the new taxa see [Appendix A and Fig. C.3](#).

### 3.2. Divergence time of main clades

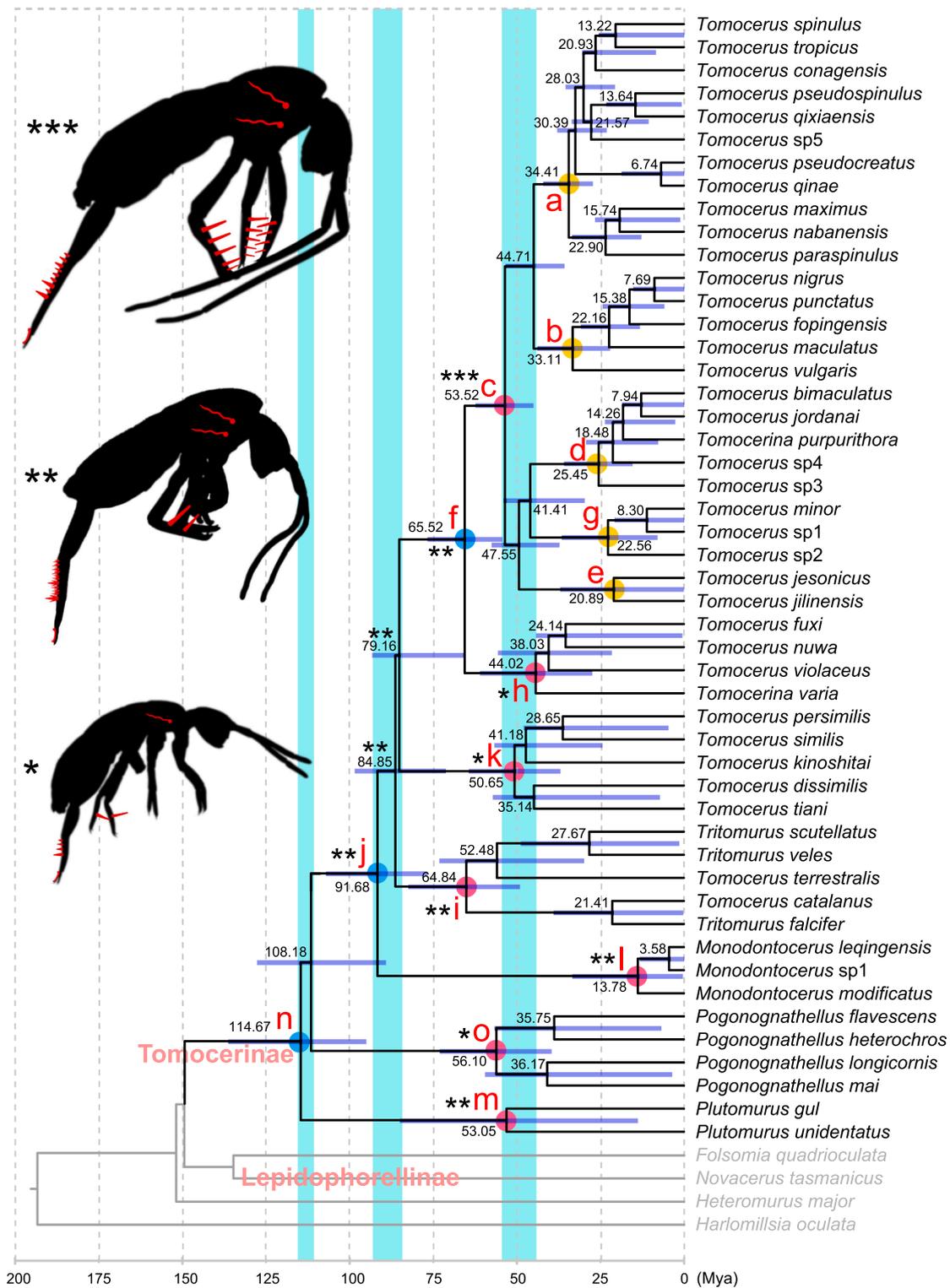
As indicated by the divergence time estimation ([Fig. 4](#)), the ages of most recent common ancestor of well supported clades (a–o) are as follows: clade a (*ocreatus*): 34.41 (27.30–42.12, 95% confidence intervals) Mya; clade b (*nigrus*): 33.11 (22.19–43.92) Mya; clade c (*Tomocerus*): 53.52 (45.03–62.42) Mya; clade d (*bimaculatus*): 25.45 (15.45–35.91) Mya; clade e (*jilinensis*): 20.89 (0.09–37.08) Mya; clade f (*Tomocerus* + *Tomocerina*): 65.52 (54.36–76.71) Mya; clade g (*minor*): 22.56 (7.94–36.61) Mya; clade h (*Tomocerina*): 44.02 (27.46–61.05) Mya; clade i (*Tritomurus*): 64.84 (49.10–82.47) Mya; clade j (largest major branch): 91.68 (76.82–107.09) Mya; clade k (*kinoshitai*): 50.65

(36.98–64.38) Mya; clade l (*Monodontocerus*): 13.78 (0.39–33.45) Mya; clade m (*Plutomurus*): 53.05 (13.83–84.97) Mya; clade n (Tomocerinae): 114.67 (95.01–136.33) Mya; clade o (*Pogonognathellus*): 56.10 (39.61–73.09) Mya. Three relatively rapid evolutionary events contributing to the supra-specific diversity are observed. The first one between 108.18 (89.13–127.68) and 114.67 (95.01–136.33) Mya resulted in the divergences between three major branches; the second one between 79.16 (65.62–93.27) and 91.68 (76.82–107.09) Mya resulted in the generic level divergence in the largest major branch (clade j); and the third one between 44.71 (35.79–53.42) and 53.52 (45.03–62.42) Mya resulted in the diversification of the largest genus *Tomocerus*.

### 3.3. Ancestral states of characters

The results generated by MP and ML methods of ACSR were congruent in most well supported nodes, except for the states of dental spines in node j (BPP > 0.95, [Fig. 5](#), [C.2](#), [Table B.4](#)). For most characters in most nodes, the ancestral states were reconstructed with a high degree of probability (>95%), whereas equivocal states were mainly shown in some deep nodes (nodes c, f, j, n).

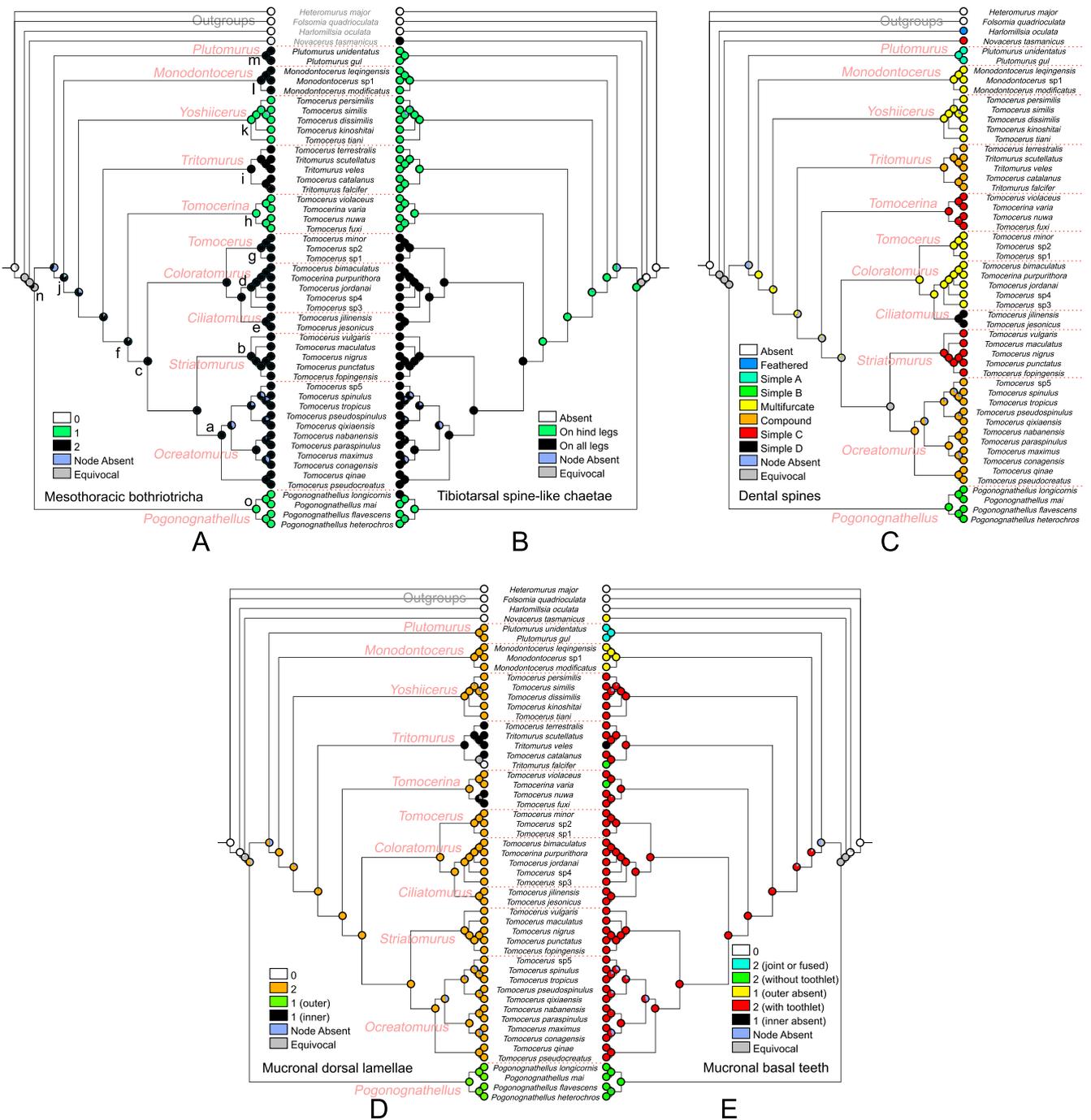
According to our results, the presence of 1 + 1 mesothoracic



**Fig. 4.** Divergence time estimation within Tomocerinae based on an ultrametric tree generated by BEAST. Node labels represent estimated divergence time. Node bars represent 95% confidence intervals of estimated divergence time. Nodes with close circles: key nodes with strong supports (BPP > 0.95), yellow—subgenera of *Tomocerus*; red—genera; blue—supra-generic level nodes. Light blue shades in the background indicate approximate time span of three events shaping current supra-specific diversity. Tip labels represent specific names before taxonomic changes. Asterisks indicate ancestral ecomorphological forms of nodes: \*edaphic, \*\*intermediate, \*\*\*epigeic. Two subfamilies Tomocerinae and Lepidophorellinae are labelled at their basal nodes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bothriotricha appeared independently in *Pogonognathellus* (clade o), the *kinoshitai*-clade (clade k) and the *Tomocerina*-clade (clade h). The presence of spine-like chaetae on front and mid tibiotarsi appeared twice, once in *P. longicornis* and once in *Tomocerus* (clade c).

Regarding characters on the jumping organ, four types of ‘simple’ dental spines appeared five independent times, with type A in *Plutomurus* (clade m); type B in *Pogonognathellus*, type C in *Tomocerina* and the *nigrus*-clade (clade b), and type D in the *jilimensis*-clade (clade e). The



**Fig. 5.** Ancestral character states reconstruction (ACSR) using likelihood method over 20,000 Bayesian trees, summarised on a Bayesian consensus tree. **A**, mesothoracic bothriotricha; **B**, tibiotarsal spine-like chaetae; **C**, dental spines; **D**, mucronal dorsal lamellae; **E**, mucronal basal teeth. Each node indicates character states with different colourations and the proportion of the state over all examined trees.

‘multifurcate’ type of dental spine present in *Monodontocerus* (clade l), the *kinoshitai*-clade, the *minor*-clade (clade g) and the *bimaculatus*-clade (clade d) was potentially the ancestral state of the largest basal clade j (supported in ML reconstruction). The ‘compound’ type of dental spine appeared independently in *Tritomurus* (clade i) and in the *ocreatus*-clade (clade a). The presence of single mucronal dorsal lamella appeared three times, once in *Pogonognathellus*, formed by the reduction of inner lamella; two independent times in *Tritomurus* and the clade of *T. fuxi* + *T. nuwa*, both formed by the reduction of outer lamella. Different states of mucronal basal teeth were characteristic across major branches, the presence of a toothlet on mucronal outer basal tooth was probably the ancestral state for clade j, while in this clade the absence of the toothlet

appeared independently in *Tritomurus falcifer* Cassagnau, 1958 and *T. varia*.

The ri value is 0.86 for the mesothoracic bothriotricha, 0.91 for the tibiotarsal spine-like chaetae, 0.9 for the type of dental spines, 0.91 for the mucronal dorsal lamellae and 0.82 for the mucronal basal teeth, therefore the former four characters show demonstrable phylogenetic conservatism (ri > 0.85).

## 4. Discussion

### 4.1. Phylogeny and classification of Tomocerinae

The results of our multi-loci molecular analyses have supported the monophyly of Tomocerinae, and shed light on the so far confusing phylogenetic relationship within this early divergent group of Collembola.

The monophyly of Tomocerinae has been recovered by a few previous studies (Park, 2009; Felderhoff et al., 2010; Yu et al., 2016b), but all these studies were based on very limited number of genera and/or species. Park (2009) included 5 species belonging to *Tomocerina* and *Tomocerus*; Felderhoff et al. (2010) concentrated on *Pogonognathellus* and selected only *T. minor* to represent other tomocerins; Yu et al. (2016) included 10 species belonging to *Pogonognathellus*, *Tomocerina* and *Tomocerus*. The important genera *Tritomurus*, *Plutomurus* and *Monodontocerus* have not been sampled for molecular analyses until the present study. Therefore, our study based on a much more comprehensive taxon sampling provides a much stronger support for the monophyly of this morphologically well-defined group of Collembola.

Moreover, all analyses consistently recovered three major branches of Tomocerinae, and had high congruence in resolving the relationship within the largest major branch including the most problematic genera. Within the largest major branch, five monophyletic and deeply divergent clades (c, h, i, k, l) are separated from each other by long branches, whereas only one clade containing three *Monodontocerus* species represents a currently accepted genus. This result is in line with morphological study supporting the validity of *Monodontocerus* (Yu et al., 2014a). Two problematic genera *Tomocerus* and *Tomocerina* as previously defined are both revealed polyphyletic in the present study. Species assigned to *Tomocerus* are scattered in several independent evolutionary lineages. Amongst these separate lineages, the largest one including the genus type *T. minor* represents the ‘true *Tomocerus*’, which can be further divided into five subclades; a distantly related lineage represents the *kinoshitai*-group defined in previous morphological-molecular integrative analyses (Yu et al., 2017a), and is described as a new genus in this study; the other species cluster in two clades either with *Tomocerina* or with *Tritomurus*, respectively. Two species of *Tomocerina* never formed a monophyletic clade. *T. purpurithora* is revealed nested in the true *Tomocerus*, whereas *T. varia*, whose specimens were used to define the genus (Yosii, 1955), clusters with the *violaceus*-group, which is the sister group of the true *Tomocerus*. Therefore, these aforementioned results strongly support previous hypothesis based on morphological assessments, that the previous definitions of *Tomocerus* and *Tomocerina* by the presence or absence of a toothlet on mucronal outer basal tooth cannot reflect natural groups (Yu et al., 2014b, 2017b). More importantly, the evolutionary lineages defined by our molecular analyses can also be distinguished by other morphological characters, notably the mesothoracic bothriotracha, tibiotarsal spine-like chaetae and dental spines. As indicated by the estimated divergence time, this major branch of Tomocerinae has experienced two periods of radiation, the first one during Late Cretaceous, leading to the primary divergence and subsequent formation of current generic level clades; and the second one during Eocene, resulting in the diversification of the true *Tomocerus*. An East Asian section of the second radiation event, according to previous molecular assessment (Zhang et al., 2014b), was likely correlated to orogenesis during this period.

Besides the polyphyly of current *Tomocerus* and *Tomocerina*, a most striking finding of the present study is the monophyletic clade consisting of three *Tritomurus* and two *Tomocerus* species. The genus *Tritomurus* as currently accepted contains three troglobionts, with generic diagnosis relying merely on the absence of eyes, which is undoubtedly subject to adaptive convergence in cave habitats. The genus used to include all blind tomocerins, but since Yosii (1956) discriminated *Plutomurus* from *Tritomurus*, it was expected that subsequent study would reveal distant relationships between these species and eventually lead to a collapse of

this genus (Cassagnau, 1958; Lukić et al., 2010). However, results of the present study indicate that the three eyeless troglobionts, together with two eyed troglaphiles of *Tomocerus*, are really closely related to each other, and distantly related to the true *Tomocerus*. Also interestingly, the five species in this clade are further grouped into two deeply divergent subclades, which do not differ in the eye regression degree, but are in accordance with their distinct and narrow geographical ranges (Pyrénées versus Dinarides), confirming that the absence of eyes in this clade is an evolutionary convergence. Similar patterns of convergent cave adaptation are common in other Collembola (e.g. Christiansen, 1961). According to the divergence time estimation, the splitting of the two subclades was approximately during Late Cretaceous–Eocene. The deep divergence and disjunct distribution suggest possible relict status of the two subclades, which requires further test with extended sampling in adjacent regions.

The other two major branches in the tree represent the so far best defined genera within Tomocerinae, i.e. *Plutomurus* and *Pogonognathellus*. Although both genera used to be questioned (Christiansen, 1964; Massoud and Ellis, 1974), they have been also supported by later morphological assessments providing more generic characteristics (Yosii, 1967; Felderhoff et al., 2010; Yu and Deharveng, 2015). In the present study, we sampled species of these two genera that exhibited the extreme infra-generic variations with respect to eye status (in *Plutomurus*), antennae (in *Pogonognathellus*), tibiotarsal spine-like chaetae (in *Pogonognathellus*), mucro, etc. With this sampling, we still recovered the monophyly of the two genera, and indicates their distinctiveness by separating them from other tomocerins in long basal branches.

The three major branches represent the primary divergences among Tomocerinae, but relationship between them has not been fully resolved by the phylogenetic analyses. As indicated by the timing tree, divergence events between the three branches took place within a short time span. This pattern results in long external and short internal branches on the tree, which make phylogenetic inference difficult (Cummins and McInerney, 2011; Salvi et al., 2019). The same problem also exists in supporting the deepest nodes within the largest branch, despite that all analyses have recovered similar topology on the trees. In comparison, relationship within the more recent clade consisting of *Tomocerus* + *Tomocerina* is better supported across analyses.

Regarding the classification of Tomocerinae, there used to be two opposite points of view. One was led by R. Yoshii (Yosii before 1980s’), who claimed ‘we are now well informed with regard to the systematic relations of each species’ (Yosii, 1967), and supported grouping tomocerins into numerous genera/subgenera (Yosii, 1955, 1956, 1970). The other was represented by K. Christiansen, who argued ‘few genera (the taxonomic position of Tomocerinae at that time) of the order (Collembola) have been fractured as much as this one’, and suggested to sink all supra-specific taxa into a single genus *Tomocerus* (Christiansen, 1964).

In general, the reconstructed phylogeny of this study supports our hypothesis that current classification only partially reflects the evolution of Tomocerinae. Most supra-specific taxa proposed or redefined by Yosii (1955, 1956, 1967) are supported, indicating that he successfully identified natural groups within the subfamily in most cases, despite that no cladistic approach was applied at that time. Nevertheless, because of the small number of known species and the lack of morphological characters at that time, several generic criteria proposed by Yosii were ambiguous, leading to subsequent confusions, for which reason we also supported partially the arguments of Christiansen, that the current use of some characters for generic level diagnosis were not suitable (Christiansen, 1964; Ma et al., 2003). In the light of molecular phylogenetic reconstruction and morphological character assessment conducted in this study, we are now able to revise several historically poorly defined genera and establish new genera and subgenera conforming to a cladistic system (for detailed description and remarks see Appendix A and Fig. C.3).

#### 4.2. Evolution of functional traits and implications for ecological divergence

The comprehensive phylogeny of Tomocerinae produced by our analyses allows us to reconstruct the evolutionary history of five ecomorphological traits, *i.e.* bothriotricha, tibiotarsal spine-like chaetae, dental spines, mucronal lamellae and mucronal basal teeth. Because these traits are assumed to be associated with airflow detection or locomotion, which are intimately correlated to the habitat niche of collembolan species (Salmon et al., 2014), our findings also have implications for the ecological divergence between lineages of Tomocerinae.

**Bothriotricha.** Morphologically specialised chaetae of this type are known in various terrestrial arthropods, and have been interpreted as sensory organs of airborne vibrations and currents (*e.g.* Drašlar, 1973; Reissland and Görner, 1985; Barth 2004). In Collembola the value of the number and position of bothriotricha for higher level classification has been widely acknowledged (Szeptycki, 1979; Betsch and Waller, 1989). However, this character was considered absolutely stable within Tomocerinae, until a recent study confirmed that some groups have only 1 + 1 bothriotricha on mesothorax in contrast to commonly accepted 2 + 2 (Yu et al., 2016a). In the present study, we found that the presence of 2 + 2 mesothoracic bothriotricha was most likely the ancestral state for deep nodes, whereas the presence of 1 + 1 mesothoracic bothriotricha likely homologous to the inner pair in the former case was independently derived in *Pogonognathellus*, *Yoshiicerus gen. n.* and *Tomocerina*. Therefore, amongst tomocerins the later state is a convergence between the three genera, but for each genus it is a synapomorphy. Moreover, conforming to their function, the bothriotricha are commonly found in collembolan species living in epigeic habitats, or with a putative epigeic ancestor, *i.e.* all species of Symphyleona Börner, 1901, Entomobryioidea Womersley, 1934 and Actaletidae Börner, 1902, most species of Tomoceroidea Szeptycki, 1979, and some epigeic genera of Isotomidae (*e.g.* *Isotomurus* Börner, 1903 and *Psammitotoma* Greenslade and Deharveng, 1986). A recent study also provided statistical support for the correlation between the presence of bothriotricha and epigeic life style (Salmon et al., 2014). In Tomocerinae, the reduction of bothriotricha in three clades suggests they or their ancestors had a more edaphic life style than those of other groups. This inference is supported by other morphological and behavioral traits in *Yoshiicerus gen. n.*, *Tomocerina*, and the basal species of *Pogonognathellus*, *i.e.* *Pogonognathellus bidentatus* (Folsom, 1913) (*sensu* Felderhoff et al., 2010), such as small body size (not in *P. bidentatus*), short antennae, small eye patches, small number of tibiotarsal spine-like chaetae and preference for lower litter and humus habitats (Yu et al., 2017a).

**Tibiotarsal spine-like inner chaetae.** Except sexual dimorphism in some groups (*e.g.* *Seira* Lubbock, 1870, *Tyrannoseira* Bellini and Zeppelini, 2011), most characters on legs, such as leg length, claw morphology and tenent hairs, are correlated to the locomotory performance of species (Ponge et al., 2006; Christiansen, 1965; Yu et al., 2017a). However, the functional importance of another specialised character, *i.e.* the thickening and hardening of inner chaetae on tibiotarsi, was previously overlooked. Amongst Collembola, such modified chaetae are often found in large, active species with long legs, such as in Tomoceridae, Entomobryidae Schäffer, 1896 and Dicyrtomidae Börner, 1906. To determine the function of these chaetae, we have conducted observation in cultured species. We found that the animals tend to stand and move on the inner side of their legs when climbing on granulated surfaces (*e.g.* soil particles), fine sticks (*e.g.* pine needles), and edges of woods and stones, while undoubtedly in this motion the strong spine-like chaetae can enhance the grasping ability of legs. In Tomocerinae the pattern of these chaetae can be generally classified as two types, *i.e.* numerous on all legs, or a few on hind legs. According to previous records and our field observation, species with the former type of tibiotarsal chaetae have a wider microhabitat range, from ground litters to trunks and branches of living plants (*e.g.* Maynard, 1951; Hisamatsu and

Matsunaga, 1994; Felderhoff et al., 2010; Park et al., 2011), indicating a higher mobility. Results of the ACSR analyses suggest that the later, less mobile type is probably the ancestral state for Tomocerinae, while the more mobile type evolved independently in *Pogonognathellus* and the true *Tomocerus*. In *Pogonognathellus*, three species with the less mobile type of tibiotarsal chaetae never cluster in a monophyletic clade, which is partially in line with a previous study showing this character is variable within the *longicornis*-clade (Felderhoff et al., 2010). In contrast, in *Tomocerus* the more mobile type is a synapomorphic character. This finding suggests that the change in mobility, which is fundamental to the habitat niche of a species (Winemiller et al., 2015), was involved in the origination of *Tomocerus*, and probably also led to the speciation within *Pogonognathellus*.

**Traits on furca.** When resting, Collembola hold the furca with tenaculum on the ventral side of body; when jumping, the furca is released, pushing the animal up into the air by hitting the ground or other substrates with its dorsal (in released status) face (Hopkin, 1997). Therefore, besides the size and shape of furca, the dorsal structures of furca can also affect the jumping performance of Collembola. Notably, some cyclomorphic species of Collembola, *e.g.* *Hypogastrura socialis* (Uzel, 1891) and *Proisotoma minima* (Absolon, 1901), enhance dorsal teeth or tubercles on dens during the jumping-active phase of life (Leinaas, 1981a, b; Potapov and Bogomolov, 2016), whereas some other *Hypogastrura* species reduce teeth and lamellae on mucro during the jumping-inactive phase (Cassagnau, 1956a,b). Although empirical evidence is still lacking, these previous findings strongly suggest an advanced function of furca with these protruding structures. In Tomocerinae, these kinds of structures are represented by dental spines, mucronal lamellae and mucronal teeth, which are relatively variable characters in this group, and have been extensively used for diagnosis. Our results showed that amongst the three characters, the states of dental spines and mucronal lamellae are phylogenetically more conservative, whereas the states of mucronal basal teeth is the least predictable. Regarding the dental spines, except that the multifurcate-type is probably a symplesiomorphy for *Monodontocerus*, *Yoshiicerus gen. n.*, *Tomocerus (Tomocerus)* and *Tomocerus (Coloratomurus) subgen. n.*, the other states represent synapomorphies for genera and subgenera. Regarding the mucronal lamellae, the presence of only outer lamella is a synapomorphy for *Pogonognathellus*, whereas the presence of two dorsal lamellae is the ancestral state of other tomocerins. The reduction of outer lamella is convergent in *Tritomurus* and *Tomocerina*. Regarding the mucronal basal teeth, the presence of a toothlet on outer basal tooth is a symplesiomorphy for *Tomocerus*, *Tomocerina*, *Tritomurus* and *Yoshiicerus gen. n.*, thus should no more be used to define *Tomocerus*; whereas the states in *Pogonognathellus*, *Plutomurus* and *Monodontocerus* are synapomorphies for these genera. Different evolutionary patterns of the three characters suggest that they may have unequal significance or play different roles in the function of furca. Although an explicit functional interpretation of various ornaments on furca is still elusive, the aforementioned evidence from other Collembola suggests that increasing the number and granularity of the ornaments can potentially enhance the jumping ability of the animal. Under this hypothesis, the evolutionary patterns of furca traits are also likely to indicate the divergence in locomotory ability and/or activity between evolutionary lineages, which is to be tested by integrating phylogenetic analyses and functional experiments.

Conclusively, the evolutionary patterns of the ecomorphological traits, especially bothriotricha and tibiotarsal spine-like chaetae, well indicate that tomocerins have undergone multiple times substantial divergences of habitat-niche and lifeforms, which has contributed to current higher taxa richness and ecological diversity of the subfamily. Notably, all three fast evolutionary events revealed in this study were either associated with or preceded by the divergence of life styles, which further demonstrates the importance of ecological divergence in the diversification of tomocerins and supports our last hypothesis.

Furthermore, given the ubiquitous functional differentiation among

Collembola and other terrestrial invertebrates (e.g. Schmallfuss 1984, Rusek 2007, Kurth and Kier 2015), similar evolutionary patterns may also be recognised in other groups. For example, available phylogenetic studies have shown that in the superfamily Entomobryoidea Womersley, 1934, body scales and types of furca, which are relevant to the defense and locomotion of Collembola, respectively (for scales, *sensu* Wolff et al., 2014, 2016), can both have multiple independent origins (Zhang et al. 2014a, 2015). Although comprehensive phylogeny is still lacking for most other groups of Collembola, the condition of some traits and their statistical links to habitat across several families, e.g. eye reduction and furcal development in Hypogastruridae, Neanuridae and Isotomidae, is widely considered as convergent evolutions. Reconstructing robust phylogeny of more groups, improving the dating accuracy and revealing the environmental drivers of functional traits will allow to understand evolutionary patterns and pathways of these convergent evolutions.

#### 4.3. Implications for trait-based ecology

In Collembola, comprehensive and detailed phylogenetic analyses have only emerged recently for a few groups (e.g. Schneider et al., 2011; Zhang et al., 2019; Lukić et al., 2020), and for the first time for Tomocerinae in the present study. According to our results, previous classification of Tomocerinae showed marked incongruence with evolutionary relationships, hence following the old system may lead to incorrect inferences of trait conservatism. In the presence of advanced taxonomic systems, a timely updating of present trait databases is recommended to ensure their accuracy (Wong et al., 2018).

Although primary and standardised measurements are preferred for accurately assigning trait values to species (Brousseau et al., 2018; Wong et al., 2018), non-morphological traits, such as life history and behaviour, are unknown or notoriously difficult to measure in organisms of minute size and cryptic life styles, such as microarthropods. In Collembola, the most frequently used ecological trait, *i.e.* the habitat requirements or preferences, were observed in only a limited number of species, and were assigned to other species merely according to apparent morphological similarities and taxonomic positions (*sensu* Rusek, 2007). For example, probably because of the conserved morphology (large size, long antennae, eyes present), non-cave species of Tomocerinae are classically placed into the same ecological category, either epedaphic (e.g. Potapov et al., 2016) or hemiedaphic (e.g. Malcicka et al., 2017), whereas our study reveals that in fact different groups have distinct habitat-niches as a result of deep ecological divergences. This is in line with a statistical analysis implying that *T. minor* and *Pogonognathellus flavescens* (Tullberg, 1871) have distinct habitats (Salmon et al., 2014). These findings of 'cryptic' ecological diversity in a previously-thought ecologically explicit group strongly suggest that similar underestimation may widely exist in the megadiverse terrestrial invertebrate fauna, while to what extent it affects the functional interpretation of community structure need to be further assessed. However, rather than calling for exhaustive primary inspections of traits on every species which is impractical notably for the prevalent large-scale studies, it is more recommendable that reliable backbones for the trait-taxon relationships should be established on the basis of robust macroevolutionary reconstructions. Such studies are numerous in other ecological groups, such as aquatic insects and pollinators (e.g. Malm et al., 2013; Sabatinelli et al., 2020), but are still lacking for the majority of soil fauna. In the present study, our results show that the phylogenetic relatedness of life styles even varies across genera, hence generic position can be used as a predictor in *Tomocerus* and *Yoshiicerus* *gen. n.*, but not in *Pogonognathellus*.

In addition, mapping trait values on a comprehensive, dated phylogeny can help to trace the historical scenarios causing the ecological divergences, which may also have implications for current Anthropogenic changes. For example, our results suggest the divergences of life styles are roughly coincident with the Aptian–Albian and the Late Cretaceous cooling periods within the Cretaceous greenhouse (Herrle

et al., 2015; O'Connor et al., 2019), which may indicate a selective pressure during climate change events. However, the inferences from a preliminary divergence time estimation should be regarded as providing a hypothetical perspective rather than concrete evidence, because on one hand, palaeoclimatical and geological events may include more factors than have been reconstructed; on the other hand, the accuracy of divergence time estimation can be affected by a complex set of factors, e.g. datasets, calibrations, model fitness and prior settings (Smith et al., 2018).

Conclusively, the present study indicates that the knowledge on macroevolutionary patterns can help to improve the accuracy and predictive power of trait-based ecological studies. For many groups of great ecological importance, such as Collembola and other terrestrial invertebrates, the phylogenetic assessments of ecological and physiological traits are in pressing need. Several recent studies based on preliminary basal phylogeny of Collembola have provided good examples of such practices (e.g. Chen et al., 2017; Malcicka et al., 2017), whereas future progress in phylogenetics are expected to bring more comprehensive patterns.

#### CRedit authorship contribution statement

**Daoyuan Yu:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Software, Validation, Visualization, Writing - original draft. **Louis Deharveng:** Conceptualization, Investigation, Resources, Writing - review & editing. **Marko Lukić:** Investigation, Resources, Funding acquisition, Writing - review & editing. **Yiming Wei:** Investigation, Data curation. **Feng Hu:** Project administration, Validation. **Manqiang Liu:** Project administration, Supervision.

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#### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ympev.2020.106995>.

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