



Integrative taxonomy of diversification treehopper *Tricentrus* (Hemiptera: Membracidae: Centrotinae) from China shed their phylogenomic relationship and the evolutionary history

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Abstract

The treehopper genus *Tricentrus* is a widespread group of insects, characterized by typical spines and, in some species, sexually dimorphic suprahumeral horns. With 238 described species worldwide, *Tricentrus* represents the most species-rich genus in the subfamily Centrotinae. Currently, 72 species are documented in China, yet the phylogenetic relationships and evolutionary history of this genus remain unknown. Here, we use an integrative approach to characterize and describe these treehoppers based on materials collected from China. We name three new species: *Tricentrus allochrous* Li & Chen **sp. nov.** and *Tricentrus pianmaensis* Li & Chen **sp. nov.** from Yunnan, *Tricentrus dexingensis* Li & Chen **sp. nov.** from Xizang, with the revision of one synonym. Combined analysis morphological comparisons, species delimitation and phylogeny reliably separate these new species from known species, and sexual dimorphism with suprahumeral horns in three species is reported for the first time. Divergence time estimation indicates that the *Tricentrus* differentiated during the Early Cretaceous (110.41 Mya). Ancestral state reconstruction reveals that the most recent common ancestor possessed suprahumeral horns in both sexes and exhibited a short tubular pygofer apex. Our analyses demonstrate four evolutionary transformations in pygofer apex morphology and seven distinct transitions in suprahumeral horn development. These morphological diversifications likely resulted from multiple mechanisms, including sexual selection, life history strategies with associated behavioral adaptations, and incomplete lineage sorting.

Keywords

phylogeny, sexual dimorphism, taxonomy, treehopper

1. Introduction

The treehopper family Membracidae (Hemiptera) comprises a widespread and species-rich group of insects. Its members exhibit not only remarkable morphological diversity in the pronotum but also significant pest attributes

affecting agricultural and forestry. These insects cause direct damage by feeding on economic crops (Yuan et al. 1986; 1999; Chou 1975), and facilitate viral transmission (Yuan and Chou 2002). Globally, 3,491 extant tree-

hopper species have been described, with the subfamily Centrotinae housing the greatest number (Dmitriev et al. 2022). Among the Centrotinae, the genus *Tricentrus* Stål 1866 was notable for its high species richness and prevalence (Dmitriev et al. 2022). The genus comprises 238 known species (Dmitriev et al. 2022). Within this total, 117 species have been reported from China, based on the work of Yuan and Chou (2002). Stål (1866) established the genus *Tricentrus* (commonly known as three-sharp-point bugs), designating *Centrotus fairmairei* Stål, 1859 as the type species. Subsequently, the period from 1908 to 2002 saw the description of numerous new species in this genus by researchers from various regions (Distant 1908, 1916; Bierman 1910; Matsumura 1912, 1938; Melichar 1914; Schmidt 1926; Lindberg 1927; Kato 1928, 1930, 1940, 1960; Jacobi 1944; Ishihara 1961; Ahmad and Yasmeen 1974, 1976, 1978, 1979; Ananthasubramanian and Ananthakrishnan 1975; Chou 1975; Yasmeen and Ahmad 1976a, b, 1978; Ananthasubramanian 1980, 1982, 1996; Thirumalai and Ananthasubramanian 1985; Sharma and Badan 1986; Thirumalai 1986; Yuan et al. 1986, 1992, 1997, 1999; Yuan 1987; Yuan and Cui 1988; Ahmad 1992; Liang and McKamey 1996; Yuan and Liang 1999; Yuan and Chou 2002). In addition, there are also cross regional researchers, e.g. Buckton (1903), Funkhouser (1914a, b, 1915, 1918a, b, 1919, 1920, 1927a, b, c, d, 1929, 1932, 1934, 1935a, b, c, 1937a, b, c, d, 1938, 1942), Metcalf and Wade (1965).

Following more detailed investigation, several former genera have been synonymized with *Tricentrus*, including *Otaris* Buckton, 1903 (Distant 1916), *Taloipa* Buckton, 1905 (Distant 1908), *Centrotoscelus* Funkhouser, 1914 (Ahmad and Yasmeen 1974), and *Arisangargara* Kato, 1928 (Ahmad and Yasmeen 1974). These taxonomic revisions were prompted by three distinct expressions of the suprahumeral horn within the genus: 1) both sexes present suprahumeral horns (Fig. 1A); 2) both sexes absent suprahumeral horns (Figs 1B, 3) sexually dimorphic expression of suprahumeral horns (Fig. 1C). The first two morphological types were commonly documented, whereas the sexually dimorphic form was seldom reported (Funkhouser 1919; Yasmeen and Ahmad 1976a; 1978; Yuan et al. 1997). Among dimorphic species, males lacking suprahumeral horns have often been confused with

males with absent suprahumeral horns in morphological assessments. For instance, such confusion has occurred between the species *T. apheliphallus* (Yuan & Li, 2002) and *T. walkeri* Metcalf & Wade, 1965, *T. arcifrontclypei* (Yuan & Li, 2002) and *T. camelloleifer* Yuan & Cui, 1997 (Walker 1851; Yuan et al. 1997; Yuan and Chou 2002). Additionally, the lack of male morphological data represents an especially acute deficiency. The female specimens have predominantly been designated as types, while the male morphology of numerous species remained unknown in previous studies, as seen in some species recorded distributed in China by Funkhouser (1937a, d, 1938, 1942) previously, and monographs published by Yuan and Chou (2002). Among the 72 documented *Tricentrus* species in China, males of 34 species remain unknown (Yuan and Chou 2002). Are there any species with sexual dimorphism in suprahumeral horns among these unknown male species? It is currently unknown.

On the other hand, previous morphological and molecular evidence has consistently shown that this genus clusters with other genera of the tribe Gargarini into a single clade (Wallace and Deitz 2004; Bai et al. 2023; Li et al. 2023). Additionally, various species groups have been proposed based on morphology, such as the *T. projectus*, *T. gibbosulus*, *T. fairmairei* group (Ahmad and Yasmeen 1978, 1979; Ahmad 1992), and the *T. fulgidus*, *T. acuticornis*, *T. brunneus*, *T. megaloplasius*, *T. curvicornis* groups (Yuan and Chou 2002). The evolutionary relationships within this genus are still unresolved, stemming from limited species representation in existing studies. For Chinese *Tricentrus* in particular, whether morphological and molecular phylogenetic results are congruent is yet to be resolved.

Here, we present a detailed report of the genus *Tricentrus* in China using an integrative approach that combines taxonomy, phylogenetic analysis, and ancestral state reconstruction, based on the available morphological and molecular data. Our results indicated that the all examined species of the genus involved in the analysis formed a single clade, and samples of different sexes were confirmed to belong to the same species through species-definition analysis. We also describe three new species, namely *Tricentrus allochrous* Li & Chen **sp. nov.**, *T. pianmaensis* Li & Chen **sp. nov.** from Yunnan, and *T. dexingensis* Li &

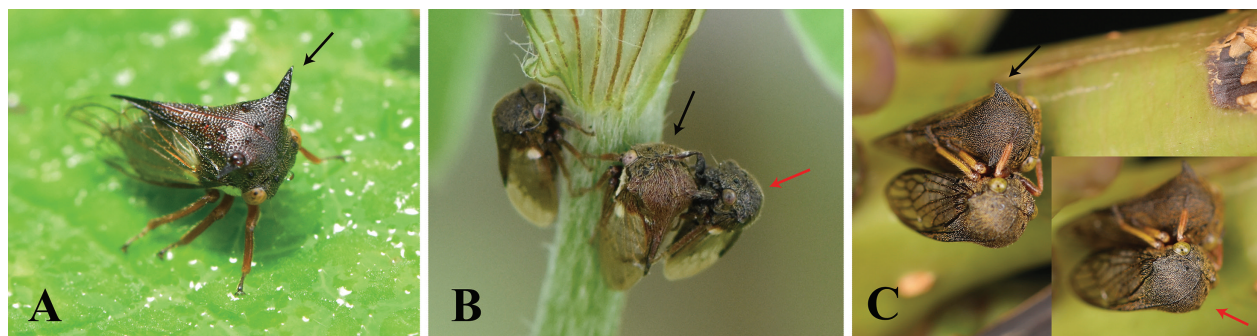


Figure 1. Photographs of species of the genus *Tricentrus*. A both sexes with suprahumeral horns, *T. sp1.* (photo by Xin-Yi Zheng); B both sexes without suprahumeral horns, *T. davidi* (photo by Xin-Yi Zheng); C sexually dimorphic with suprahumeral horns, *T. sp2* (photo by Feng-E Li). The black and red arrows indicate females and males, respectively.

Chen **sp. nov.** from Xizang, where *T. dexingensis* exhibits sexual dimorphism in suprahumeral horns. And, one new synonymy is proposed based on morphological evidence. Ancestral state reconstruction indicates that the presence of suprahumeral horns in both sexes and a short, tubular-shaped pygofer apex represent the ancestral condition in genus *Tricentrus*, with seven and four morphological transitions in these traits, respectively. Our study provides new insights on the evolution of *Tricentrus*.

2. Materials and methods

2.1. Materials

For taxonomic and phylogenetic study, we examined species of *Tricentrus* and sampled from Yunnan, Guizhou, Guangdong, Guangxi, Xizang, Shandong, Shanxi, Sichuan, Fujian province respectively (Table S1). All the specimens examined are deposited in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

2.2. Morphology

General morphological terminology follows Deitz (1975) and Dietrich et al. (2001) except for the morphology of the female genitalia, which follows Mejdalani (1998). For the morphological study, habitus photographs were taken using Canon® EOS5D with camera shot MP-E 65mm f/2.8 1–5×, multiple layers were stacked using Helicon Focus 6. Forewings and hindwing photographs were taken using a KEYENCE® VHX-1000. The genital segments of the specimens examined were cleared in 10% NaOH and drawn from preparations in glycerin jelly using a Leica® MZ 125 stereomicroscope. The photographs and the illustrations were imported into Adobe Photoshop CS5 for plate composition and labeling.

2.3. DNA extraction, sequencing, and sequence assembly

The genomic DNA was extracted from the thorax of adults using a DNA Kit (TIANGEN®, Beijing, China). For sequencing of the mitochondrial genomes, a total amount of 1.5µg DNA per sample was used as input material. Sequencing libraries were generated using the Truseq Nano DNA HT Sample preparation Kit (Illumina USA) following manufacturer's recommendations. These libraries constructed above were sequenced on the Illumina NovaSeq platform, 150bp paired-end reads were generated with an insert size around 350bp. Mitogenomes were assembled using MitoZ v2.4 (Meng et al. 2019) with *Leptobelus gazella* (Fairmaire, 1847) (NC_023219) as reference, followed by annotation in Geneious Prime 2021.1.1 (Kearse et al. 2012). A total of 13 protein-coding genes were predicted by determining their open reading

frames using the invertebrate mitochondrial genetic codon; rRNA genes and AT-rich regions were identified by alignment with homologous genes from other treehopper species; the locations and secondary structures of tRNA genes were predicted using the MITOS web server (<http://mitos.bioinf.uni-leipzig.de/index.py>) (Bernt et al. 2013).

2.4. Species delimitation analyses

Based on the mitochondrial *COI* sequences obtained, we used four DNA-based species delimitation approaches to define species partitions: automatic barcode gap discovery (ABGD; Puillandre et al. 2012) assemble species by automatic partitioning (ASAP; Puillandre et al. 2021), Poisson tree processes (bPTP; Zhang et al. 2013), and the generalized mixed Yule coalescent (GMYC; Fujisawa and Barraclough 2013). The ABGD and ASAP methods utilize predefined thresholds to discriminate between interspecific and intraspecific genetic variation, partitioning species by applying hierarchical clustering algorithms to pairwise genetic distances calculated from single-locus sequence data.

ABGD and ASAP analyses were performed on a *COI* multiple sequence alignment using the online portals (<https://bioinfo.mnhn.fr/abi/public/asap/asapold.html>; <https://bioinfo.mnhn.fr/abi/public/abgd/abgdold.html>; accessed April 25, 2025). As both websites are no longer accessible (as of February 20, 2026), the sequence data and results are provided in File S1. PTP can give a species delimitation hypothesis based on a gene tree inferred from molecular sequences. bPTP was a Bayesian implementation (BI) of the PTP model. In this analysis, the Newick-formatted BI tree from MrBayes was uploaded as input on the bPTP web-server (<https://species.h-its.org/ptp>). The GMYC model requires an ultrametric tree as input, estimated divergence times using the Birth-Death model with exponential priors (Monaghan et al. 2009; Michonneau 2015) on a consensus tree generated in BEAST v2.4.7 (Bouckaert et al. 2014). This tree was then submitted to the GMYC web server (<https://species.h-its.org/gmyc>) for species delimitation analysis (Pons et al. 2006).

2.5. Phylogenetic analysis

The phylogenetic analysis included 53 samples, comprising 50 *Tricentrus* species and one representative each from the tribes Darthulini, Ceresini, Polyglyptini (Table S1). Sequence data were obtained from nine NCBI (the National Center of Biotechnology Information) (<https://www.ncbi.nlm.nih.gov>) accessions and 44 newly sequenced specimens (NCBI GenBank under the accession numbers: PV826162–PV826205).

The nucleotide sequences of 13 PCGs were extracted using the introduction PhyloSuite v.1.2.2 (Zhang et al. 2018). The alignment of 13 PCGs was based on amino acid sequences translated with the invertebrate mitochondrial genetic codon table using MUSCLE (Edgar 2004)

compiled in MEGA v.6.0 (Tamura et al. 2013). Individual gene (nucleotide sequences) alignments were concatenated into a database using SequenceMatrix v.1.7 (Vaidya et al. 2011). The best partition schemes (Table S2) and substitution models were estimated using PartitionFinder v.2.1.1 (Lanfear et al. 2017). The final dataset was analyzed using maximum likelihood (ML) and Bayesian inference (BI) inferred analyses, respectively, using IQ-TREE v.1.6.8 (Nguyen et al. 2014) and MrBayes v3.2.6 (Ronquist et al. 2012). The Edge-linked partition model for 10,000 ultrafast (Minh et al. 2013) bootstraps, as well as 1000 SH-aLRT (Guindon et al. 2010) replicates, were set in the ML analyses. The BI analysis was performed under the following conditions: four simultaneous Markov chain Monte Carlo (MCMC) runs of 30,000,000 generations, sampling every 1000th generation, and the first 25% discarded as burn-in. When the average standard deviation of split frequencies fell below 0.01 and remained stable, stationarity was considered to have reached.

Furthermore, an effective sample size (ESS) value of more than 200 was used as a convergence diagnostic using TRACER v.1.6 (Rambaut et al. 2018). When the bootstrap percentage (BP) was >75% or the Bayesian posterior probability (BPP) was >0.9, the results were considered credible. Consensus trees were viewed and edited using FigTree v.1.4.2 (Mousavi et al. 2014).

2.6. Divergence time estimates, ancestral state reconstructions (ASRs)

The time scale of the diversification of *Tricentrus* was estimated by using BEAST v2.4.7 (Bouckaert et al. 2014). The molecular dataset above and the topology resulting from the combined dataset based on the above BI analyses were used. The best partitions and models identical to those used for the above phylogenetic analyses in BEAUTI (Bouckaert et al. 2014). We used a relaxed molecular clock model (Drummond et al. 2006) and an exponential prior, with time tree and clock model linked across partitions. We applied a node-dating approach with a birth death tree prior (Kendall 1948). Based on the divergence time estimation by Dietrich et al. (2017), the treehopper lineage (Aetalionidae, Melizoderidae, and Membracidae) originated approximately 134 MYA, while crown group diversification commenced 18 million years later, with modern subfamilies emerging during the late Cretaceous to early Paleogene. To calibrate nodes on the phylogeny, we employed a well-constrained timeline based on inferred chronometric data (134 MYA) from Dietrich et al. (2017). This MCMC was run for 100 million generations; trees were sampled for every 1000 generations. Discarding the first 25% of the run, the maximum clade credibility tree with median heights coupled with 95% highest posterior density heights interval (95% HDP) was summarized in TreeAnnotator v.1.8 (Bouckaert et al. 2014). TRACER v.1.7 was used to assess convergence and estimate the effective sample size (ESS) of each parameter. The chronogram was viewed and edited using FigTree v.1.4.2.

To elucidate the evolution of morphological characters among *Tricentrus* and to evaluate their diagnostic value for higher-level classification, we examined two key characters and reconstructed their ancestral states on the molecular phylogenetic tree. The characters examined and their respective states were defined as follows (Table S3): Character 1 (Suprahumeral horns): (A) present in both sexes (B) absent in both sexes (C) sexually dimorphic with suprahumeral horns (present in female, absent in male); Character 2 (pygofer apex morphology): (A) pygofer apex short, tubular shape (ventral margins slightly exceed dorsal margins or both margins flush) (B) pygofer apex angular shape (dorsal margins exceed ventral margins obviously). Ancestral state reconstructions were performed on the Bayesian consensus tree generated by BEAST v2.4.7, employing the Bayesian Binary Markov Chain Monte Carlo (BBM) method as implemented in RASP v4.0 (Yu et al. 2015).

3. Results

3.1. Phylogeny

The ML and BI analyses based on nucleotide and amino acid molecular dataset produced congruent tree topologies, with discrepancies limited to weakly supported internal nodes (Figs S1–S3). The phylogenetic analyses reveals that all examined species of this genus *Tricentrus* cluster within a single well-supported clade with high support (Fig. 2) (ML bootstrap = 100; BI posterior probability = 1) (Fig. S1). The four main branches of the genus *Tricentrus* were presented in the phylogenetic tree as sister groups to each other. The species, *T. camelliae*, as a single branch at the base of the tree.

In clade 2, specimens of both sexes from *T. obesus* and *T. walkeri* (sampled across Guangdong, Guangxi, and Guizhou Provinces) formed a single, well-supported clade (ML bootstrap = 100; BI posterior probability = 1), demonstrating their conspecificity despite sexual dimorphism with suprahumeral horns. Phylogenetic analyses resolved these taxa as sister groups, with the topology ((*T. obesus* + *T. walkeri*) + *T. folicornatus*) under both BI (posterior probability = 1) and ML (bootstrap = 100) criteria (Fig. S1).

As well as *T. obesus* and *T. walkeri*, the species *T. colligatoclypei*, *T. floripinnae*, and *T. dexingensis* Li & Chen **sp. nov.** exhibit pronounced sexual dimorphism. The phylogenetic analyses showed these taxa as reciprocally monophyletic sister lineages, terminal of clade 4 (ML bootstrap = 100; BI posterior probability = 1). These species collectively formed a clade with *T. quernales*, yielding the topology ((*T. colligatoclypei* + *T. floripinnae*) + (*T. dexingensis* Li & Chen **sp. nov.** + *T. quernales*)) across all analyses.

Phylogenetic analyses placed the two new species, *T. allochrous* Li & Chen **sp. nov.** and *T. pianmaensis* Li & Chen **sp. nov.**, within a strongly supported subclade of

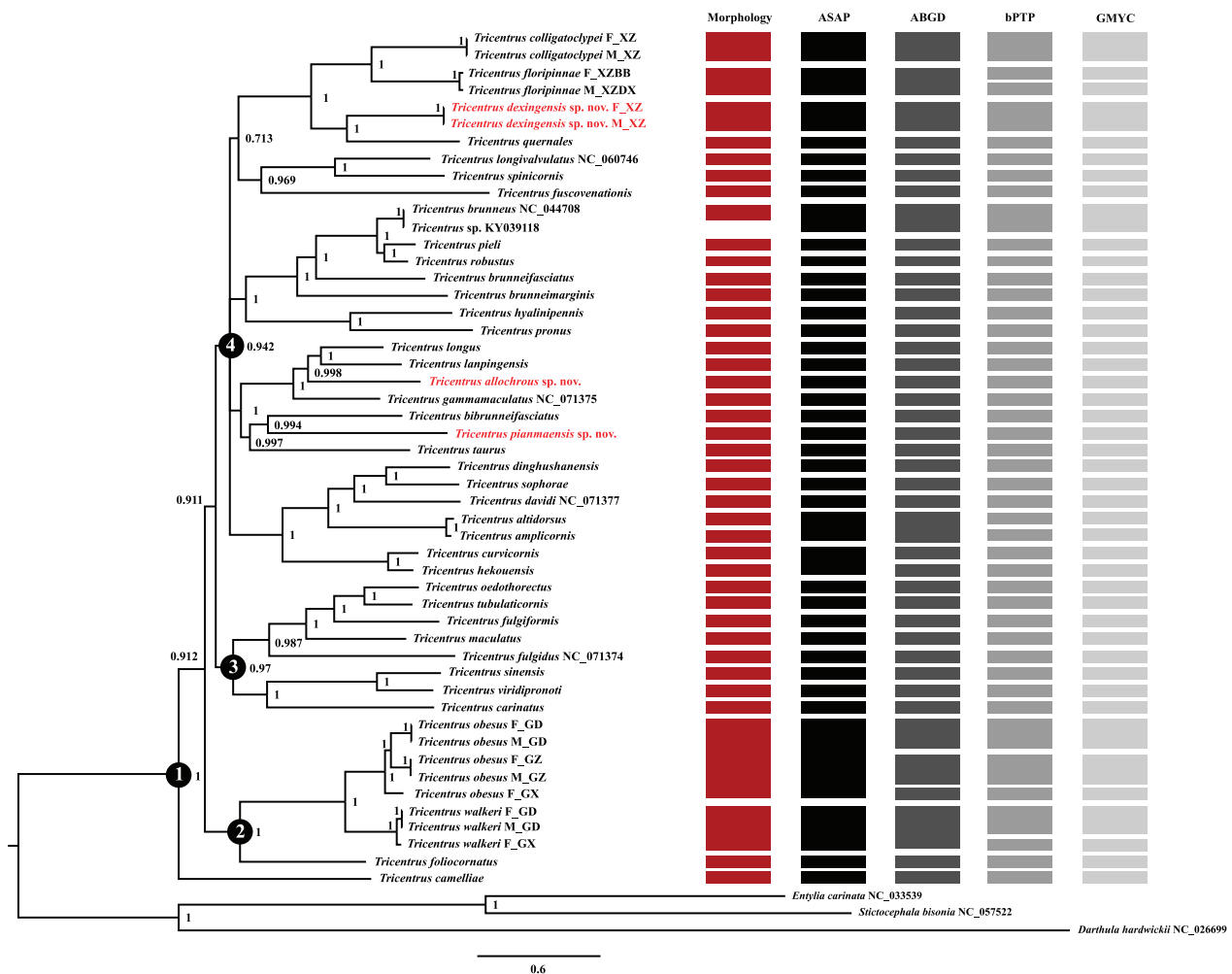


Figure 2. Phylogenetic trees of treehoppers, inferred using MrBayes analysis based on the nucleotide sequences of the 13 protein-coding genes. Bayesian posterior probabilities (BPPs) are indicated on branches. Black circles represent annotated branches. The boxes of different colors on the right represent the results of morphology and species definition.

clade 4 with near central region (Fig. 2) alongside *T. longus*, *T. lanpingensis*, *T. gammamaculatus*, *T. bibrunneifasciatus*, and *T. taurus*. The consensus topology was resolved as: (((*T. longus* + *T. lanpingensis*) + *T. allochrous* Li & Chen **sp. nov.**) + *T. gammamaculatus*) + ((*T. bibrunneifasciatus* + *T. pianmaensis* Li & Chen **sp. nov.**) + *T. taurus*).

The clade 3 comprised eight species forming a basal polytomy in the phylogenetic tree, with sturdy support (ML bootstrap = 99.4; BI posterior probability = 0.97) (Fig. S1).

3.2. Molecular species delimitation analysis

Species boundaries of *Tricentrus* inferred from four delimitation methods (ASAP, ABGD, bPTP, and GMYC) using *COI* sequences with *Tricentrus* were illustrated (Fig. 2). Most of the four molecular delimitation methods yielded concordant results, delineating 38–41 species that correspond closely to well-supported phylogenetic clades recovered in both BI and ML analyses. Despite several instances of incongruence between the results of species

delimitation methods, all consistently separated the three new species as a distinct entity respectively (Fig. 2), and both sexes were consistently recovered as conspecific across all delimitation analyses, with male and female specimens clustering within the same molecular operational taxonomic units (MOTUs). The ASAP algorithm (Kimura 2-parameter model, K2P) recovered 38 molecular operational taxonomic units (MOTUs) at its optimal partition score (7.5). In contrast, ABGD produced discordant species delimitations among the three interspecific comparisons, *T. curvicornis*, *T. hekouensis* and *T. obesus*. The bPTP analysis delineated 41 MOTUs. Within the *T. floripinnae*, males and females were delimited as distinct evolutionary lineages. Congruently, the GMYC model corroborated all bPTP-delimited clades.

3.3. Divergence time estimation

The dated phylogeny (Fig. 3) based on nucleotide data showed the divergence between *Tricentrus* and the outgroup at 136.40 Mya [95% highest posterior density (HPD): 134.02–149.67] during the Early Cretaceous. The diversification within the genus *Tricentrus* was dat-

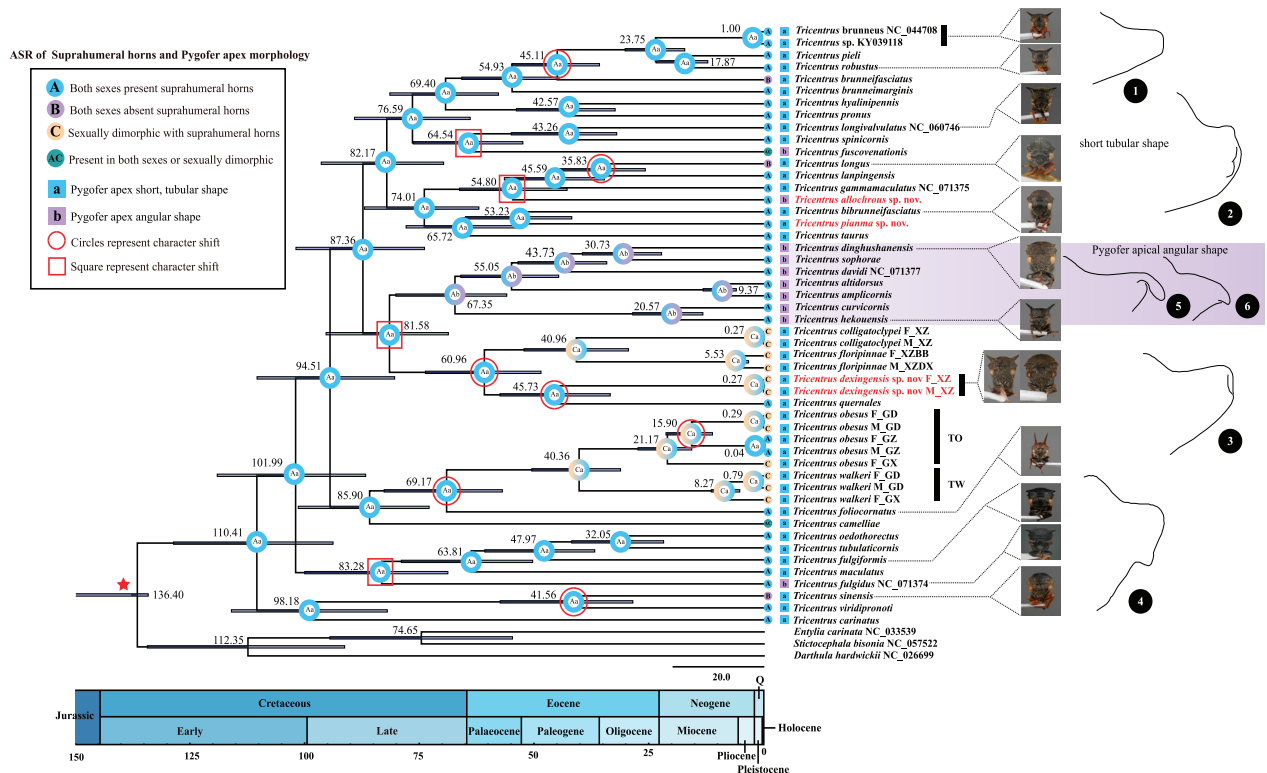


Figure 3. Chronogram showing the ancestral state reconstructions and temporal divergences of the genus *Tricentrus*. Pie charts on nodes indicate most likely states only. Blue bars indicate time intervals for 95% probability of actual age (Fig. S4). The color and shape of nodes at the end of the tree and the color of letters in brackets correspond to states of the characters presence of the treehopper suprahumeral horn and pygofer apex morphology on the left box of the figure. Calibration nodes by the red star. The figure on the right is the frontal view of habitus of the treehoppers, and circles 1–6 lateral view sketch of apical pygofer morphology.

ed to the period from the Early Cretaceous 110.41 Mya (95% HPD: 93.85–128.52). The initial divergence between species *T. obesus* (TO) and *T. walkeri* (TW) and *T. folicornatus* was dated at 69.19 Mya (95% HPD: 57.05–82.76). The sexually dimorphic clade TO group was estimated to have diverged from the TW group at 40.36 Mya (95% HPD: 31.34–50.67). And other sexual dimorphism species (*T. colligatoclypei*, *T. floripinnae*, *T. dexingensis* Li & Chen **sp. nov.**, not *T. quernales*, since this species' male is unknown) began to form in the Palaeocene at 60.96 Mya (95% HPD: 48.64–73.79), the *T. colligatoclypei* + *T. floripinnae*, *T. dexingensis* Li & Chen **sp. nov.** divergence in the Eocene, at 40.96 Mya (95% HPD: 29.61–52.34) and 45.73 Mya (95% HPD: 33.60–57.56) and the remaining two new species, *T. allochrous* Li & Chen **sp. nov.**, *T. pianmaensis* Li & Chen **sp. nov.**, showed divergences starting in the Palaeocene at 53.23 Mya (95% HPD: 41.95–65.05) and Eocene 45.69 Mya (95% HPD: 42.97–66.38), respectively. The differentiation time of the remaining species can be found in the Figure S4.

3.4. Ancestral state reconstructions

ASR analyses of suprahumeral horns variation in the treehopper genus *Tricentrus* indicated that the ancestral condition for this genus featured suprahumeral horns present in both sexes (Figs 3, S5). Our analyses revealed

seven evolutionary transitions in this character, representing three distinct patterns of morphological change. ASR identified three independent evolutionary transitions from ancestral state A (suprahumeral horns present in both sexes) to state B (suprahumeral horns absent in both sexes), occurred along the branches leading to: *T. sinensis*, *T. longus*, and *T. brunneifasciatus*, while the other three evolutionary transitions from state A to state C (sexual dimorphism with suprahumeral horns) occurred in the following species branches: *T. walkeri*, *T. obesus*, *T. dexingensis* Li & Chen **sp. nov.**, *T. floripinnae*, and *T. colligatoclypei*. On the contrary, the evolutionary transition from state C to state A occurred only once, in the *T. obesus* group.

The ASR analyses of female pygofer apex morphology demonstrated that the ancestral condition for this genus was characterized by a short tubular shape (ventral margins slightly exceed dorsal margins or both margins flush) (Figs 3, S6). The analyses identified four evolutionary transitions in pygofer apex morphology, all following a single pattern of morphological change. All five morphological transitions are directed from the ancestral state A (short tubular shape) to the derived state B (angular shape: dorsal margins exceed ventral margins obviously), and occurred along the branches leading to: *T. fulgidus*, *T. oedothorectus*, *T. hekouensis*, *T. curvicornis*, *T. amplicornis*, *T. altdorsus*, *T. davidi*, *T. sophorae*, *T. dinghushanensis*, *T. allochrous* Li & Chen **sp. nov.**, *T. fuscoventionis*, *T. brunneifasciatus*.

3.5. Taxonomy

3.5.1. *Tricentrus* Stål, 1866

Tricentrus Stål, 1866

Tricentrus Stål, 1866: 89; Distant, 1907: 53; Funkhouser, 1927: 495; Goding, 1931: 303; Wu, 1935: 62; Metcalf & Wade, 1965: 379; Ahmad & Yasmeen, 1974: 183; Ananthasubramanian & Ananthakrishnan, 1975: 224; Yuan & Chou, 2002: 362–363.

Tricentrus Metcalf & Wade, 1965: 411.

Taloipa Metcalf & Wade, 1965: 1479.

Otaris Buckton, 1903: 249; Metcalf & Wade, 1965: 421.

Taloipa Buckton, 1905: 334.

Centrotus Matsumura, 1914: 72.

Centrotoscelus Funkhouser, 1914: 72; Yuan & Chou, 2002: 330.

Arisangargara Kato, 1928: 48.

Type species. *Centrotus fairmairei* Stål, 1859

Diagnosis. Modified from Wallace and Deitz (2004). Suprahumeral horns present or absent; posterior pronotal process straight at base, appressed against scutellum. Scutellum most apices visible. Frontoclypeal margins expanding gradually towards apex. Frontoclypeal lobes distinct or indistinct, not extending to apex of frontoclypeus. Metathoracic leg trochanter with very large spines. Forewing with R_1 , R_{2+3} , R_{4+5} , M_{1+2} , M_{3+4} ; apex unfused (5 apical cells). Female second valvulae without significant broadening.

3.5.2. *Tricentrus allochrous* Li & Chen sp. nov.

<https://zoobank.org/7F79C904-1596-49A8-B82D-D429B88D6878>

Figures S7–S9

Diagnosis. Pronotum rusty orange in female (Fig. S7A, B, E); male wine-red with darker margins (except metopidium and callosity, black in both) (Fig. S7C, D, F). Forewing smoke-yellow, bearing a transverse light brown band at mid-length (Fig. S7G).

Description. Measurements: Body length: males ($n = 11$): 6.7–6.9mm, females ($n = 12$): 7.1–7.3mm; forewing length: males ($n = 11$): 6.0–6.3mm, females ($n = 12$): 6.5–6.6mm; width between humeral angles apices: males ($n = 11$): 2.3–2.5mm, females ($n = 12$): 2.6–2.7mm; width between suprahumeral horns apices: males ($n = 11$): 2.7–3.0mm, females ($n = 12$): 3.2–3.6mm. — **Coloration:** Both sexes body orange-yellow, although males exhibit a darker overall coloration. Head black, eyes yellowish-brown, ocelli light yellow. Thorax black, legs femur with apical, tibia and tarsus orange, claw dark brown. Forewing veins concolorous with the membrane; male veins more deeply pigmented (Fig. S7G). — **Head:** Vertex with dorsal and ventral margins slightly arcuated and wave-shaped respectively (Fig. S7E, F). Ocelli

slightly closer to inner margins of eyes than to each other. Frontoclypeal margins expanding gradually towards apex and frontoclypeal lobes distinct not extending to apex of frontoclypeus (Fig. S7E, F). — **Thorax:** Suprahumeral horns base thick and sturdy, the end extends upwards to the side, and apical blunt. Posterior pronotal process straight and extended, apex stays in the vein M_{3+4} base (Fig. S7A–D). Metathoracic leg trochanter with very large spines (Fig. S7I). — **Male genitalia:** Pygofer sub-rectangular in lateral view, tube shaped at the posterodorsal (Fig. S8A, B, D). Sternite IX with concave ventral margin in ventral view (Fig. S8B). Lateral plate triangular in dorsal half, right portion weakly depressed, margins setose (Fig. S8G). Basal more than half of subgenital plate fused (Fig. S8B). Style clasp angled dorsally; distally end lateral recurved and slender, inner surface with setae; connective n-shaped (Fig. S8C). Aedeagus in lateral view U-shaped, tapered distally with coarse denticles in distal half of dorsal margin; gonopore oval, near apex on posterior surface (Fig. S8E, F). — **Female genitalia:** Pygofer sub-rectangular in lateral view, densely covered with setae, its apex slightly curved ventrally (Fig. S9A, B). Sternite VII longer than width in ventral view, with posterior margin deeply concave, accounting for two-thirds of the width (Fig. S9C). First valvulae knife-shaped, exhibiting gentle curvature; dorsal margin medially depressed, with fine longitudinal striae proximally and an acuminate apex (Fig. S9D). Second valvulae similar in shape to the first valvulae, dorsal margin of the posterior half bearing contiguous denticles, with the base denticle distinctively isolated (Fig. S9E). Third valvulae (gonoplac) broadly rounded distally (Fig. S9F).

Material examined. Holotype: CHINA • ♂; Yunnan Prov., Dehong City, Yingjiang County, Zhina Town (25°16'9.43"N, 98°2'4.44"E), 1850m; 25 May 2023; Min Li leg. **Paratypes:** CHINA • 10♂♂12♀♀; same locality as holotype; Min Li, Guang-Li Gou leg.

Type deposition statement. The holotype and paratype specimens of the new species described herein have been deposited in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

Distribution. China (Yunnan).

Etymology. The word “*allochrous*” is a Latinized adjective, referring to sexual dichromatism, specifically differing pigmentation between males and females.

Remarks. This species is similar to *T. albomaculatus* Distant, 1907, but differs from this in (1) forewing with a transverse light brown band at mid-length (absent brown band in *T. albomaculatus*); (2) forewing smoke-yellow (black brown on the terminus in *T. albomaculatus*); (3) metopidium uniform pigmentation, rusty orange or black (anterior margin of metopidium black and the remaining brown in female, male all black in *T. albomaculatus*).

3.5.3. *Tricentrus dexingensis* Li & Chen sp. nov.

<https://zoobank.org/FAFC6168-D33F-42DF-A619-E46FB6724883>

Figures S10–S12

Diagnosis. Suprahumeral horns base thick and sturdy, elongate sideways and upwards, dorsal side flattened; absence in male. Posterior pronotal process weak depression on the base, strongly expanded near middle not exceeding apex of suprahumeral horns (Fig. S10A–D). Forewing light brown, bearing two spacers of transparent and tawny band, tornus transparent; veins brown except area of transparent (Fig. S10H, I).

Description. Measurements: Body length: males (n = 2): 3.9–4.0mm, females (n = 2): 4.6–4.7mm; forewing length: males (n = 2): 3.5–3.7mm, females (n = 2): 4.0–4.1mm; width between humeral angles apices: males (n = 2): 1.9–2.0mm, females (n = 2): 2.0–2.1 mm; width between suprahumeral horns apices: females (n = 2): 2.3–2.5mm. — **Coloration:** Female body reddish brown with darker margins, male black (Fig. S10A–D). Eyes yellowish brown, male darker; ocelli tangerine yellow, male white (Fig. S10E, F). Legs coxae, trochanter, femur black; apical of femur, tibia, tarsus rusty brown, and claw yellow (Fig. S10G). — **Head:** Vertex with dorsal margins bow-shaped, slight depression in the center; ventral margins oblique and weakly wavy (Fig. S10E, F). Ocelli slightly closer to inner margins of eyes than to each other. Frontoclypeal margins expanding gradually towards apex in a rectangle, on the same arc with the frontoclypeal lobes apex (Fig. S10E, F). — **Thorax:** Metathoracic leg trochanter with very large spines (Fig. S10G). — **Male genitalia:** Pygofer rectangular in lateral view, dorsal margins base convex (Fig. S11A, B, D). Sternite IX rectangular with slightly concave ventral margin in ventral view (Fig. S11D). Lateral plate finger-like in dorsal half, base thick and sturdy, right portion weakly depressed, margins setose (Fig. S11G). Basal 2/3 of subgenital plate fused (Fig. S11D). Style clasp angled dorsally; apex laterally recurved, style shank slender, inner surface with setae; connective n-shaped (Fig. S11C). Aedeagus uncinat, a quarter apical taper in lateral view, distally with coarse denticles in distal half of dorsal margin; gonopore oval at the apex (Fig. S11E, F). — **Female genitalia:** Pygofer with clearly angulate base and weakly tubular distal portion in lateral view; surface densely setose throughout (Fig. S12A, B). Sternite VII U-shaped, triangular shaped on both sides, with posterior margin deeply concave, accounting for nearly all of the width (Fig. S12C). First valvulae knife-shaped, exhibiting weak curvature; dorsal margin depressed, base convex, with fine longitudinal striae on about half of its length, and terminating in an acuminate apex (Fig. S12D). Second valvulae similar in shape to the first valvulae, dorsal margin of nearly the posterior third bearing contiguous denticles (Fig. S12E).

Third valvulae (gonoplac) broadly rounded distally (Fig. S12F).

Material examined. Holotype: CHINA • ♂; Xizang Prov., Linzhi City, Motuo County, Dexing Town (29°19'52.482"N, 95°18'38.6784"E), 735 m; 11 August 2020; Yong-Jin Sui leg. — **Paratype:** CHINA • 1♂2♀; same data as holotype; Yongjin Sui, Xian-Yi Wang leg.

Type deposition statement. The holotype and paratype specimens of the new species described herein have been deposited in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

Distribution. China (Xizang).

Etymology. The species is named after the type locality.

Remarks. This species is similar to *T. dorsocameloides* Yuan & Cui, 1997, but differs from this in (1) suprahumeral horns near quadrilateral in shape with blunt apical margins (triangular with acuminate apices in *T. dorsocameloides*); (2) forewings dark brown to blackish; with a hyaline transverse band on the median, and fulvous transverse bands in the subapical area (yellowish-brown with brown on apex in *T. dorsocameloides*); (3) leg coxae, trochanter, femur black; apical of femur, tibia, tarsus rusty brown, and claw yellow (trochanter, femur dark brown and the remaining brown in *T. dorsocameloides*); (4) forewing veins dark brown (yellow in *T. dorsocameloides*).

3.5.4. *Tricentrus pianmaensis* Li & Chen sp. nov.

<https://zoobank.org/E1AD5DAE-D8EE-40DF-93D4-7383CB61EF8A>

Figure S13–S15

Diagnosis. Pronotum and head reddish brown in female; male dark burgundy with darker margins (except metopidium, callosity and head black) (Fig. S13A–D). Suprahumeral horns base thick and sturdy, nearly upright. Female forewing reddish brown, bearing brown at distal end; veins same colouration as forewing. Male forewing deeply smoke-yellow, veins deeply brown (Fig. S13G).

Description. Measurements: Body length: males (n = 9): 6.3–6.5mm, females (n = 8): 7.2–7.6mm; forewing length: males (n = 9): 5.4–5.6mm, females (n = 8): 6.4–6.7mm; width between humeral angles apices: males (n = 9): 2.7–2.8mm, females (n = 8): 3.4–3.5mm; width between suprahumeral horns apices: males (n = 9): 2.7–2.9 mm, females (n = 8): 3.6–3.7mm. — **Coloration:** Eyes dark yellowish brown with brown scattered patches, ocelli light orange (Fig. S13E, F). Thorax same pronotum, legs tarsus and claw brown in female; male black,

legs reddish brown and black mix (Fig. S13I). — **Head:** Vertex with dorsal margins arcuate and ventral margins oblique. Ocelli slightly closer to inner margins of eyes than to each other. Frontoclypeal margins expanding gradually towards apex and frontoclypeal lobes distinct, slightly above vertex, ventral margins not extending to apex of frontoclypeus (Fig. S13E, F). — **Thorax:** Posterior pronotal process straight and extended, apex stays in the anal angle (Fig. S13A–D). Metathoracic leg trochanter with very large spines (Fig. S13I). — **Male genitalia:** Pygofer rectangular in lateral view, dorsal margins base convex (Fig. S14A, B). Sternite IX with slightly concave ventral margin in ventral view (Fig. S14B). Lateral plate finger-like in dorsal half, right portion weakly depressed, margins setose (Fig. S14G). Basal nearly half of subgenital plate fused (Fig. S14B). Style clasp angled dorsally; distally end lateral recurved, inner surface with setae; connective n-shaped (Fig. S14C). Aedeagus in lateral view U-shaped, distally with coarse denticles in distal half of dorsal margin; gonopore oval, near apex on posterior surface (Fig. S14E, F). — **Female genitalia:** Pygofer with angulate base and weakly tubular distal portion in lateral view; surface densely setose throughout (Fig. S15A, B). Sternite VII longer than width in ventral view, with posterior margin deeply concave, accounting for nearly all of the width (Fig. S15C). First valvulae knife-shaped, exhibiting obvious curvature; dorsal margin depressed, with fine longitudinal striae exceeding two-thirds, and terminating in an acuminate apex (Fig. S15D). Second valvulae similar in shape to the first valvulae, dorsal margin of the posterior third bearing contiguous denticles, with the base denticle distinctively isolated (Fig. S15E). Third valvulae (gonoplac) broadly rounded distally (Fig. S15F).

Material examined. Holotype: CHINA • ♂; Yunnan Prov., Nujiang City, Lushui County, Pianma Town (26°03'17.69"N, 98°36'49.81"E), 2000 m; 6 August 2018; Feng-E Li leg. **Paratypes:** CHINA • 8♂♂8♀♀; same locality as holotype; 6 September 2023; Yong-Jin Sui, Li-Kun Zhong, Min Tang leg.

Type deposition statement. The holotype and paratype specimens of the new species described herein have been deposited in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

Distribution. China (Yunnan).

Etymology. The species is named after the type locality.

Remarks. This species is similar to *T. oedothorectus* Yuan & Cui, 1987, but differs from this in (1) coloration of body reddish brown, the presence of a lateral carina of suprahumeral horns (black; without lateral carina of suprahumeral horns in *T. albomaculatus*); (2) posterior pronotal process planar (tapered in *T. albomaculatus*); (3) forewing yellowish brown (veins and extremity brown in *T. albomaculatus*); (4) frontoclypeal lobes distinct (small and distinct in *T. albomaculatus*).

3.5.5. *Tricentrus colligatoclypei* Yuan & Cui, 1988

Figures S16–S18

Tricentrus colligatoclypei Yuan & Cui, 1988: 134; Yuan & Chou, 2002: 394–395.

Diagnosis. Suprahumeral horns base thick and sturdy, elongate sideways and upwards; absent in male. Posterior pronotal process straight and extended, apex stays in the tornus (Fig. S16A–D). Frontoclypeal margins expanding gradually towards apex, on the same arc with the frontoclypeal lobes apex. The frontoclypeus demonstrates coplanar alignment with the vertex ventral margins (Fig. S16E, F).

Redescription. Measurements: Body length: males (n = 2): 4.4–4.5mm, females (n = 2): 4.9–5.0mm; forewing length: males (n = 2): 3.4–3.5mm, females (n = 2): 3.7–4.5mm; width between humeral angles apices: males (n = 2): 2.4–2.5mm, females (n = 2): 2.8–3.3mm; width between suprahumeral horns apices: females (n = 2): 2.2–2.6mm. — **Coloration:** Female body black brown, male black (Fig. S16A–D). Eyes yellowish brown with brown scattered patches, ocelli yellowish brown (Fig. S16E, F). Legs coxae, trochanter, femur black; tibia, tarsus and claw brown. Forewing yellow-brown, tornus neighboring brown; veins R₁ medial, r-m, m-cu, Cu apical, brown; male basal half transparent (Fig. S16G, H). — **Head:** Vertex with dorsal margins convex, slight depression in the center; ventral margins oblique and weakly wavy. Ocelli slightly closer to inner margins of eyes than to each other. — **Male genitalia:** Pygofer rectangular in lateral view, dorsal margins convex (Fig. S17A, B, D). Sternite IX trapezoidal with slightly concave ventral margin in ventral view (Fig. S17D). Lateral plate finger-like in dorsal half, right portion weakly depressed, margins setose (Fig. S17G). More than basal half of subgenital plate fused (Fig. S17D). Style clasp angled dorsally; apex laterally recurved, inner surface with setae; connective n-shaped (Fig. S17C). Aedeagus uncinat in lateral view, distally with coarse denticles in distal half of dorsal margin; gonopore oval occupying a quarter of the aedeagus (Fig. S17E, F). — **Female genitalia:** Pygofer with angulate, obvious base and weakly tubular distal portion in lateral view; surface densely setose throughout (Fig. S18A, B). Sternite VII with posterior margin deeply concave, accounting for nearly all of the width (Fig. S18C). First valvulae knife-shaped, exhibiting weak curvature; dorsal margin depressed, with fine longitudinal striae on the one-third and terminating in an acuminate apex (Fig. S18D). Second valvulae similar in shape to the first valvulae, dorsal margin of the posterior third bearing contiguous denticles, with the base denticle distinctively isolated (Fig. S18E). Third valvulae (gonoplac) broadly rounded distally (Fig. S18F).

Material examined. CHINA • 2♂♂2♀♀; Xizang Prov., Linzhi City, Motuo County, Beibeng Town

(29°15'14.857"N, 95°12'16.013"E), 935 m; 30 June 2022; Hong-Li He leg.

Distribution. China (Xizang).

Remarks. This species was initially documented based on a female specimen collected in Beibeng Town, Motuo County, China (Xizang). Following this original discovery, no further records were documented for over a century until our recent recollection at the type locality. Here, we provide the first comprehensive morphological description of male specimens, complemented by complete mitochondrial genome sequencing. These critical additions enable accurate identification and pairing of male specimens within this taxon.

3.5.6. *Tricentrus floripinnae* Yuan & Cui, 1987

Figures S19–S21

Tricentrus floripinnae Yuan & Cui, 1987: 136; Yuan & Chou, 2002: 396–397; Li et al, 2020, 252, 254.

Diagnosis. Suprahumeral horns base thick and sturdy, reaching out to the sides, not exceeding humeral angle in frontal view; absent in male. Posterior pronotal process gabled, apex stays in the tornus (Fig. S19A–D). Forewing darker tawny, veins R_1 , r-m, m-cu, cu dark brown, tornus transparent; blackish brown anteriorly and posteriorly near the tornus and at the extremity of the forewings (Fig. S19G).

Redescription. Measurements: Body length: males (n = 3): 4.5–4.6mm, females (n = 4): 5.0–5.4mm; forewing length: males (n = 3): 3.9–4.0mm, females (n = 4): 4.4–4.7mm; width between humeral angles apices: males (n = 3): 2.1–2.2mm, females (n = 4): 2.4–2.8mm; width between suprahumeral horns apices: females (n = 3): 2.4–2.8mm. — **Coloration:** Both sexes black. Eyes yellowish brown or silvery grey with black brown border; ocelli tangerine yellow (Fig. S19E, F). Legs black except apical of femur and tibia rusty brown; claw and tarsus tawny. — **Head:** Vertex with dorsal margins bow-shaped; ventral margins oblique and weakly wavy on the base. Ocelli slightly closer to inner margins of eyes than to each other. Frontoclypeal margins expanding gradually towards apex in arcuate, on the same arc with the frontoclypeal lobes apex (Fig. S19E, F). — **Male genitalia:** Pygofer rectangular in lateral view, dorsal margins base convex, suffer with distinct lateral carina (Fig. S20A, B, D). Sternite IX rectangular with slightly concave ventral margin in ventral view (Fig. S20D). Lateral plate finger-like in dorsal half, base thick and sturdy, right portion weakly depressed, margins setose (Fig. S20G). Basal two-thirds of subgenital plate fused (Fig. S20D). Style clasp angled dorsally; apex laterally recurved, style shank slender, inner surface with setae; connective n-shaped (Fig. S20C).

Aedeagus uncinata, apical with one-third narrow in lateral view, distally with coarse denticles in more than half of the dorsal margin; gonopore oval in the apical (Fig. S20E, F). — **Female genitalia:** Pygofer with angulate base and apex blunt; weakly tubular distal portion in lateral view; surface densely setose throughout (Fig. S21A, B). Sternite VII U-shaped, triangular shaped on both sides, with posterior margin deeply concave, accounting for nearly all of the width (Fig. S21C). First valvulae knife-shaped, exhibiting curvature; dorsal margin depressed, with fine longitudinal striae on nearly a half and terminating in an acuminate apex (Fig. S21D). Second valvulae similar in shape to the first valvulae, dorsoposterior margin bearing arranged denticles along the distal third, with two enlarged basal denticles forming distinct intersegmental spacing structures (Fig. S21E). Third valvulae (gonoplac) broadly rounded distally (Fig. S21F).

Material examined. CHINA • 3♂♂3♀♀; Xizang Prov., Linzhi City, Motuo County, Dexing Town (29°19'52.482"N, 95°18'38.6784"E), 735 m; 11 August 2020; Yong-Jing Sui leg. CHINA • 1♀; Xizang Prov., Linzhi City, Motuo County, Beibeng Town (29°14'36.3804"N, 95°10'12.774"E), 775 m; 11 August 2020; Yong-Jing Sui leg.

Distribution. China (Xizang).

Remarks. This species was originally described by Yuan and Cui (1987) based on female specimens collected in Xizang, China and subsequently came into the China faunal checklist (Yuan and Chou 2002). Both foundational records were based solely on female specimens, leaving male morphological characteristics undocumented until the recent work of Li et al. (2020), which provided the first confirmed description of diagnostic male features. However, through comparative analysis of morphology we confirm these specimens represent distinct taxonomic entities. The *Tricentrus floripinnae* (Li et al. 2020) is hereby reclassified as a misapplied taxonomic concept within the genus *Tricentrus*, based on morphological incongruences between the material and newly acquired specimens from the original locality. Here, through integrated morphological and molecular analysis of newly collected type locality material, we validated it to be a sexually dimorphic species and confirmed males of this species.

3.5.7. *Tricentrus obesus* Funkhouser, 1942

Figures S22–S25

Tricentrus obesus Funkhouser, 1942: 61.

Tricentrus aleuritidis Chou, 1975: 426; Yuan, 1987: 152; Yuan & Chou, 2002: 438. **Syn. nov.**

Diagnosis. Suprahumeral horns base thick and sturdy, elongate sideways and upwards; absence or presence in

male (Fig. S23A–E3, a–e3). Forewing smoke-yellow, bearing four alternating transverse bands: two transparent (basal and medial) alternating with two light brown bands, brown at distal end; venation concolorous except veins most of the R_{2+3} , R_{4+5} , and r-m, m-cu; male base transparent; male with wing base transparent and veins more deeply pigmented. (Fig. S23A4–E4). Aedeagus uncinuate in lateral view, dorsal margin bearing three paired spinose processes located in the medial, subapical, apical areas respectively; gonopore slender-elliptical, occupying half of the aedeagus (Fig. S23a5–6–e5–e6 and Fig. S24E, F).

Redescription. Measurements: Body length: males (n = 16): 6.2–6.4mm, females (n = 16): 7.2–7.8mm; forewing length: males (n = 16): 5.4–5.6mm, females (n = 16): 6.4–6.5mm; width between humeral angles apices: males (n = 16): 3.1–3.4mm, females (n = 16): 3.7–4.0mm; width between suprahumeral horns apices: males (n = 16): 2.8–4.5mm, females (n = 16): 4.5–5.0mm. — **Coloration:** Both sexes body black, brown, or dark brown (Fig. S23A1–E1, a1–e1). Eyes yellowish brown with brown scattered patches, ocelli orange-brown (Fig. S22A–C and Fig. S22A1–E1, a1–e1). Legs coxae, trochanter, femur, claw black; tibia, tarsus yellow brown (Fig. S23A2–E2, a2–e2). — **Head:** Vertex with dorsal margins convex, slight depression in the center. Ocelli slightly closer to inner margins of eyes than to each other. Frontoclypeal margins expanding gradually towards apex and frontoclypeal lobes distinct, slightly above vertex, ventral margins reaching to the middle of frontoclypeus (Fig. S23A3–E3, a3–e3). — **Thorax:** Posterior pronotal process gabled, weak depression on the base, apex dorsal margins slightly deflexed ventrad (Fig. S23A3–E3, a3–e3). — **Male genitalia:** Pygofer narrow rectangular in lateral view, suffer with distinct lateral carina (Fig. S24A, B, D). Sternite IX with slightly concave ventral margin in ventral view (Fig. S24B). Lateral plate scalene triangle, right portion weakly depressed, margins setose (Fig. S24G). Basal three-quarters of subgenital plate fused (Fig. S24B). Style clasp angled dorsally; style shank arc, apex laterally recurved and margin exhibits a truncate configuration, inner surface with setae; connective n-shaped (Fig. S23a7–e7 and Fig. S24C). — **Female genitalia:** Pygofer with obvious angulate base and weakly tubular distal portion in lateral view; surface densely setose throughout (Fig. S25A, B). Sternite VII with posterior margin deeply concave, accounting for nearly all of the width (Fig. S25C). First valvulae knife-shaped, exhibiting weak curvature; dorsal margin depressed, with fine longitudinal striae on nearly half and terminating in an acuminate apex (Fig. S25D). Second valvulae similar in shape to the first valvulae, dorsal margin of the posterior third bearing contiguous denticles (Fig. S25E). Third valvulae (gonoplac) broadly rounded distally (Fig. S25F).

Material examined. CHINA • 1♂3♀♀; Guangxi Prov., Guilin City, Lingui District, Wantian Town (25°36′43.989″N, 109°57′39.131″E), 1600 m; 4 July

2023; Yongjin Sui, Feng-E Li leg. CHINA • 2♂♂6♀♀; Guangdong Prov., Ruyuan City, Shixing County, Luoba Town (24°50′36.230″N, 114°13′3.440″E), 261 m; 14 June 2023; Shasha Lv, Feng-E Li leg. CHINA • 11♂♂3♀♀; Fujian Prov., Jianou City, Fangdao Town (27°3′8.587″N, 118°9′27.080″E); 21 May 2012; Jian-Kun Long leg. CHINA • 1♂1♀; Guizhou Prov., Tongren City, Dejiang County, Fuxing Town (28°6′30.640″N, 107°54′3.797″E); 7 June 2021; Yin-Lin Mu leg. CHINA • 1♂3♀♀; Shandong Prov., Linyi City, Yinan County, Mamuchi Town (35°41′30.651″N, 118°16′50.623″E); 17 July 2020; Yongjin Sui leg.

Distribution. China (Guangxi, Guangdong, Fujian, Guizhou, Sichuan, Shaanxi).

Remarks. Specimens from four biogeographically distinct localities were examined, revealing all males completely lack suprahumeral horns. While sexual dimorphism has been documented in this genus *Tricentrus*, this discovery provides critical insights into evolutionary developmental pathways regulating sexual dimorphism. We have added the relevant morphological characters of the males and their mitochondrial genome sequences to make them correctly paired males. Examination of the type material (Fig. S22) indicates that *Tricentrus aleuritis* Chou, 1975 is conspecific with *T. obesus* Funkhouser, 1942; the former is consequently placed as a junior synonym.

3.5.8. *Tricentrus walkeri* Metcalf & Wade, 1965

Figures S26–S28

Centrotus capreolus Walker, 1851: 627.

Tricentrus capreolus Stål, 1870: 728; Funkhouser, 1927: 498; Goding, 1939: 317, 324; Funkhouser, 1950: 209.

Tricentrus walkeri Metcalf & Wade, 1965: 412; Yuan & Chou, 2002: 439.

Diagnosis. Suprahumeral horns slim and short, apex blunt, elongate sideways and upwards, dorsal side flattened; absence in male. Aedeagus uncinuate in lateral view, slender in posterior view; base with ventral margins slightly concavity, dorsal margin bearing two paired spinose processes located in the medial, and apical respectively, medial maximum development, subapical smallest; gonopore slender-elliptical, occupying nearly a half of the aedeagus (Fig. S27E, F).

Redescription. Measurements: Body length: males (n = 4): 6.0–6.2mm, females (n = 10): 6.1–7.0mm; forewing length: male (n = 4): 5.4–5.5mm, females (n = 10): 5.1–6.2mm; width between humeral angles apices: males (n = 4): 3.1–3.2mm, females (n = 10): 3.1–3.5mm; width between suprahumeral horns apices: females (n = 10): 3.5–4.0mm. — **Coloration:** Body black-brown with gold hairs (Fig. 23A1–C1, a1–b1). Forewing smoke-yellow,

bearing four alternating transverse bands: two transparent (basal and medial) alternating with two light brown bands, brown at distal end (Fig. 23A4–C4). Legs coxae, trochanter, femur black; tibia black-brown, tarsus orange, claw yellow brown. — **Head:** Vertex with dorsal margins bow-shaped obviously, slightly depression in the center; ventral margins oblique and weakly wavy. Ocelli slightly closer to inner margins of eyes than to each other. Frontoclypeal margins expanding gradually towards apex and frontoclypeal lobes distinct not extending to apex of frontoclypeus (Fig. 23A3–C3, a3–b3). — **Thorax:** Posterior pronotal process ridged, weak depression on the base, apex dorsal margins slightly deflexed ventrad (Fig. 23A2–C2, a2–b2). — **Male genitalia:** Pygofer narrow rectangular in lateral view, suffer with distinct lateral carina (Fig. 24A–B, D). Sternite IX rectangular with slightly concave ventral and lateral margin in ventral view (Fig. 24D). Lateral plate exhibits a scalene triangular configuration, with the dextral aspect demonstrating shallow concavity (Fig. 24G). Basal more than a half of subgenital plate fused (Fig. 24D). Style clasp angled dorsally; style shank arc, apex lateral recurved, and margins acuminate, inner surface with setae; connective n-shaped (Fig. 24C). — **Female genitalia:** Pygofer with elliptical base and weakly tubular distal portion in lateral view; surface densely setose throughout (Fig. 25A–B). Sternite VII exhibits V-shaped, with posterior margin deeply concave, account for near all of the width (Fig. 25C). First valvulae knife-shaped, exhibiting weakly curvature in the near medial; dorsal margin with fine longitudinal striae more than a half and terminating in an acuminate apex (Fig. 25D). Second valvulae similar in shape to the first valvulae, dorsal margin of the posterior thirds bearing contiguous denticles, and base denticle obvious (Fig. 25E). Third valvulae (gonoploc) broadly rounded distally (Fig. 25F).

Material examined. CHINA • 4♀♀; Guangxi Prov., Guilin City, Lingui District, Wantian Town (25°36'43.989"N, 109°57'39.131"E), 1600 m; 4 July 2023, Yongjin Sui, Fenge Li leg. CHINA • 3♂♂4♀♀; Guangdong Prov., Ruyuan City, Shixing County, Luoba Town (24°50'36.230"N, 114°13'3.440"E), 261m; 14 June 2023; Shasha Lv, Yongjing Sui leg. CHINA • 1♂♂2♀♀; Guizhou Prov., Kaili City, Rongjiang County (26°18'19.867"N, 108°21'29.996"E), Ying-Jian Wang leg.

Distribution. China (Anhui, Hubei, Fujian, Hunan, Guangxi, Guangdong); Philippines.

Remarks. This species is similar to *T. obesus* Funkhouser, 1942 in morphological features of pronotum and forewing, but differs from the later in: (1) suprahumeral horns triangular in dorsal view, ungenerous in head and pronotum in anterior view (exhibits a sub-rectangular configuration in dorsal view, thick and sturdy in *T. obesus*); (2) aedeagus with medial spinose processes obviously longer, and slender in posterior view (medial spinose processes normality and not slender in *T. obesus*); (3) style clasp apex with margins acuminate (a truncate configuration in *T. obesus*).

4. Discussion

4.1. Diversification history and ancestral characteristics of the genus *Tricentrus*

Our molecular dating and ancestral state analysis (Fig. 3) provide new insights into the evolution of *Tricentrus*. The diversification of *Tricentrus* was dated to the Early Cretaceous (110.41 Mya, 95% HPD: 93.85–128.52), which is slightly older than the estimate by Li et al. (2023). The inconsistency is probably attributable to the insufficient materials of *Tricentrus* analysed in the study by Li et al. (2023). After the Early Cretaceous initial divergence, most of the *Tricentrus* species divergences took place during the Late Cretaceous, Eocene and Oligocene and a few in the Quaternary. The succession of Early Cretaceous ecological transitions, plate tectonic reorganizations, and the Cretaceous–Paleogene mass extinction (Hu 2005; Wang 2006; Yang et al. 2024) led to a phase of high diversification, in which multiple animals and plants underwent rapid biotic radiations during the Paleogene recovery interval (Lowery et al. 2018; Lyson et al. 2019; Magallón et al. 2019; Dimitrov et al. 2023). It is interesting that the main divergence of treehoppers occurred at the same frequency as the main radiation of their angiosperm host plants during the Early Cretaceous (Foster et al. 2016; Dietrich et al. 2017). Our result of the molecular dating analysis of the genus *Tricentrus* was consistent with the above findings. Both nymphal and adult stages of treehoppers demonstrate consistent feeding preferences for angiosperm hosts, as documented across multiple field studies (Yuan and Chou 2002; Wallace and Deitz 2004). As a genus with a large number of taxa, *Tricentrus*, like other treehoppers, shares the typical treehopper preference for thermophilic habitats, utilizing semi-evergreen or evergreen angiosperms as primary host plants (Wood 1993; Yuan and Chou 2002; Wallace and Deitz 2004). Based on this, we infer that the Early to Mid-Cretaceous temperature variations (Xi et al. 2024) expanded thermally suitable habitats and coincided with an increase in potential host taxa (Foster et al. 2016) for the genus *Tricentrus*.

In addition, the results of the ASR analysis of the suprahumeral horns showed that the presence of suprahumeral horns in both sexes was the ancestral state in the genus *Tricentrus* (Fig. 3). This result was similar to previous research on the *Tricentrus* genus, in which suprahumeral horns underwent multiple morphological transformations, including from absent to present (Li et al. 2023). This morphological transformation likely represents the integrated outcome of multiple evolutionary factors. Firstly, incomplete lineage sorting (ILS) is one of the possible reasons for this. Multiple descendant species arose through rapid cladogenesis from a common ancestor, resulting in the stochastic segregation of ancestral polymorphisms during subsequent lineage divergence. The phenomenon where similar traits arise independently in different species due to the stochastic inheritance of ancestral characteristics has been documented across

multiple animal groups, including insects (Fontaine et al. 2015) and marsupials (Feng et al. 2022). Second, complex life-history strategies, coupled with the pressure to make behavioral choices, may be another contributing factor. As commonly known, most treehopper species, with the exception of a small number of solitary species, have highly developed sub-social behaviors (Wood 1993; Yuan and Chou 2002), e.g. maternal care, aggregation and ant mutualism (Wood 1979; Lin 2006). This leads to a high proportion of females in the offspring (Wood 1984), thereby prolonging the entire life cycle and intensifying species competition.

On the other hand, the results of the ASR analysis of the pygofer apex morphology show that short and tubular was the ancestral state in the genus *Tricentrus* (Fig. 3). Similar to suprahumeral horns, the pygofer apex may have undergone morphological changes due to ILS. Furthermore, excluding the species *T. fulgidus*, *T. allochrous*, and *T. fuscobeniensis*, the clade of primary morphological transformations in pygofer apex structures emerged during the Cretaceous-Paleogene extinction interval. Increased competition as a result of the mass extinction event may have contributed to this morphological transition. The pygofer apex was usually involved in reproduction and excretion, with honeydew secretion being the main metabolite of treehoppers, which was a sugar-rich waste product (Wood 1993). Honeydew usually attracts ants to feed on it and a symbiotic relationship formed (Yuan and Chou 2002; Nelson and Mooney 2022). The angular morphology of the pygofer may confer energetic benefits to cicadas by reducing metabolic costs during honeydew processing, and avoiding species competition.

Finally, the existing morphological groupings of Chinese *Tricentrus* were not fully supported by our molecular phylogenetic data. From the perspective of the character pygofer apex, only the majority of species with the angular shape of the pygofer cluster into one branch (the base in the fourth branch of Fig. 2), while a few species were dispersed. And the remaining species with tubular pygofer apices group on different branches of the phylogenetic tree. Most of the species were classified conform to the group *T. brunneus* (Yuan and Chou 2002). Besides, interestingly, the top branch (Fig. 2), i.e. ((*T. colligatochlypei* + *T. floripinnae*) + (*T. dexingensis* Li & Chen **sp. nov.** + *T. quernales*)), these species show frontoclypeal margins expanding gradually towards the apex in a rectangle, on the same arc with the frontoclypeal lobes apex. This important characteristic was the clustering feature of the group *T. projectus* (Ahmad & Yasmeen, 1979). And yet such discordance between morphological and molecular phylogenetic results was not uncommon in taxonomic studies (Fontaine et al. 2015; Feng et al. 2022).

4.2. Patterns of sexual dimorphism with suprahumeral horns and geographical variation

Our morphological and molecular analyses revealed three distinct species of *Tricentrus* inhabiting Yunnan and Xi-

zang province. The three new species, *T. allochrous* Li & Chen **sp. nov.**, *T. pianmaensis* Li & Chen **sp. nov.** and *T. dexingensis* Li & Chen **sp. nov.**, were clearly distinct in their morphology of the pronotum and female genitalia; our descriptions and illustrations (Figs S7, S10, S13) herein make their identification in the field straightforward. The three species exhibit a combination of morphological features, including metathoracic leg trochanters with very large spines, and straight, elongated posterior pronotal processes that cover most of the scutellum. This character suite was shared among known members of the genus *Tricentrus* (Ahmad and Yasmeen 1974). With the increase of the number of species, however, some species with these features were easy to confuse with the genus *Centrotoscelus* (Funkhouser 1914a) (without suprahumeral horns in the both sexes), which was later synonymized with *Tricentrus* based on evidence from morphology and phylogeny (Wallace and Deitz 2004). For the suprahumeral horns, this genus exhibits three distinct expression patterns: species with presence in both sexes, species with absence in both sexes, and species displaying sexual dimorphism. Although sexually dimorphic species constitute a small portion of the genus, new cases continue to be documented with ongoing research (Funkhouser 1919; Yasmeen and Ahmad 1976a, 1978; Yuan et al. 1997). This morphological convergence presents substantial challenges for species delimitation within the genus.

In our results, one newly described and three previously known species demonstrated pronounced sexual dimorphism in suprahumeral horn morphology (Figs S10, S16, S19, S22, S23, S26). Notably, this study provided the first documented records of male specimens for three of these species, enabling comprehensive intersexual comparisons. Actually, sexual dimorphism is phylogenetically widespread across insects, being well-documented in Diptera, Lepidoptera, Hymenoptera, and Hemiptera (Hildreth 1965; Allen et al. 2011; Yang et al. 2015; Wang et al. 2022). The phenotypic divergence may stem from multiple evolutionary mechanisms: sexual selection and its key transcription factors, mating systems, the synergistic interplay between rapidly evolving and highly conserved elements (Andersson 1996; Chenoweth et al. 2008; Allen et al. 2011; Hopkins and Kopp 2021; Chikami et al. 2022; Laslo et al. 2023).

Cytogenetic analyses revealed that treehoppers generally possessed an XO sex-determination system, with the sexually dimorphic species *T. acuticornis* representing a derived exception with an XY chromosomal mechanism (Tian and Yuan 1995). Furthermore, the treehopper lineages defining modern subfamilies were estimated to have arisen during the late Cretaceous or early Paleogene (Dietrich et al. 2017). This derived sex-determination mechanism, combined with rapid Cretaceous diversification, likely drove the evolution of sexual dimorphism in this lineage.

Additionally, male specimens lacking suprahumeral horns were herein reported for *T. obesus* for the first time, representing a significant morphological variation within this species (Fig. S23a3–e3). Previous taxonomic

treatments (Chou 1975; Yuan and Chou 2002) reported significant intraspecific variation in male suprahumeral horn morphology for this species, encompassing a continuum from rudimentary protuberances to fully developed suprahumeral horn structures, with the complete absence of suprahumeral horns representing the only exception to this morphological spectrum. Variation in the suprahumeral horns exhibits consistent morphological patterns across males of multiple species, e.g. *T. bifurcus*, *T. pseudobifurcus*, *T. russellae*, *T. variabilis* (Ahmad and Yasmeen 1979, figs 10, 27, 31, 38, 46), *T. obesus* and *T. walkeri* (Figs S22, S23, S26). Interestingly, this morphological variation also exists in female individuals (female polymorphism), e.g. *T. angularis* (Yasmeen and Ahmad 1976, figs 7, 8), and females exhibit more variational modifications and morphological change in the suprahumeral horns ranging from small to large, e.g. *T. bifurcus*, *T. pseudobifurcus*, *T. russellae*, *T. variabilis*, *T. latiformis*, and *T. qadrii* (Ahmad and Yasmeen 1979, figs 11, 31, 39, 47; Yasmeen and Ahmad 1976, figs. 18, 28). Such morphological variation of same-sex species was documented in other genera beyond the focal taxon, e.g. *Oxyrhachis taranda* (Ananthasubramanian 1987, figs 2–5), *Membracis mexicana* (De-la-Mora and Pinero 2023, Fig. 1), and *Hypsolyrium kempii* (Yuan and Chou 2002, Fig. 43). In addition to variations in suprahumeral horns, there were also intraspecific variations in the male genitalia of the species *T. obesus*. Geographic variation was evident in the position, size, and arrangement of the three pairs of aedeagus spines among samples examined of the species *T. obesus* (Fig. S23a5–e5), and in the position of the style, equally with the connective (Fig. S23a6–e6). The species *T. walkeri* exhibits congruent geographical variation in these characters (Fig. S26a5–7, b5–7). This variation was shaped by genetics and the environment (Willmore et al. 2007), e.g. environmental gradients (Ji et al. 2024), host plants (Rebar and Rodríguez 2014; Gadelha et al. 2017), geographic distribution (Jamie et al. 2023). For treehoppers, different geographical distributions and ecological niches likely represent a primary driver of intraspecific morphological variation.

In summary, this study substantially improves the understanding of *Tricentrus* treehoppers from China and increases the known diversity by three new species. And sexual dimorphism in the presence of suprahumeral horns was reported in three species for the first time. Attached to the above study was a legend and discussion of the results using the synthesized methodology. We have no doubt that further investigations will reveal additional diversity in this genus and sexual dimorphism in suprahumeral horns, particularly in Xizang and Yunnan of China, where a combination of climatic and topographical heterogeneity appears to have resulted in extensive diversification in these animals (Fan et al. 2024).

5. Declarations

Conflict of interest. The authors declare that they have no conflicts of interest in relation to this work.

Data availability. Sequence data used in this study are all available via GenBank. New DNA sequences obtained during this study have been deposited in NCBI GenBank under the accession numbers: PV826162–PV826205. All examined specimens were deposited in the Institute of Entomology, Guizhou University.

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Supplementary Material 1

Figures S1–S28

Authors: Li F-E, Yang L, Long J-K, Chang Z-M, Chen X-S (2026)

Data type: .docx

Explanation notes: **Figure S1.** Phylogenetic trees were inferred using ML analysis based on the nucleotide sequences of the 13 PCGs. — **Figure S2.** Phylogenetic trees were inferred using ML analysis based on the nucleotide sequences of the AA. — **Figure S3.** Phylogenetic trees were inferred using MrBayes analysis based on the nucleotide sequences of the AA. — **Figure S4.** The temporal divergences of the genus *Tricentrus*. — **Figure S5.** the results of the ASR for sexual dimorphism with suprahumeral horns morphology. — **Figure S6.** The results of the ASR for apical pygofer morphology. — **Figures S7–9.** *Tricentrus allochrous* Li & Chen **sp. nov.** habitus, male and female genitalia. — **Figures S10–12.** *T. dextingensis* Li & Chen **sp. nov.** habitus, male and female genitalia. — **Figures S13–15.** *T. pianmaensis* Li & Chen **sp. nov.** habitus, male and female genitalia. — **Figures S16–18.** *T. colligatoclypei* Yuan & Cui, 1988 habitus, male and female genitalia. — **Figures S19–21.** *T. floripinnae* Yuan & Cui, 1987 habitus, male and female genitalia. — **Figures S22–25.** *T. obesus* Funkhouser, 1942 habitus, male and female genitalia. — **Figures S26–28.** *T. walkeri* Metcalf & Wade, 1965 habitus, male and female genitalia.

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Supplementary Material 2

Tables S1–S3

Authors: Li F-E, Yang L, Long J-K, Chang Z-M, Chen X-S (2026)

Data type: .docx

Explanation notes: **Table S1.** Information on the 53 specimens included in this study. Abbreviated: F, Female; M, Male. — **Table S2.** Best partitioning schemes and models based on different datasets for phylogenetic analysis, Abbreviated: AA, amino acid sequences; PCG, protein-coding genes sequences. — **Table S3.** The character states of the two characters used for the ancestral state reconstructions in the genus *Tricentrus*. Abbreviated: F, Female; M, Male; GD, Guangdong; GZ, Guizhou; GX, Guangxi; XZ, Xizang.

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Link: <https://doi.org/10.3897/asp.84.e164719.suppl2>

Supplementary Material 3

File S1

Authors: Li F-E, Yang L, Long J-K, Chang Z-M, Chen X-S (2026)

Data type: .zip

Explanation notes: **COX1S.** The COI gene alignment sequences from the 53 insect samples included in this study [.fas file]. — **RS.** ABGD and ASAP species delimitation Results [.txt file].

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