

**First Molecular Phylogeny Estimate of the Tribe Mecopini (Curculionidae: Conoderinae)
Unveils its Polyphyletic Nature at the Tribal and Generic Level**

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Mecopini has received limited attention since the last century, highlighting an important knowledge gap in its systematics and taxonomy. The morphological characteristics of several genera within this tribe contradict the widely accepted tribal diagnosis, suggesting that the current classification is unsustainable. In this study, we examined mecopine specimens from Taiwan and the Philippines,

reconstructed the first molecular phylogeny estimate for this obscure tribe, and examined type series of all described *Pempheres* Pascoe and *Chirozetes* (*Chirozetes*) *arotes* Heller and *C. (Mesochirozetes) formosanus* Heller, representing two subgenera within the genus *Chirozetes* Pascoe, to propose taxonomic acts on these genera. Our results reveal the polyphyletic relationships within Mecopini at both tribal and generic levels. Based on the phylogenetic framework and morphological characters, we propose excluding *Agametis* Pascoe from this tribe and elevating the subgenus *Mesochirozetes* Heller to full generic status. We also designate the lectotypes of *Mesochirozetes formosanus* Heller and two *Pempheres* species. Our study highlights the uncertainties of current classification of Mecopini, raising questions not only about the tribal composition but also the monophyly of genera within this tribe. Further studies are necessary to address these systematics issues, which may prompt a reevaluation and redefinition of this little-known tribe.

Key words: *Agametis*, *Chirozetes*, *Mesochirozetes*, New synonym, New placement

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BACKGROUND

The tribe Mecopini Lacordaire, 1866 (Curculionidae: Conoderinae) comprises 22 genera and 139 described species exclusively inhabiting tropical and subtropical areas across the Oriental, Palearctic, and Ethiopian regions (Marshall 1941; Alonso-Zarazaga and Lyal 1999; Alonso-Zarazaga et al. 2024). Among these, *Agametis* Pascoe, *Chirozetes* Pascoe, *Mecopus* Schönherr, and *Phylaitis* Pascoe exhibit a disproportionately high species diversity, harboring 92 of the described mecopine species. In contrast, eight genera and one subgenus are monotypic, most of which are known only from the original description without further records, indicating a lack of

comprehensive taxonomic work on Mecopini. In terms of morphological characteristics, mecopine species, similar to other conoderines, are characterized by large eyes nearly occupying the entire heads (Kojima and Lyal 2002). They exhibit a preference for fallen timber in open environments and are usually active under the direct sunlight (Pascoe 1871; Lyal 1986). It is noteworthy that some mecopine species display distinct fly-mimic behaviors similar to those conoderine weevils observed in the Americas (Lyal 1986; Anzaldo et al. 2020). Despite their unique habitat preferences and behavior, these weevils have received limited attention by entomologists for a long time, leaving aspects of their biology, behavior, and systematics largely unexplored.

Lacordaire (1866) established the tribe Zygotides and delineated it into two distinct geographical sections: Section I, exclusive to tropical America, and Section II, spanning Africa, the East Indies, and Polynesia. He further proposed the Mecopides as a subgroup within Section II, encompassing the genera *Mecopus* and *Macrobamon* Lacordaire (= *Odoacis* Pascoe). Pascoe (1870) subsequently elevated Zygotides to subfamilial status and incorporated *Mecopus*, *Chirozetes*, *Agamētis* and *Macrobamon* into the Mecopides (Pascoe 1870). Over the ensuing six decades, Mecopini received considerable attention, with the establishment of 16 out of the 22 described genera and description of a majority of named species (Pascoe 1871; Heller 1894, 1898, 1915, 1922, 1924, 1929, 1931; Hustache 1920, 1921, 1931). The tribal placement of these taxa remained unspecified until Hustache (1934) provided the first catalog, listing twenty-three genera in this tribe and thereby bringing clarity to the generic composition of Mecopini. However, since Hustache's work, Mecopini has received limited attention up to the present. Marshall (1939) treated *Heurippa* Pascoe as a junior synonym of *Synophthalmus* Lacordaire (= *Phytophilus* Schönherr), automatically reassigning it to the tribe Coryssomerini. Two years later, Marshall (1941) recognized *Pempherulus* Marshall from *Pempheres* Pascoe. The generic composition of Mecopini remained unchanged for several decades until Wibmer and O'Brien (1986) transferred *Hedycera* Pascoe to the tribe Lechriopini. The most recent generic catalogue, proposed by Alonso-Zarazaga and Lyal (1999), generally adhered to Hustache's treatment.

The diagnostic characteristics of Mecopini remain controversial. Traditionally, the funicle with

six antennomeres serve as the tribal diagnosis (Morimoto 1962; Anzaldo 2017; Legalov 2018). However, the exceptional cases occur in several genera. For instance, it has been reported that *Emexaure* Pascoe and *Mecopoidellus* Hustache exhibit seven funicular antennomeres (Pascoe 1871; Hustache 1931). This discordance raises doubts about the validity of the current classification of Mecopini. As mentioned above, this group has been understudied for a long time. Its unreliable tribal diagnosis suggests the uncertainty about its monophyly, which is a significant knowledge gap in the systematics of Conoderinae. Therefore, in this study, we revisited the morphological characters and applied four molecular markers to reconstruct the first phylogeny estimate of Mecopini, utilizing specimens from Taiwan and the Philippines. Our objectives are twofold: 1) to evaluate the validity of the current generic composition of Mecopini and propose a revised diagnosis of this tribe, and 2) to reassess the taxonomic status of mecopine genera from Taiwan and the Philippines.

MATERIALS AND METHODS

Morphological examination

The specimens examined in this study were deposited in the following institutions:

NHMUK: British Museum of Natural History, London, UK. MSNG: Museo Civico di Storia Naturale di Genova "Giacomo Doria", Genova, Italy. NMNS: Natural Museum of Natural Sciences, Taichung, Taiwan. SDEI: Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany. SNSD: Senckenberg Naturhistorische Sammlungen Dresden, Germany.

We obtained 20 dry specimens from Taiwan and the Philippines to infer the phylogenetic relationship within Mecopini, representing nine species of seven genera and one subgenus. We also included four conoderine species as outgroups, with an unidentified Bariditae species serving as the most distant outgroup. Closer outgroups included an unidentified Conoderitae species and two

species of Coryssomerini (*Metialma* sp. and *Phytophilus amoena* (Pascoe, 1871)). The examined specimens were acquired from, or subsequently deposited in, the NMNS. Specimens were identified to the generic level based on the keys of Pascoe (1871) and Heller (1894, 1931) and to the species level based on the original descriptions and illustrations. The identifications of five species were further compared to the type specimens, including *Talanthia phalangium* Pascoe and *Mecopus hopei* Rosenschöld referred to the figures of Grebennikov and Zyskowski (2018) and Tseng and Cheng (2023), as well as *Chirozetes arotes* Heller, *C. (Mesochirozetes) formosanus* Heller and *Pempheres habena* Pascoe from the photos of type specimens deposited in SNSD and NHMUK. To conduct a detailed morphological comparison between *Pempheres* and *Mesochirozetes*, we examined 19 additional specimens and acquired photos of type series from all described species of both taxa. These included *P. habena*, *P. trilineata* Pascoe, *P. picta* Heller and *C. (Mesochirozetes) formosanus*, deposited at NMNS, MSNG, SDEI, and SNSD.

Label data of type specimens are cited verbatim, with a double slash (//) denoting data from different labels, a single one (/) those on different lines on a label and square brackets ([]) describing the color and status of the label. Examinations and dissections of the specimens were conducted using a Nikon SMZ 800N stereomicroscope. Muscles from meso- and metathorax were removed during dissection and preserved in 95% EtOH at -20°C until DNA extraction. Photographs were captured using the same stereomicroscope with the SGviews software (Sage Vision CO., LTD, Taiwan), and a Nikon D610 equipped with a Nikon AF-S FX Micro 105mm F2.8 G IF-ED VR lens. Image stacking was achieved using Helicon focus 7.5.1 (Helicon Soft Ltd., Ukraine).

DNA extraction and sequencing, and bioinformatics

Genomic DNA was extracted from thoracic muscles using the QIAamp DNA Micro kit (Qiagen, Hilden, Germany). Our study employed four molecular markers: mitochondrial cytochrome *c* oxidase subunit I (*COI*), as well as three nuclear loci - *28S rRNA*, Arginine Kinase (*ArgK*) and Elongation factor 1- α (*EF1 α*). Polymerase chain reactions (PCR) were conducted for all

four markers within a total reaction volume of 25.5 μL , comprising 3 μL of template DNA, 9 μL H_2O , 0.5 μL of each 10 μM primer and 12.5 μL EmeraldAmp[®] MAX HS PCR Master Mix. Detailed primer information and PCR conditions are provided in table S1. PCR products were visualized by 1% agarose gel electrophoresis. Sequencing was performed using an ABI PRISM 3730 Genetic Analyser, facilitated by the National Yang Ming Chiao Tung University Cancer Progression Research Center (Taipei, Taiwan). Sequences were checked and edited by Geneious 11.0.5. (Kearse et al. 2012). The protein-coding genes were translated into amino acid to confirm any potential stop codons. We accessed sequences from GenBank for two mecopine species (*Talanthia* sp. and *Mecopus bispinosus* (Weber, 1801), with accession numbers provided in Table S2). Sequences alignments for each locus were conducted using MAFFT v.7. (Rozewicki et al. 2019), and subsequently concatenated using Mesquite v.3.6. (Maddison and Maddison 2022).

Phylogenetic analyses

Phylogenetic reconstruction employed both maximum likelihood (ML) and Bayesian inferences (BI) algorithms. ML analysis was conducted using RAxML v. 8.2.10. (Stamatakis 2014), utilizing the default GTR + G substitution model with sequences partitioned by locus. Node support values were obtained through rapid bootstrap analysis with 1000 iterations. Rapid bootstrap values greater than 75 but less than 90 were considered moderately supported, while those exceeding 90 were regarded as robustly supported. For BI analysis, the best substitution model for each locus was estimated using jModelTest2 (Darriba et al. 2012), which suggested GTR + I + G for *COI*, TVM + I + G for *28S rRNA*, TIM2ef + G for *ArgK*, and TIM1 + I + G for *EF1 α* . The BI analysis was performed using MrBayes v.3.1.2 (Ronquist et al. 2012) within the CIPRES science gateway (Miller et al. 2010), involving 10 million generations, a sampling frequency of 1,000 generations and a 25% burn-in. We considered posterior probabilities greater than 0.75 but less than 0.95 as moderately supported, and probabilities exceeding 0.95 as robustly supported. The topologies from ML and BI analyses were visualized using Interactive Tree Of Life (iTOL) v5 (Letunic and Bork

RESULTS

Morphological examination

Nine mecopine species were recognized for phylogenetic reconstruction, including *Agametis festiva* Pascoe, 1870, *Chirozetes (Chirozetes) arotos* Heller, 1915, *C. (Mesochirozetes) formosanus* Heller, 1931, *Pempheres habena* Pascoe, 1871, *Talanthia phalangium* Pascoe, 1871, *Mecopus bispinosus* (Weber, 1801) and *M. hopei* Rosenschöld, 1838. Two specimens remain unidentified at the species level. One specimen is tentatively designated as *Phylaitis* cf. *v-album* Pascoe, 1871, based on its similarity of dorsal habitus, despite its geographical distance from the type locality. The other is an undescribed *Pempherulus* species. The sampling includes five speciose genera of Mecopini: *Agametis* (14 species), *Chirozetes* (2 subgenera and 20 species), *Mecopus* (48 species), *Phylaitis* (10 species), and *Pempherulus* (8 described species), as well as two genera with relatively fewer species: *Pempheres* (3 species) and *Talanthia* (4 species). Notably, *A. festiva*, *T. phalangium*, and *M. bispinosus* are the type species for their respective genera, and *C. (M.) formosanus* is the type species of the subgenus *Mesochirozetes* Heller, 1931. Detailed images of the dorsal habitus of voucher specimens have been deposited in Zenodo (<https://zenodo.org/doi/10.5281/zenodo.8156265>), and specimen details are provided in table S2.

Morphological comparisons between the genus *Pempheres* and the subgenus *Mesochirozetes* reveal similarities between these two taxa. Males of three out of four described species, with the exception of *P. picta* (known only from a single female specimen), do not exhibit prosternal spines and hairs on the ventral side of protarsi, which are common in other mecopine genera. Sexual dimorphism is evident in the abdomens of *Pempheres* and *Mesochirozetes*. Males of *P. trilineata* and *P. habena* exhibit a pair of tubercles in the middle of ventrite I, which are somewhat denticulate

and project inward on the posterior margin, forming a canaliculate structure. *C. (M.) formosanus* exhibits similar canaliculate structures, but differs in the morphology of tubercles that are not denticulate and have distinct hairs on the inner margin. Additionally, the canaliculate structures of *Mesochirozetes* can also be found on ventrite V. Detailed comparisons can be found in the following taxonomic section and discussion.

Phylogenetic analyses

(Fig. 1)

The final concatenated matrix includes 24 individuals, comprising a total of 3658 bp. The specific number and length of all loci are as follows: 19 individuals for *COI* (ranging from 569 to 1219 bp), 21 for 28S *rRNA* (ranging from 451 to 677 bp), 17 for *ArgK* (ranging from 534 to 788 bp), and 18 for *EF1 α* (ranging from 608 to 640 bp). No indels or stop codons were detected in the protein-coding loci (*COI*, *ArgK* and *EF1 α*). All sequences have been deposited in GenBank, and the accession numbers are provided in table S2.

The ML and BI analyses consistently produce nearly identical topologies, with the only difference occurring in the relationship between *Bariditae* sp. and *Agametis festiva* (the BI topology is provided in Fig. S1). In both topologies, a polyphyletic Mecopini was recovered, with *Agametis* locating at a relatively early diverging position distantly separated from other mecopine genera. Conversely, seven other genera/subgenus collectively form a robustly supported clade, with bootstrap value at 100 and posterior probability at 1. Within this clade, *Chirozetes arotes* is the first derived lineage, followed by a monophyletic group comprising *C. (M.) formosanus* and *Pempheres habena*. The remaining four genera constitute a moderately supported clade, with *Phylaitis* forming a sister group of *Talanthia*, and *Pempherulus* aligning as a sister to *Mecopus*. It is important to highlight that two *Chirozetes* subgenera display a polyphyletic relationship. The nominal subgenus represents an independent lineage, and *Mesochirozetes* is positioned as a sister to *Pempheres*.

TAXONOMY

Tribe Mecopini Lacordaire, 1866

Diagnosis: Funicle with six antennomeres. We re-identify the absence of a prosternal canal as a diagnostic characteristic, as a consequence of excluding the genus *Agametis* from this tribe (see DISCUSSION).

Genus *Pempheres* Pascoe, 1871

Type species: *Pempheres trilineata* Pascoe, 1871 (by present designation).

Diagnosis (modified after Pascoe (1871) and Heller (1894)): Funicle with antennomere 2 twice longer than 1; male without prosternal spines (Fig. 3C, D) and hairs on the ventral of protarsi; abdominal ventrite I with medial canaliculate structures (Fig. 4C, D). We regard two diagnostic characters—the sinuated protibia and the proximity of antennal scape to rostral base—as invalid for distinguishing this genus from other mecopine genera (see details in the discussion).

Remarks: The type species of this genus was not designated in the original description and remained so until now (Pascoe 1871; Alonso-Zarazaga and Lyal 1999). Among the two species described in the original description of *Pempheres*, we designate *P. trilineata* as the type species. The decision is based on the type series of *P. trilineata* containing both male and female specimens, in contrast to the type series of *P. habena* containing only females, which provide less morphological information.

The presence of canaliculate structures on the abdomen of males suggests that *Mecopus serrirostris* Pascoe, 1871 and *M. ceylanensis* Heller, 1893 probably belong to this genus (Heller 1894).

Pempheres trilineata Pascoe, 1871

(Figs. 2A; 3A, B)

Diagnosis: Pronotum with lateral stripe straight, space between longitudinal stripes without spotted scales; elytra with distinct longitudinal lateral stripe, with lateral stripe continuous, medial stripe uniform in width along entire length; scales whitish.

Types: Lectotype: 1 ♀, Type [red circular label, print] // Batchian [blue oval label, hand writing] // Pempheris / trilineata / Pasc [white rectangular label, hand writing] // Pascoe Coll. / 93–60 [white rectangular label, print] // NHMUK015009734 (NHMUK). Paralectotypes: 1 ♂, Morty [blue oval label, hand writing] // Pascoe Coll. / 93–60 [white rectangular label, print] // NHMUK015014006 (NHMUK); 1 ♂, Amboyna [blue oval label, hand writing] // *Pempheris / trilineata* Pasc [white rectangular label, hand writing] // Pascoe Coll. / 93–60 [white rectangular label, print] // NHMUK015014005 (NHMUK).

Distribution: Maluku Islands, Indonesia (Pascoe 1871).

Remark: Pascoe (1871) did not explicitly designate a primary type in the original description, resulting in all specimens used for the description being considered syntypes with equal nomenclatural status. The exact number of specimens used for the species description was not specified, but he mentioned that the specimens were collected from three localities: “*Hab.* Batchian, Morty, Amboyna.” There are three such specimens in his collection at NHMUK, recognized as the syntypes. To establish a definitive, name-bearing type for *P. trilineata*, we designate the female syntype from Batchian (labeled “type”), which closely matches Pascoe’s description, as the lectotype of *P. trilineata*. The other two male specimens from the type series are designated as paralectotypes.

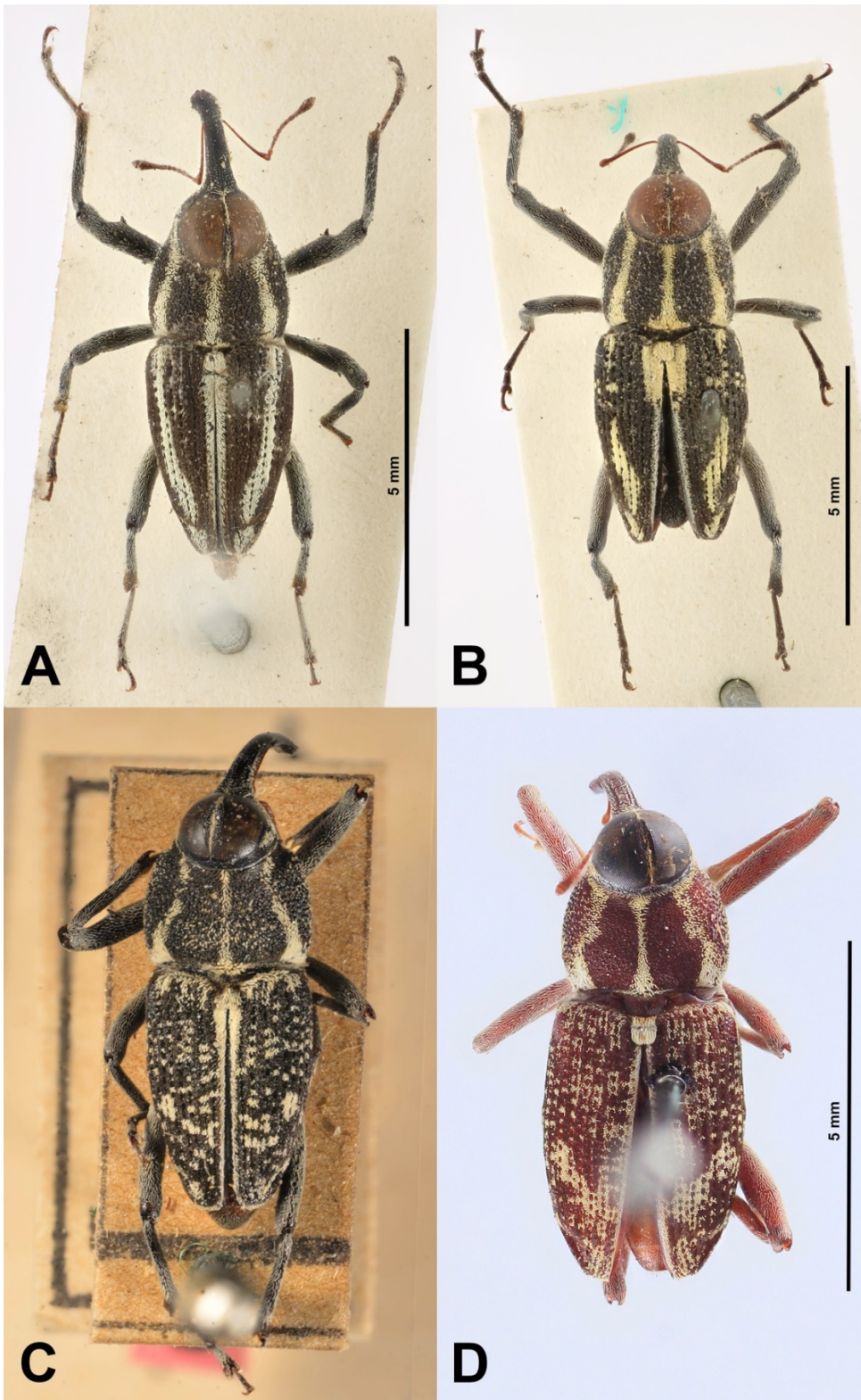


Fig. 2. Type specimens of *Pempheres* and *Mesochirozetes* in dorsal view. A: lectotype of *Pempheres trilineata* Pascoe, 1871; B: lectotype of *Pempheres habena* Pascoe, 1871; C: holotype of *Pempheres picta* Heller, 1894; D: lectotype of *Chirozetes* (*Mesochirozetes*) *formosanus* Heller, 1931. Photo credits: A–B, Keita Matsumoto (NHMUK); C, Roberto Poggi (MSNG).

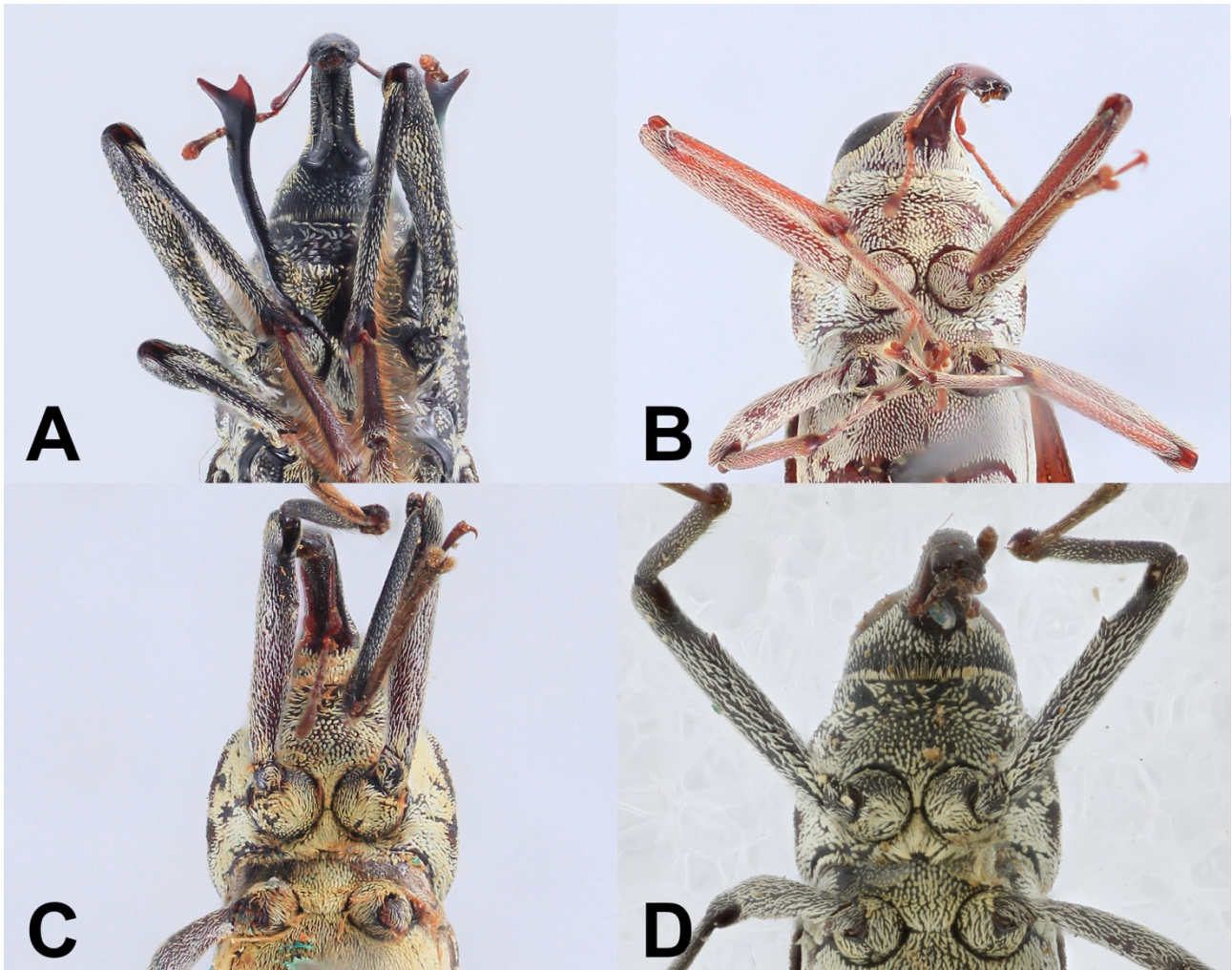


Fig. 3. Comparison of male prosternum of *Chirozetes*, *Mesochirozetes* and *Pempheris* spp. Males of *Chirozetes* exhibit distinct prosternal spines, where *Mesochirozetes* and *Pempheris* do not. A: *Chirozetes arotus* Heller, 1915; B: *Mesochirozetes formosanus* (Heller, 1931); C: *Pempheris habena* Pascoe, 1871; D: *Pempheris trilineata* Pascoe, 1871. Photo credits: D, Keita Matsumoto (NHMUK).

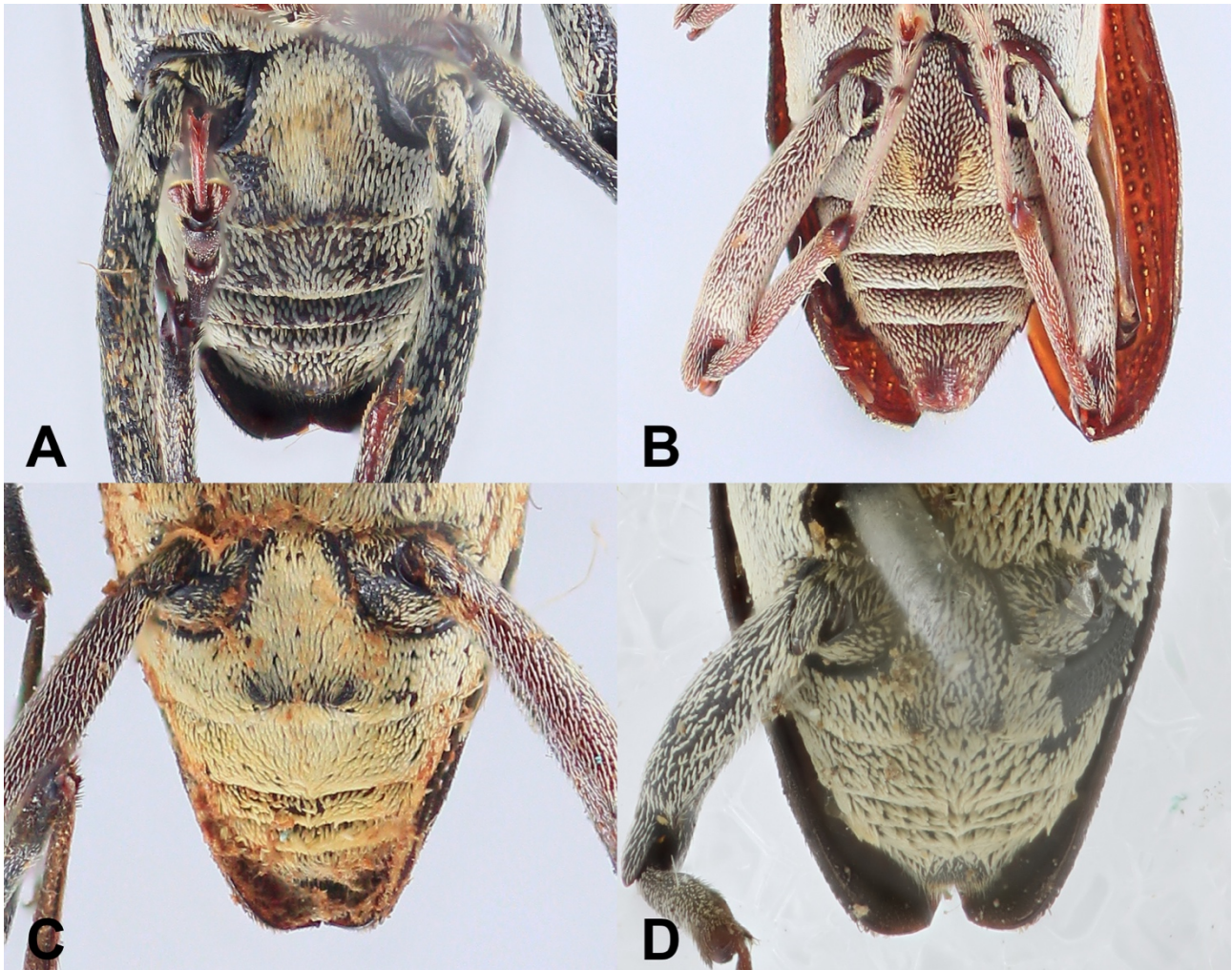


Fig. 4. Comparison of male abdomens of *Chirozetes*, *Mesochirozetes* and *Pempheres* spp. Males of *Mesochirozetes* and *Pempheres* exhibit distinct canaliculate structures, where *Pempheres* occurs on ventrite I, while *Mesochirozetes* on ventrite I and V. A: *Chirozetes arotos* Heller, 1915; B: *Mesochirozetes formosanus* (Heller, 1931); C: *Pempheres habena* Pascoe, 1871; D: *Pempheres trilineata* Pascoe, 1871. Photo credits: D, Keita Matsumoto (NHMUK).

***Pempheres habena* Pascoe, 1871**

***Mecopus abdominalis* Kirsch, 1875 (synonymized by Heller 1894: 12)**

(Figs. 2B; 3C, D)

Diagnosis: Pronotum with lateral stripe straight, space between longitudinal stripes without spotted scales; elytra with distinct longitudinal lateral stripe, with lateral stripe interrupted on basal half, medial stripe widest anteriorly, narrowed posteriorly; scales yellowish.

Types: Lectotype: 1 ♀, Type [red circular label, print] // Singapore [blue oval label, hand

writing] // Pempheris / habena / Pasc [white rectangular label, hand writing] // Pascoe Coll. / 93–60 [white rectangular label, print] // NHMUK015009754 (NHMUK). Paralectotype: 1 ♀, Sumatra [blue oval label, hand writing] // *Pempheris / habena* Pasc [white rectangular label, hand writing] // Pascoe Coll. / 93–60 [white rectangular label, print] // NHMUK015009755 (NHMUK).

Other material: MALAYSIA: 1 ♂, Malacca [yellow rectangular label, hand writing] // Typus [pink rectangular label, print] // 1023 [yellow rectangular label, hand writing] // *Mecopus abdomina-* / *lis* Kirsch = *Pempheris / habena* Pascoe [white rectangular label, print] // Staatl. Museum für / Tierkunde, Dresden [white rectangular label, print] (SNSD); 1 ex., Perak / Malacca / (Doherty) [rectangular label, print] // 119. [rectangular label, hand writing] // *Pempheris / habena / Pascoe / det. Heller 1893-1912* [rectangular label, hand writing] // MUSEO GENOVA / coll. Angelo Solari / (acquisto 2000) [white rectangular label, print] (MSNG); 1 ♀, PERAK, F. M. S. / Batang Padang / Jor Camp 1500 ft. / May 29 1923 / H.M. Pendlebury leg. [rectangular label, print and hand write] // *Pempheris / habena* Pasc. / det. G.A.K. Marshall [rectangular label, print and hand write] // Ex F.M.S. / Museum / B.M. 1955-354. [rectangular label, print] // NHMUK015014004 (NHMUK); 1 ♂, MALAY PENINS / Endong Roose / Pelialing gajal / 20.6.1928 [rectangular label, print and hand write] // PEMPHERES / HABENA, Pasc. [rectangular label, hand write] // 589 [rectangular label, hand write] // Ex F.M.S. / Museum / B.M. 1955-354. [rectangular label, print] // NHMUK015014003 (NHMUK). PHILIPPINES: 1 ♂, Kasibu, Nueva Viscaya, North Luzon, V.2020, local collector leg. // WZPCC_03596 (NMNS); 1 ♀, Roxas, Palawan, II.2021, local collector leg. // WZPCC_03597 (NMNS).

Distribution: Singapore; Sumatra Island, Indonesia; Peninsular Malaysia; Philippines (Pascoe 1871; Heller 1894; Schultze 1916).

Remark: Pascoe (1871) did not explicitly designate a primary type in the original description, resulting in all specimens used for the description being syntypes with equal nomenclatural status. The exact number of specimens used for the species description was also not specified, but he mentioned that the specimens were collected from two localities: “*Hab.* Singapore, Sumatra.” There are two such specimens in his collection at NHMUK, recognized as the syntypes. To establish a

definitive, name-bearing type for *P. habena*, we designate the female syntype from Singapore (labeled “type”), which closely matches the original description, as the lectotype of *P. habena*. The other female specimen from the type series is designated as a paralectotype.

***Pempheres picta* Heller, 1894**

(Fig. 2C)

Diagnosis: Pronotum with lateral stripe sinuate, space between longitudinal stripes with spotted scales; elytra without or only with indistinct longitudinal lateral stripe, apical half densely covered with spotted, patchy scales; metepisternum covered with a patch of black scales.

Types: Holotype: 1 ♀, Tenasserim / Thagatà / Fea. Apr. 1887 [rectangular label, print] // Typus [red rectangular label, hand writing] // *Pempheres (?) pictus* Heller / Determ: K.M. Heller. ♀ [rectangular label, print and hand writing] // *picta* / Heller [rectangular label, hand writing] // *Pempheres / picta*, Heller / typus! [yellow rectangular label, hand writing] // Museo Civico / di Genova [white rectangular label, print] (MSNG).

Other material: LAOS: 1ex., Laos / Kiong Kouang / Vitalis 1919 [rectangular label, hand writing] // *picta* / Hllr. / det. Solari, 920 [rectangular label, hand writing] // MUSEO GENOVA / coll. Angelo Solari / (acquisto 2000) [white rectangular label, print] (MSNG).

Distribution: Tenasserim, Myanmar (Heller 1894); Laos (new distribution record).

Remarks: Heller (1894) did not designate a primary type in the original description. However, the species description appears to be based on a single specimen, for which he provided only one measurement and explicitly stated the label details as “Patria: Tenasserim, Thagala, legit Fea, April 1887, Mus. Civico Genua”. There is indeed only one such specimen in his collection at MSNG, which is labeled as “Typus” and recognized as the holotype in this study.

Heller (1894) mentioned the uncertainty regarding the generic placement of this species, as

indicated by a question mark in the original description and on the holotype label. Our examinations reveal the morphological similarities between *P. picta* and *Mesochirozetes formosanus*, such as sinuated lateral stripes on the pronotum and spotted scale patches on the elytra, suggesting a close relationship between these species. Additional specimens and further morphological and molecular examinations are necessary for verifying the taxonomic status of this species.

Genus *Mesochirozetes* Heller, 1931 stat. nov.

Type species: Chirozetes (Mesochirozetes) formosanus Heller, 1931 (by monotypy)

Diagnosis (modified after Heller (1931)): Funicle with antennomere 2 as long as, or slightly longer than 1; male without prosternal spines (Fig. 3B) and hairs on the ventral of protarsi; abdominal ventrite I and V with medial canaliculate structures (Fig. 4B).

***Mesochirozetes formosanus* (Heller, 1931) comb. nov.**

***Chirozetes (Mesochirozetes) formosanus* Heller, 1931**

(Figs. 2D; 3E, F)

Diagnosis: Pronotum with lateral stripe sinuate, space between longitudinal stripes with spotted scales; elytra without or only with indistinct longitudinal stripe, apical half densely covered with spotted, patchy scales; integument reddish brown; metepisternum covered with white scales.

Types: Lectotype: TAIWAN: 1 ♂, Formosa / Kosempo / H. Sauter'09 [yellow rectangular label, print and hand writing] // 1909 / 22 [white rectangular label, print and hand writing] // Typus! [red rectangular label, print] // ♂ [white rectangular label, hand writing] // Staatl. Museum für / Tierkunde, Dresden [white rectangular label, print] (SNSD). Paralectotypes: 1 ♂, Formosa / Kosempo / H. Sauter'09 [yellow rectangular label, print and hand writing] // 1909 / 22 [white rectangular label, print and hand writing] // Paratypus / *formosanus* Hell. [red rectangular label, print and hand writing] // ♂ [white rectangular label, hand writing] // Staatl. Museum für /

Tierkunde, Dresden [white rectangular label, print] (SNSD); 1 ♂, 1909 / 22 [white rectangular label, print and hand writing] // Formosa / Kosempo / H. Sauter'09 [yellow rectangular label, print and hand writing] // ♂ Paratypus / *formosanus* Hell. [red rectangular label, print and hand writing] // Staatl. Museum für / Tierkunde, Dresden [white rectangular label, print] (SNSD); 1 ♀, 1909 / 22 [white rectangular label, print and hand writing] // Formosa / Kosempo / H. Sauter'09 [yellow rectangular label, print and hand writing] // ♀ Typus / *formosanus* Hell. [red rectangular label, print and hand writing] // ♀ [white rectangular label, hand writing] // Staatl. Museum für / Tierkunde, Dresden [white rectangular label, print] (SNSD); 1 ♂, Formosa / Kosempo / H. Sauter'09 [yellow rectangular label, print and hand writing] // 1909 / 22 [white rectangular label, print and hand writing] // Syntypus [red rectangular label, print] // Cotypus / *P. formosana* / Heller [red rectangular label, print and hand writing] // *Pempheres* / *formosana* m / Det. K.M. Heller 1913 [rectangular label, print and hand writing] // SDEI Coleoptera / # 304541 (SDEI); 1 ♂, XI Formosa / Kosempo / H. Sauter 1944 08 [white rectangular label, print and hand writing] // g.n. / *Mesochirozetes* [white rectangular label, hand writing] // (*Pempheres*) *Mesochirozetes* / *formosana* n.sp. / Det. K.M. Heller 1920 [white rectangular label, print and hand writing] // SDEI Coleoptera / # 304543 (SDEI); 1 ex., Formosa / Kosempo / Sauter_VIII_.07-09 [white rectangular label, print and hand writing] // SDEI Coleoptera / # 304544 (SDEI); 1 ex., XI Formosa / Kosempo / H. Sauter 1944 08 [white rectangular label, print and hand writing] // SDEI Coleoptera / # 304546 (SDEI); 1 ♀, Kosempo (Formosa) / H. Sauter VI 19429 [white rectangular label, print and hand writing] // SDEI Coleoptera / # 304547 (SDEI).

Other materials: TAIWAN: 1 ♂, Formosa / Hoozan / H. Sauter 1910 [yellow rectangular label, print] // *Pempheres* / *formosana* m. / Det. K.M. Heller 1912 [rectangular label, print and hand writing] // MUSEO GENOVA / coll. Angelo Solari (acquisto 2000) [white rectangular label, print] (MSNG); 1 ♂, ♂ [white rectangular label, hand writing] // Kankau (Koshun) / Formosa / H. Sauter VI.1912 [white rectangular label, print] // SDEI Coleoptera / # 304542 (SDEI); 1 ex., Formosa / Hoozan 08-10 / Sauter [white rectangular label, print] // SDEI Coleoptera / # 304545 (SDEI); 1 ♀, Lienhuachih, Yuchi Township, Nantou County, 9.IV.–19.V.1998, collected by Malaise trap, C.-S.

Lin & W.-T. Yang leg. // NMNS ENT 3161-437 (NMNS); 1 ♂ 1 ♀, Chunyang, Ran'ai Township, Nantou County, 7.V.–11.VI.2002, collected by Malaise trap, C.-S. Lin & W.-T. Yang leg. // NMNS ENT 5237-3693; NMNS ENT 5237-3946 (NMNS); 1 ♂ 1 ♀, Lienhuachih, Yuchi Township, Nantou County, 9.IX.–4.X.2004, collected by Malaise trap, C.-S. Lin & W.-T. Yang leg. // NMNS ENT 6541-161; NMNS ENT 6755-23 (NMNS); 1 ♀, Kenting Forest Recreation Area, Hengchun Township, Pingtung County, 13.IV.–8.VI.2005, collected by Malaise trap, C.-S. Lin & W.-T. Yang leg. // NMNS ENT 5737-1905 (NMNS); 1 ♀, Lienhuachih, Yuchi Township, Nantou County, 3.X.–10.XI.2005, collected by Malaise trap, C.-S. Lin & W.-T. Yang leg. // NMNS ENT 6776-242 (NMNS); 1 ♀, Chunyang, Ran'ai Township, Nantou County, 10.IV.–8.V.2007, collected by Malaise trap, C.-S. Lin & W.-T. Yang leg. // NMNS ENT 7530-1014 (NMNS); 1 ♂, Huisun Forest Area (Sheshui Trail), N24.088830 E121.030011, Ran'ai Township, Nantou County, 29.IV.–16.V.2018, collected by Malaise trap, W.-R. Liang leg. // WZPCC_01310 (NMNS); 1 ♂, Kenting Forest Recreation Area, N21.96253 E120.81293, Hengchun Township, Pingtung County, 13.XI.2021, collected by hand, B.-H. Ho leg. // WZPCC_03629 (NMNS).

Distribution: Taiwan (Heller 1931).

Remark: Heller (1931) did not designate a primary type or specify the number of specimens being examined in the original description. However, it is apparent that his description was based on multiple specimens from a single locality “...— Kosempo.”. He also indicated that these specimens were deposited in SNSD and SDEI. There are four such specimens in the SNSD and five in the SDEI, indicating that all nine specimens are syntypes with equal nomenclatural status. To establish a definitive, name-bearing type for *C. (M.) formosanus*, we designate the male syntype labeled as "type!", which closely matches the original description, as the lectotype of *C. (M.) formosanus*. The other specimens from the type series are thus designated as paralectotypes.

DISCUSSION

The validity of any systematic classification is questionable if it is not robustly phylogenetically supported, as is the case with Mecopini. To address this concern, we reconstructed the first molecular phylogenetic framework of this tribe, utilizing specimens collected from Taiwan and the Philippines. Our results indicate that the sampled mecopine genera as well as the infrageneric classification of the genus *Chirozetes* exhibit a polyphyletic nature, with species failing to form monophyletic groups. These findings strongly advocate for the necessity of revising the existing systematic hypothesis of Mecopini.

***Agametis* is excluded from Mecopini**

Phylogenetic analyses reveal that *Agametis* is distant from other mecopine genera (Fig. 1), and we have identified several morphological characteristics that support this remote relationship. For instance, *Agametis* exhibits an arcuate rostrum and the tapered ventral eye margin, which are distinct from other mecopine genera but closely resemble Neotropical conoderines (Fig. 1). Additionally, the presence of an unmodified mesoventrite and prosternal canal is also akin to that of Neotropical Zygopini (Anzaldo 2017). Given the distant phylogenetic relationship and morphological distinction, we propose the exclusion of *Agametis* from Mecopini and treating this genus as *incertae sedis* under Conoderitae.

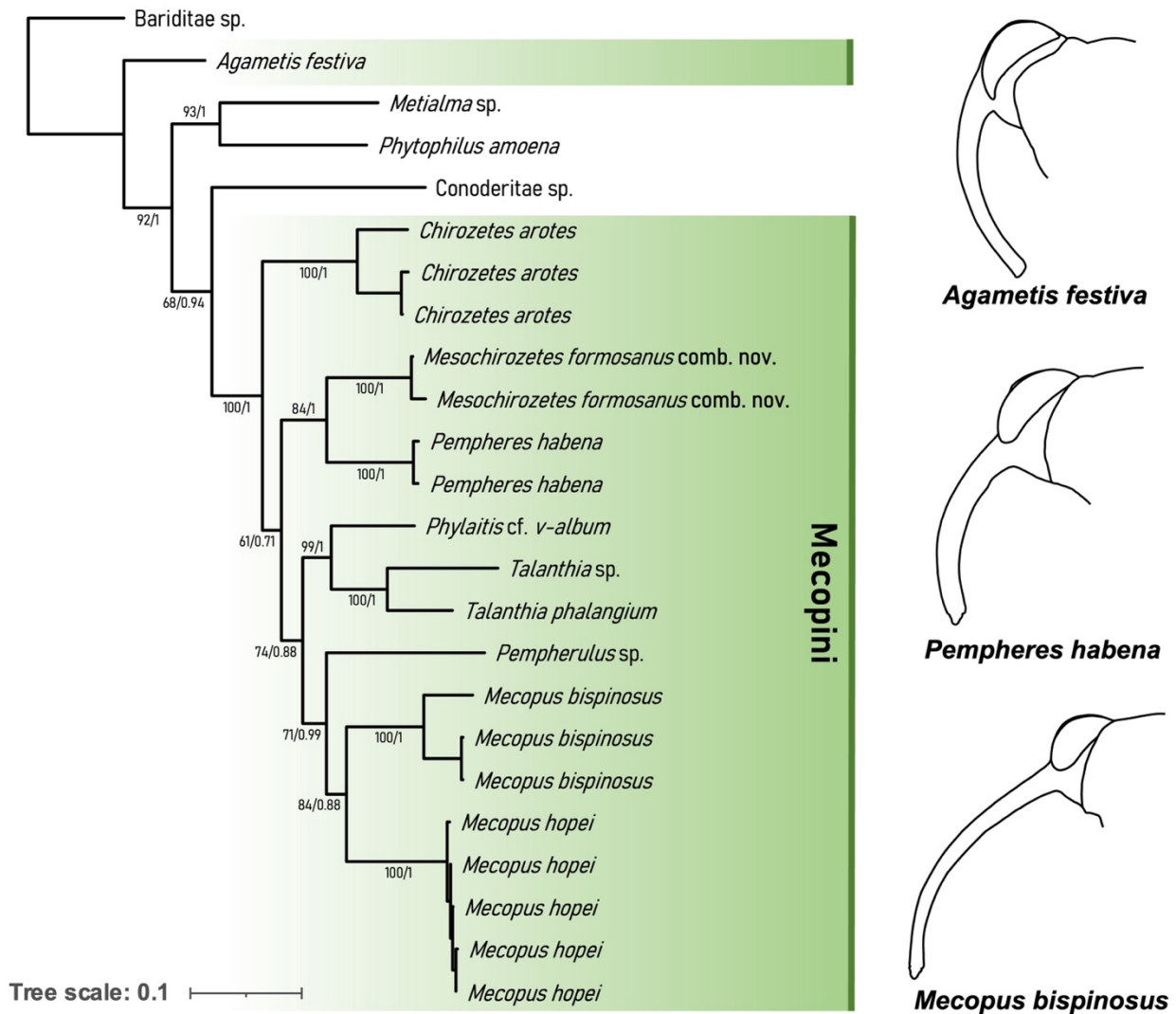


Fig. 1. Phylogenetic tree based on four molecular markers. The node support is presented with bootstrap values (left) and posterior probability (right) under each branch. Mecopine species are highlighted, and the head morphologies of three species are illustrated on the right.

The exclusion of *Agametis* highlights the demand for a comprehensive taxonomic revision of Mecopini. For instance, two genera, *Agametina* Heller, 1915 and *Ganyopsis* Pascoe, 1871, share characteristics like the arcuate rostrum and tapered ventral eye margin with *Agametis*, suggesting that they might not belong to Mecopini as well. Furthermore, the taxonomic status of genera possessing seven funicular antennomeres, in contrast to the widely accepted diagnosis of Mecopini (Heller 1894; Morimoto 1962; Anzaldo 2017; Legalov 2018), should also be reevaluated. A comprehensive taxonomic revision, coupled with robust phylogenetic analysis, is essential for reshaping the systematics of this understudied tribe.

***Mesochirozetes* is raised to full generic level**

Our phylogenetic analyses reveal a polyphyletic relationship between two subgenera of *Chirozetes* (the nominal subgenus and *Mesochirozetes*), and support a sister affinity between *Mesochirozetes* and *Pempheres* (Fig. 1). This result highlights the need for a proper taxonomic treatment of *Mesochirozetes* to ensure the monophyly of genus *Chirozetes*. *Mesochirozetes* is a monotypic subgenus of *Chirozetes* established based on its type species, *Chirozetes* (*Mesochirozetes*) *formosanus* Heller, collected in Kosempo, Southern Taiwan. In the original description of *Mesochirozetes*, Heller (1931) designed an identification key to distinguish this subgenus from the nominal subgenus *Chirozetes* and the genera *Daedania* and *Pempheres*. According to his classification, *Daedania* and *Pempheres* exhibit obtuse, wedge-shaped elytra [Flügeldecken stumpf keilförmig], whereas *Chirozetes* and *Mesochirozetes* have elytra that are somewhat cylindrical with obtusely-rounded apex [Flügeldeckenziemlich walzenförmig, hinten stumpf verrundet]. However, some *Chirozetes* species also exhibit a wedge-shaped elytra (e.g., *C. lineolatus* as shown in the figure 1 of Heller 1924), suggesting that elytral shape may not be suitable for distinguishing *Chirozetes* from *Daedania* and *Pempheres*.

Furthermore, the sexually dimorphic characteristics of *Mesochirozetes* are distinct from *Chirozetes* but similar to *Pempheres*. Specifically, males of *Mesochirozetes* and *Pempheres*, except for *P. picta* Heller (known from a single female specimen), do not exhibit prosternal spines (Fig. 3B–D) and hairs on the ventral side of protarsi, which are present in the males of *Chirozetes* species (Fig. 3A). The sexual dimorphism of both taxa present in the abdomen, where males of *Mesochirozetes* and *Pempheres* species have canaliculate structures in the middle of ventrites (Fig. 4B–D). Heller described this character in *Pempheres* (Heller 1894: 12) and *Mesochirozetes* (Heller 1931: 109), but never recognized it as a diagnostic characteristic for either taxon. However, despite the morphological similarity between *Mesochirozetes* and *Pempheres*, we still observed characteristics that differ between *Mesochirozetes* and *Pempheres* species. For example,

Mesochirozetes has two canaliculate structures in ventrites I and V (Fig. 4B), while *Pempheres* species have a single structure in ventrite I (Fig. 4C–D). The relative length of the first two antennomeres also differs, which *Pempheres* species exhibit antennomere 2 twice as long as 1, while antennomere 2 of *Mesochirozetes* is as long as, or slightly longer than 1. Based on the results of phylogenetic analyses and morphological examinations, we propose raising the subgenus *Mesochirozetes* to full generic level to maintain the monophyly of *Chirozetes*.

Additionally, we modified the diagnoses of *Pempheres* and *Mesochirozetes*, after Pascoe (1871) and Heller (1894, 1931). The sexually dimorphic characteristics are important diagnoses for both genera, including the males without prosternal spines and hairs on the ventral side of protarsi, and with canaliculate structures on ventrites. The number of canaliculate structures can further distinguish *Pempheres* and *Mesochirozetes*, where *Pempheres* has a single structure on ventrite I while *Mesochirozetes* has two on ventrites I and V. Antennal funicles are also crucial to distinguish both genera. *Pempheres* species have antennomere 2 twice as long as 1, while the antennomere 2 of *Mesochirozetes* is equal to, or slightly longer than 1. Several diagnostic characteristics of *Pempheres*, namely the sinuated protibia and proximity of antennal scape to rostral base, are not suitable for distinguishing this genus. We find that the protibia is straight in all described species (Fig. 2A–C) and the proximity between scape and rostral base is common in mecopine genera, such as *Mecopus*, *Mecopomorphus* Hustache, 1920 and *Neomecopus* Hustache, 1921. Therefore, we propose excluding these characters from the diagnosis of *Pempheres*.

CONCLUSIONS

The systematics of Mecopini, a mysterious group of weevils, has been overlooked for decades, lacking a phylogenetic framework. In this study, we provided a molecular phylogeny estimate of Mecopini based on multi-locus data for the first time. By integrating molecular and morphological evidences, we suggest excluding *Agametis* from Mecopini and synonymizing the subgenus *Mesochirozetes* with the genus *Pempheres*. Our study provide the first systematics hypothesis of

Mecopini and highlight the necessity of comprehensive phylogenetic and systematic investigations of this insufficiently studied tribe in the future.

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Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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Supplementary materials

Fig. S1. Bayesian inference (BI) topology of Mecopini. The posterior probability is shown as the node supports. (download)

Table S1. The primer-pairs used in this study. (download)

Table S2. List of specimens examined in this study. (download)