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New Genus and Species of Empheriidae (Insecta: Psocodea: Trogiomorpha) and Their Implication for the Phylogeny of Infraorder Atropetae

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Two species of psocids discovered from the Mid-Cretaceous Burmese amber, *Latempheria kachinensis* Li, Yoshizawa, and Yao, gen. et sp. nov. and *Burmempheria curvatavena* Li, Yoshizawa, and Yao, sp. nov., are described and assigned to the Empheriidae (Trogiomorpha: Atropetae) family. A phylogenetic analysis of the infraorder Atropetae is conducted based on 38 morphological characters of three outgroups and fifteen ingroups, which supported the monophyly of Atropetae including fossil and extant taxa. In the phylogenetic result, all the genera of fossil families Empheriidae and Archaeatropidae form a monophyletic group, sister to the extant members of Atropetae. The two fossil families also share a lot of similarities in morphology, locality, and geological period. Recently discovered fossil species exhibited combined morphological characters of both families. Based on these observations and the results of the phylogenetic analysis, Archaeatropidae is treated here as a new junior synonym of Empheriidae.

Keywords: Archaeatropidae, new taxon, phylogeny, synonymy, Trogiomorpha, psocoptera

INTRODUCTION

The infraorder Atropetae Pearman, 1936 represents the largest group in the suborder Trogiomorpha, with more than 400 species mainly occurring in warm and humid regions (Lienhard and Smithers, 2002). These species are classified into two extinct families (Empheriidae and Archaeatropidae) (Smithers, 1972; Baz and Ortuño, 2000, 2001; Azar and Nel, 2004; Azar et al., 2010, 2014; Li et al., 2020) and three extant families (Psoquillidae, Lepidopsocidae, and Trogiidae) (Roesler, 1944; Badonnel, 1951). Fossil Psocodea have been studied for over 100 years; however, because of limitations in fossil specimens and incomplete preservation, and different interpretations of taxonomic characteristics, many species were classified into uncertain positions. For example, based on morphological characters, two families in Trogiomorpha, i.e., Empheriidae and Archaeatropidae, are hard to distinguish (Baz and Ortuño, 2000, 2001; Perrichot et al., 2003; Li et al., 2020).

Atropetae fossils are known in five families (including three extant families) and thirty-five genera. Their geological history ranged from Cretaceous to Paleogene, and they were distributed in Lebanon (Azar and Nel, 2004), Spain (Baz and Ortuño, 2000, 2001), Myanmar (Azar and Nel, 2004; Li et al., 2020; Liang et al., in press), France SW (Azar et al., 2014), New Jersey (Azar et al., 2010), France Oise (Nel et al., 2005), Siberia (Vishnyakova, 1975; Hakim et al., 2021), and Baltic region (Hagen, 1856; Enderlein, 1911). Most of the fossil species are placed in the extinct families Empheriidae and Archaeatropidae. Empheriidae was established by Kolbe (1884), with eight genera and eleven species (Hagen, 1856, 1882; Baz and Ortuño, 2001; Nel et al., 2005; Azar et al., 2010; Li et al., 2020; Hakim et al., 2021). Archaeatropidae was established by Baz and Ortuño (2000) based on amber specimens from Spain. The family is now composed of eight genera with twelve species recorded mainly from Lebanon, Myanmar, and France SW (Baz and Ortuño, 2000; Perrichot et al., 2003; Azar and Nel, 2004; Azar et al., 2014; Cumming and Le Tirant, 2021; Liang et al., in press). Li et al. (2020) mentioned that based on high similarity in morphological characters, living period, and fossil locality, Empheriidae and Archaeatropidae are likely to be synonyms. Previous phylogenetic analyses showed that Atropetae is a monophyletic group that comprises three extant families (Smithers, 1972; Yoshizawa et al., 2006; de Moya et al., 2021). However, these analyses did not include the extinct families of Atropetae, Empheriidae, and Archaeatropidae. Consequently, the phylogenetic placement of the two families remains unsolved to date.

In this study, all ambers were collected from the Hukawng Valley, Myitkyina District, Kachin State, Myanmar (Lin et al., 2019; Zhao et al., 2020). Herein, a new genus, *Latempheria* Li, Yoshizawa and Yao, gen. nov., distinguished by broad external valves and a new species of *Burmempheria* Li et al., 2020 in Empheriidae are described. Based on present observations and published information, 38 morphological characters for three outgroups and fifteen ingroups are coded. Using this data matrix, phylogenetic analyses were conducted to estimate the phylogenetic relationships among the families of Atropetae, including fossil taxa, for the first time. The result suggests that Empheriidae and Archaeatropidae, together form a monophyletic group, and their morphological differences are obscure. Therefore, we synonymize the latter family with Empheriidae.

MATERIALS AND METHODS

Materials

The amber specimens were collected from Kachin (Hukawng Valley) in Northern Myanmar. The specimens are housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNU, Curator: Yunzhi Yao). The specimens were acquired before 2013 and then studied in 2019, with no conflict (Wang et al., 2016; Engel, 2020; Shi et al., 2021).

The specimens were examined and photographed under a Nikon SMZ25 microscope with an attached Nikon DS-Ri2 digital camera system. The morphological terminology mainly follows Yoshizawa (2005). Abbreviations: mx, maxillary palp; la, labium; Sc, subcostal vein; Sc', distal part of the subcostal vein; R, radius vein; Rs, radial sector; M, median vein; Cu, cubital vein; A, anal vein; ep, epiproct; p, paraproct; pa, parameres; s, subgenital plate; V3, external valve; mt: tarsus of mid leg; ht: tarsus of hind leg.

Taxon Sampling and Character Choice

The outgroups were selected from Prionoglarididae, Psyllipsocidae, and Cormopsocidae, and the ingroups from Atropetae (**Supplementary Table 1**). For coding the morphological data from the fossil taxa, we selected those that were widespread and that had extensive information available on morphology. Thirty-eight multistate characters were treated as non-additive (= unordered) and equally weighted. The data matrix used in this phylogenetic analysis is provided in **Supplementary Data Sheet 1**. Inapplicable states were assigned as a gap value ("—") and treated as equivalent to missing data ("?").

Phylogenetic Analysis

The character matrix (**Supplementary Datasheet**) was compiled using Nexus Data Editor v0.5.0 (Page, 2001). A phylogenetic analysis was conducted by maximum parsimony analysis in WINCLADA v1.00.08 (Nixon, 2002) with NONA script (Goloboff, 1997; Nixon, 2002) and TNT v1.5 (Goloboff and Catalano, 2016). The analysis conducted in WINCLADA was set to keep 10,000 maximum trees, 1,000 replications, and 100 starting trees per replication. A repeated analysis was run in TNT using "Traditional Search."

RESULTS

The maximum parsimony analyses using TNT and WINCLADA both yielded 6 most parsimonious trees (tree length of 86 steps, consistency index (CI) of.51, and retention index (RI) of.6), and a strict consensus tree with a tree length of 93 steps, consistency index (CI) of.47, and retention index (RI) of.54 (**Figure 1** and **Supplementary Figure 1**). Bremer Supports are shown in **Figure 1**. The result supported that Empheriidae + Archaeatropidae constitutes a monophyletic group, and that Lepidopsocidae + Psoquillidae + Trogiidae constitutes a monophyletic group. These two groups formed a monophyletic group, the infraorder Atropetae.

Infraorder Atropetae

The monophyly of Atropetae including fossil and extant taxa was demonstrated for the first time, with the following four character states supporting its monophyly: mx2 with sensillum (character 5, state 1); Areola Postica long (character13, state 1); M_{1+2} longer than the second section of M (character 22, state 2); long and thin female external valves (character 34, state 1).

Clade Lepidopsocidae + Psoquillidae + Trogiidae

In Atropetae, the families Lepidopsocidae, Psoquillidae, and Trogiidae, i.e., the extant members of the infraorder, formed a monophyletic group, with two character states

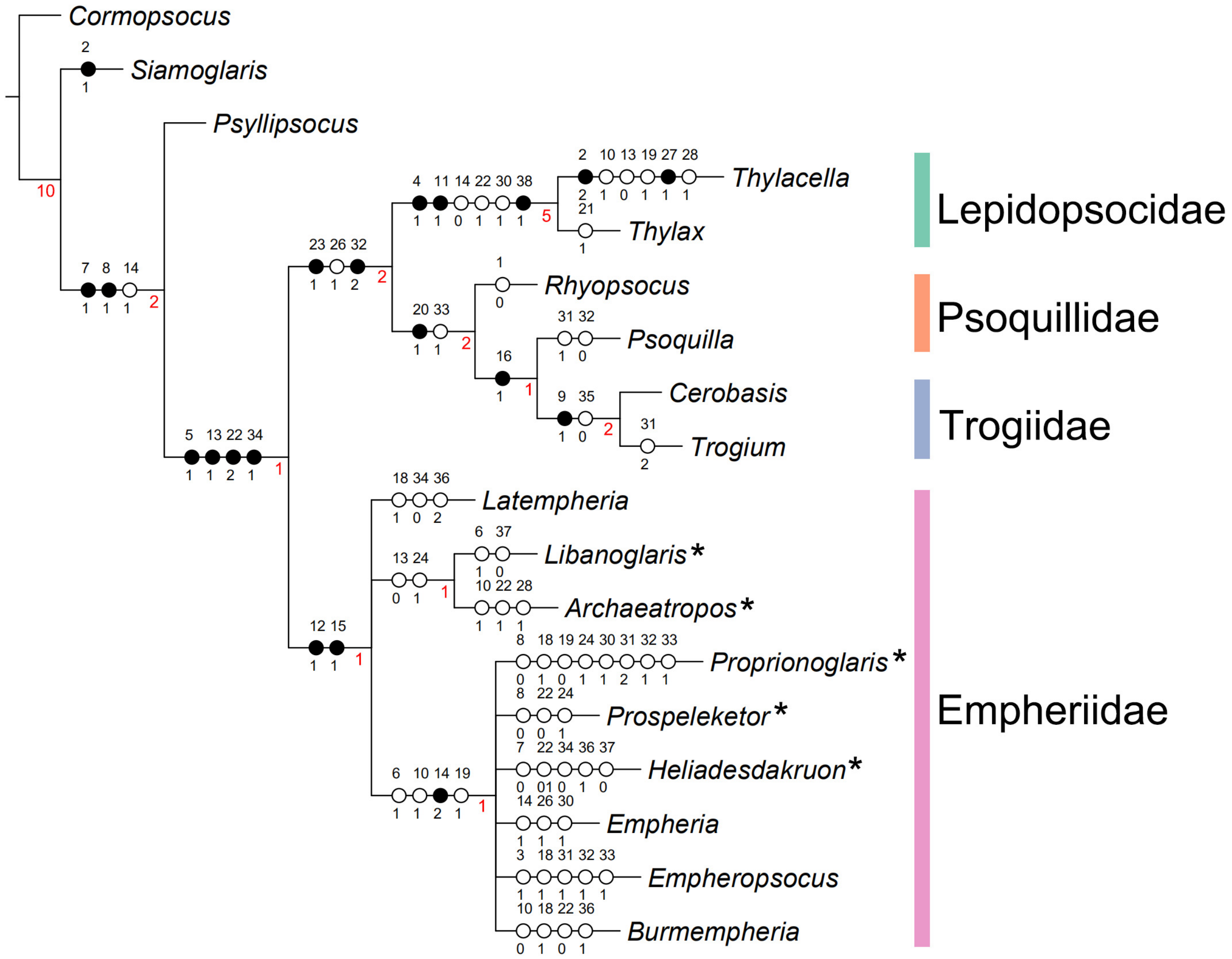

FIGURE 1 | Strict consensus tree of the most parsimonious tree. Phylogeny of Atropetae based on 18 species and 38 characters, with characters being non-additive, under equal weighting. Analyzed with WINCLADA v1.00.08 with NONA script (length = 93, CI = 0.47, RI = 0.54). * Represents the genus originally placed in Archaeatropidae.

supporting this clade: (1) Radial cell absent in forewing (character 23, state 1); (2) pulvillus broad (character 32, state 2). In this clade, Psoquillidae + Trogiidae formed a monophyletic group, the supporting character for this clade was: forewing Rs and R_1 not connected by a short crossvein (character 20, state 1). In the present analysis, the monophyly of Lepidopsocidae has been well-supported by three character states: (1) ocelli arranged far apart (character 4, state 1); (2) forewing pointed (character 11, state 1); (3) body covered by scales (character 38, state 1).

Clade Empheriidae + Archaeatropidae

Empheriidae and Archaeatropidae formed a monophyletic group (**Figure 1**), with two characters supporting this clade: (1) forewing membrane with setae (character 12, state 1); (2) forewing veins with setae (character 15, state 1). In this lineage, the relationship of each genus remained unclear.

Systematic Paleontology

Suborder Trogiomorpha Roesler, 1940.

Infraorder Atropetae Pearman, 1936.

Family Empheriidae Kolbe, 1884.

Empheriidae Kolbe, 1884: 37 [Type genus: *Empheria* Hagen, 1856: *Berliner Entomologische Zeitschrift.* 28, 35–38].

Archaeatropidae Baz and Ortuño, 2000: 369 [Type genus: *Archaeatropos* Baz and Ortuño, 2000: Annals of the Entomological Society of America. 93, 367–373]. New junior synonymy of Empheriidae.

Included genera (* represents this genus originally placed in Archaeatropidae): *Empheropsocus* Baz and Ortuño, 2001; *Preempheria* Baz and Ortuño, 2001; *Jerseyempheria* Azar et al., 2010; *Eoempheria* Nel et al., 2005; *Empheria* Hagen, 1856; *Trichempheria* Enderlein, 1911; *Burmempheria* Li et al., 2020; *Empherium* Hakim et al., 2021; **Archaeatropos* Baz and Ortuño, 2000; **Bcharreglaris* Azar and Nel, 2004; **Libanoglaris* Perrichot et al., 2003; **Proprionoglaris* Perrichot et al., 2003;

**Prospeleketor* Perrichot et al., 2003; **Setoglaris* Azar and Nel, 2004; **Heliadesdakruon* Cumming and Le Tirant, 2021; **Longiantennum* Liang et al., in press*; *Latempheria* Li, Yoshizawa, and Yao, gen. nov.

Genus: *Latempheria* Li, Yoshizawa and Yao, gen. nov.

Etymology: The generic name is a combination of Latin words "*lat*" (broad) and "*empheria*" (type genus of Empheriidae), referring to the broad external valves of the type species. The gender is feminine.

Type species: *Latempheria kachinensis* Li, Yoshizawa and Yao, gen. et sp. nov.

Diagnosis: Forewing Sc long, almost half length of forewing, ended in the middle of Radial cell; all tibiae with two apical spurs, and tibiae covered with two rows of obvious setae; external valves broad and elongate, lobate-liked.

Remarks: *Latempheria* shares a series of characters with Trogiomorpha: (1) antennae with more than 20 segments; (2) tarsi with three segments; (3) forewing pterostigma slightly opaque; (4) ventral and dorsal valves of gonapophyses strongly reduced (or absent), external valves well-developed and setose; (5) subgenital plate short, covering at most basal part of external valves (Yoshizawa et al., 2006). In addition, *Latempheria* can be classified into Atropetae by the following characters: (1) forewing basal segment of Sc well-developed; (2) hind wing A simple; (3) external valves of gonapophyses elongated and partially joined together on midline by membrane; (4) paraproct with anal spine (Yoshizawa et al., 2006). *Latempheria* can be assigned to Empheriidae according to (1) wings well-developed, rounded at apex; (2) forewing Sc bend to R; (3) venation covered with setae; (4) claws without preapical tooth (Baz and Ortuño, 2001).

In the family, *Latempheria* shares similar characteristics with *Burmempheria* Li et al., 2020 in forewing venation, legs, and antennae. The main difference between *Latempheria* and *Burmempheria* are: (1) *Latempheria* with broad and elongated external valves (vs. rod-like external valves in *Burmempheria*); (2) all tibiae with two rows of obvious spur in *Latempheria* (vs. *Burmempheria* with tibia bearing setae or bare).

Latempheria kachinensis Li, Yoshizawa and Yao, gen. et sp. nov. (**Figures 2**, **3**).

urn:lsid:zoobank.org:act:8500CE76-8F78-402B-AB7D-376B939FC0A9.

Etymology: "*Kachin*" indicates the type locality of the new species.

Material: Holotype, CNU-PSO-MA2015001 (female, head covered by impurities). Paratype, CNU-PSO-MA2015002 (female with head well preserved, gonapophyses distorted).

Locality and horizon: Hukawng Valley, Kachin State, Northern Myanmar; mid-Cretaceous, lowermost Cenomanian.

Diagnosis: All tibiae with two rows of obvious setae, with two apical spurs; external valves without setae; CuP and A_1 fused for long distance before wing margin; CuA_1 obviously curved, nearly 2 times longer than CuA_2.

Description: Female, body completely preserved, head with some impurities (**Figures 2A,B**), antennae broken (**Figure 2C**); mouthpart well-preserved; three ocelli present, arranged in inverted triangle. Body length 1.71 mm (measured from frons to terminalia). Forewing length 1.812 mm, width.809 mm; hind wing length 1.46 mm, width.509 mm. IO/d = 2.23. Mt = 307 mm; ht = 0.361 mm.

Head: head narrow, compound eyes small, diameter less than 1/2 the length of interorbital distance; antennae long, obviously broken, left 25 segments preserved, right 7 segments preserved, distal part of flagellum with soft and thin setae, secondary annulations absent (**Figures 3A,B**). Maxillary palps with four segments (**Figure 3C**), second segments longest, terminal article hatchet-shaped, with sensillum (**Figure 3D**). Labium palps with two articles, terminal augment rounded (**Figure 3E**).

Thorax: prothorax broad, mesothorax well-developed, and mesonotum triangular.

Legs: All legs covered with setae, all tibiae with two rows of obvious setae, with two apical spurs (**Figures 3F,G**); tarsus three segmented, claws without pulvillus and preapical tooth.

Forewings: Macropterous, forewing oval (**Figure 2D**), margin glabrous, veins with long setae except CuP, membrane glabrous except vannal region. Veins with Sc, M, Cu, and A with long setae arranged along both edges of veins; other veins with one row of long setae; Sc long, basally fused with R for short distance, distally curved strongly, ended at R_1 vein, short vein arises from top of curved Sc reaching to anterior margin; Sc' long, pterostigma quadrilateral, not thickened; Rs and M fused for short distance; Rs fork distal to M fork; M_{1+2} longer than second section of M, almost 2.5 times longer with it. CuA_1 and CuA_2 long, CuA_1 curved, nearly 2 times longer than CuA_2; CuP weaker than other veins; CuP and A_1 fused for long distance before reaching wing margin (**Figure 3H**).

Hind wing oval (**Figure 2E**). Hind wing margin and membrane glabrous (**Figure 2E**). Not preserved well. Distal part of R_1 curved; R_1 and Rs + M connected by a short crossvein; CuA unforked; A not visible.

Abdomen: Epiproct and paraproct covered with setae; epiproct with anal spine; dorsal valves degraded, external valves elongate, broad, lobate-liked, and partially joined together on midline by membrane (**Figures 3I,J**).

Genus: *Burmempheria* Li et al., 2020.

Type species: *Burmempheria densuschaetae* Li et al., 2020.

Burmempheria curvatavena Li, Yoshizawa and Yao, sp. nov. (**Figures 4**, **5**).

urn:lsid:zoobank.org:act:89231F37-E4CC-44BA-85F0-CCDE453FB3AA.

Etymology: A combination of Latin words "*curvata*" (bent) and "*vena*" (vein), indicating that CuA_1 is obviously curved.

Material: Holotype, CNU-PSO-MA2015003, male, well-preserved, with genitalia covered by impurities.

Locality and horizon: Hukawng Valley, Kachin State, Northern Myanmar; mid-Cretaceous, lowermost Cenomanian.

Diagnosis: All tibiae with two rows of sparse and short setae; tibia with three apical spurs; distal part of forewing CuA_1 obviously curved; M_{1+2} extremely long, almost 3 times longer than the distal section of M.

Description: Male, well -preserved, with folded distal left forewing. Body length 1.71 mm (measured from frons to terminalia). Forewing length 1.887 mm, width.762 mm; hind wing length 1.354 mm, width.453 mm. IO/d = 2.16. Mt = 0.375 mm; ht = 0.417 mm.

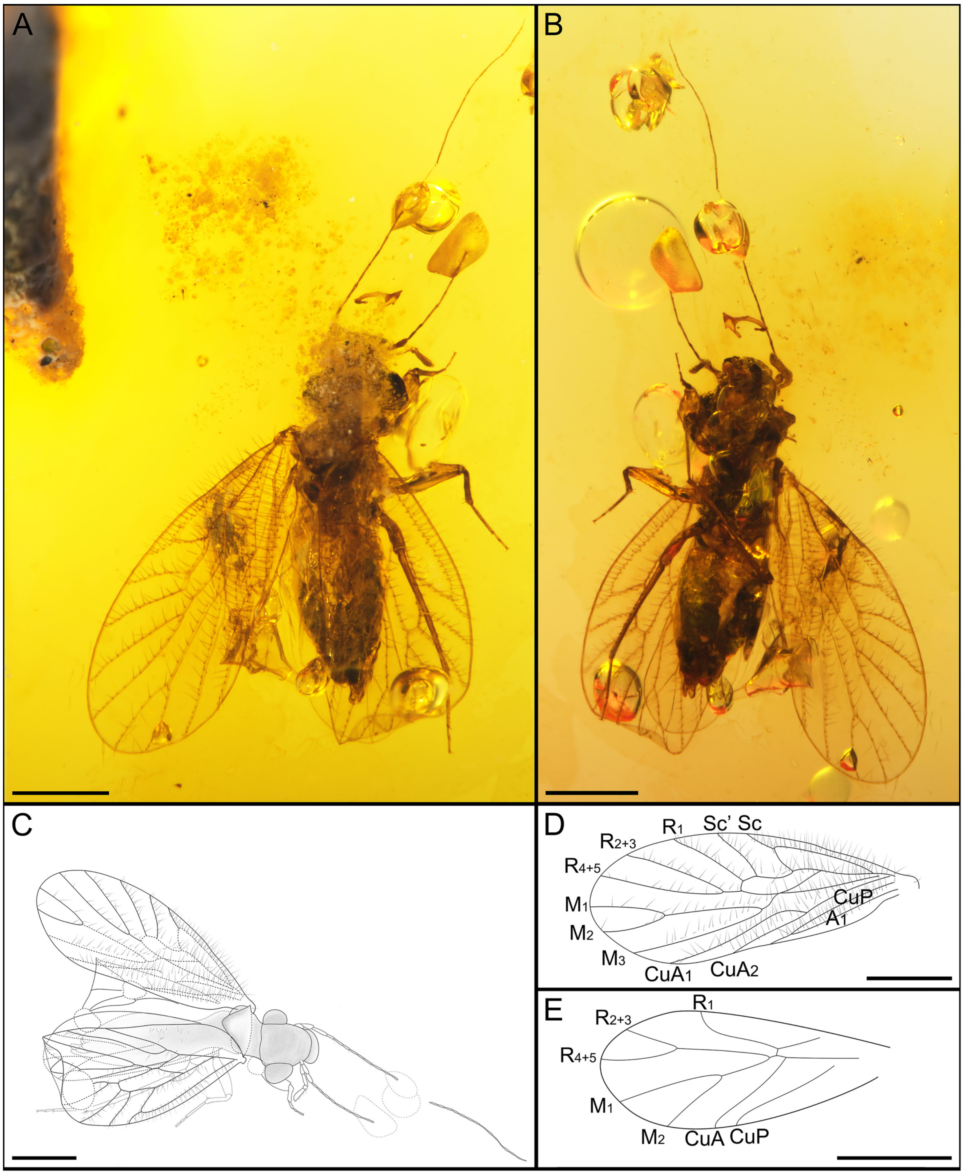

FIGURE 2 | Habitus of *Latempheria kachinensis* Li, Yoshizawa and Yao, gen. et sp. nov. CNU-PSO-2015001. **(A)** Photograph in dorsal view; **(B)** photograph in ventral view; **(C)** line drawing in dorsal view; **(D)** line drawing of forewing; **(E)** line drawing of hind wing. Scale bars:0.5 mm.

Head: vertex broad, covered with sparse and long setae (**Figures 4A,B**); compound eyes large, diameter longer than 1/2 the length of interorbital distance; three ocelli present, arranged in inverted triangle. Antennae long (**Figure 4C**), right flagellum with 30 segments, left with 32 flagellomeres, basal 10 segments covered with setae, secondary annulations absent (**Figures 5A,B**). Maxillary palps with four segments, covered with setae, terminal article hatchet-shaped, second article longest (**Figures 5C,D**).

Thorax: slight deformation, prothorax invisible, mesothorax well-developed, mesonotum triangular.

Legs. All legs long, all tibiae covered two rows of obvious setae, with three apical spurs (**Figures 5E,F**); tarsus three segmented, terminal segment with two claws, without pulvillus and preapical tooth.

Forewing: Macropterous, forewing oval (**Figure 4D**), margin glabrous, all veins with long setae except CuP, membrane glabrous except vannal region. Sc, R, M, and Cu with setae along both edges of veins, other veins with single row of setae; Sc long, basally fused with R for short distance and distally curved, short vein arises from top of curved Sc, reaching to the anterior margin; Sc' long, not curved; distal R_1 slightly curved; pterostigma quadrilateral, not thickened; M_{1+2} very long, almost 3 times longer than the second section of M; CuA with two branches, CuA_1 is twice as CuA_2, CuA_1 distinctly curved; CuP

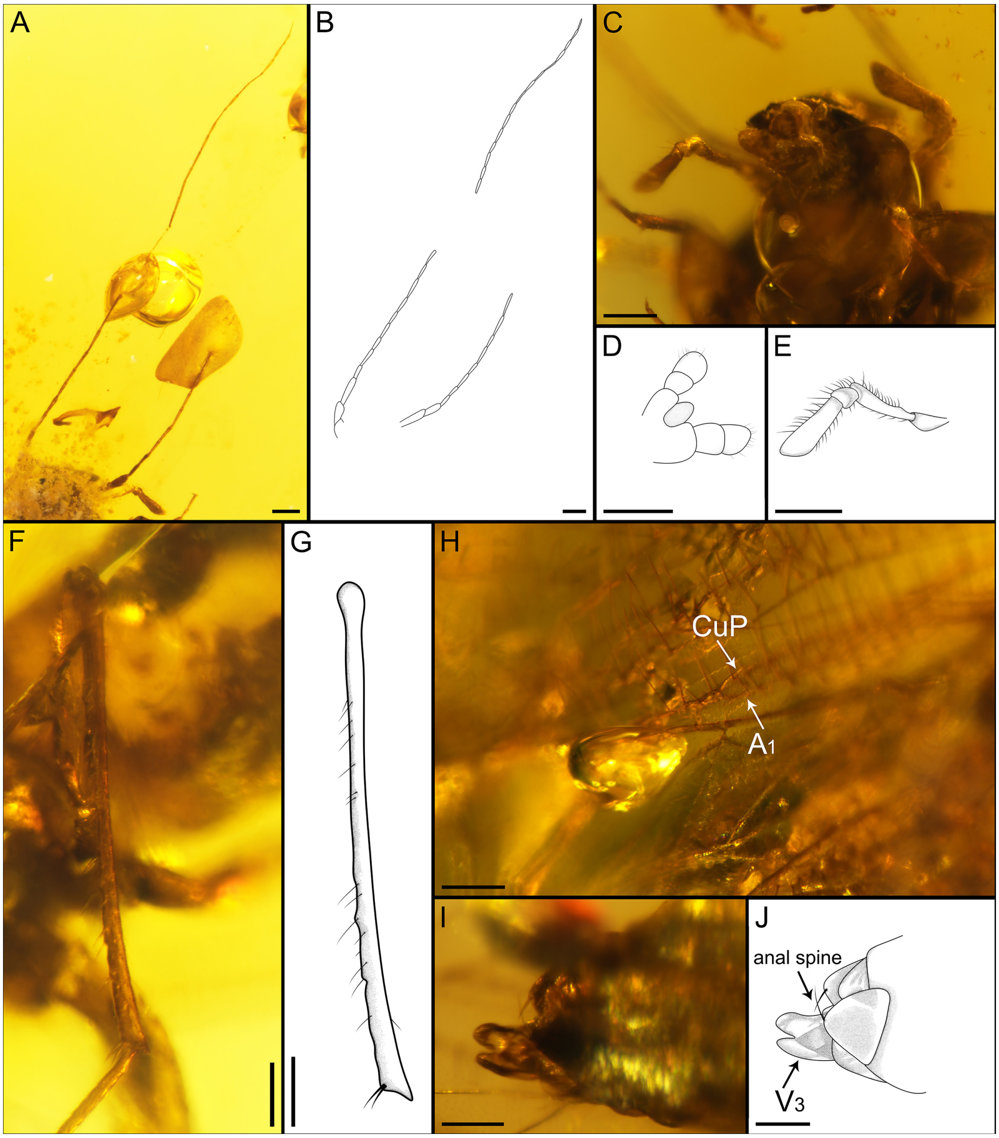

FIGURE 3 | Detailed photograph of *Latempheria kachinensis* Li, Yoshizawa and Yao, gen. et sp. nov. **(A)** Photograph of antennae; **(B)** line drawing of antennae; **(C)** photograph of mouthpart; **(D)** line drawing of right maxillary palps (dorsal view); **(E)** line drawing of labial palps; **(F)** photograph of left hind leg (dorsal view); **(G)** line drawing of left hind leg (dorsal view); **(H)** photograph of CuP and A1 in left forewing; **(I)** photograph of female terminalia; **(J)** line drawing of female terminalia. Scale bars:0.1 mm.

weaker than other veins, CuP and A1 merged for short distance before reaching wing margin (**Figure 5G**).

Hind wing oval (**Figure 4E**), hind wing margin and membrane glabrous, right hind wing folded; R1 slightly curved; M_1 and M_2 relatively long; CuA unforked; A not visible.

Abdomen: genitalia covered by impurities, not well-preserved.

Remarks: *Burmempheria curvatavena* can be assigned into *Burmempheria* based on: (1) flagellum more than 30 segments; (2) Sc long and reaching to the anterior margin; (3) lack of pulvillus. There are obvious differences between *B. curvatavena* and other species: (1) tibiae with three apical spurs (vs. two apical spurs in *B. densuschaetae* and *B. raruschaetae*); (2) M_{1+2} extremely long, almost thrice the distal section of M (vs. M_{1+2} nearly twice the distal section of M in *B. densuschaetae* and *B. raruschaetae*).

DISCUSSION

The monophyly of Atropetae, including the fossil taxa, is recovered in the current analysis for the first time. Based on the extant species, Smithers (1972) mentioned that the reduction of female genitalia to setose, lobar external valves is the main apomorphy of Atropetae. Previous molecular research also supported the monophyly of Atropetae (Yoshizawa et al., 2006; de Moya et al., 2021). Based on their result,

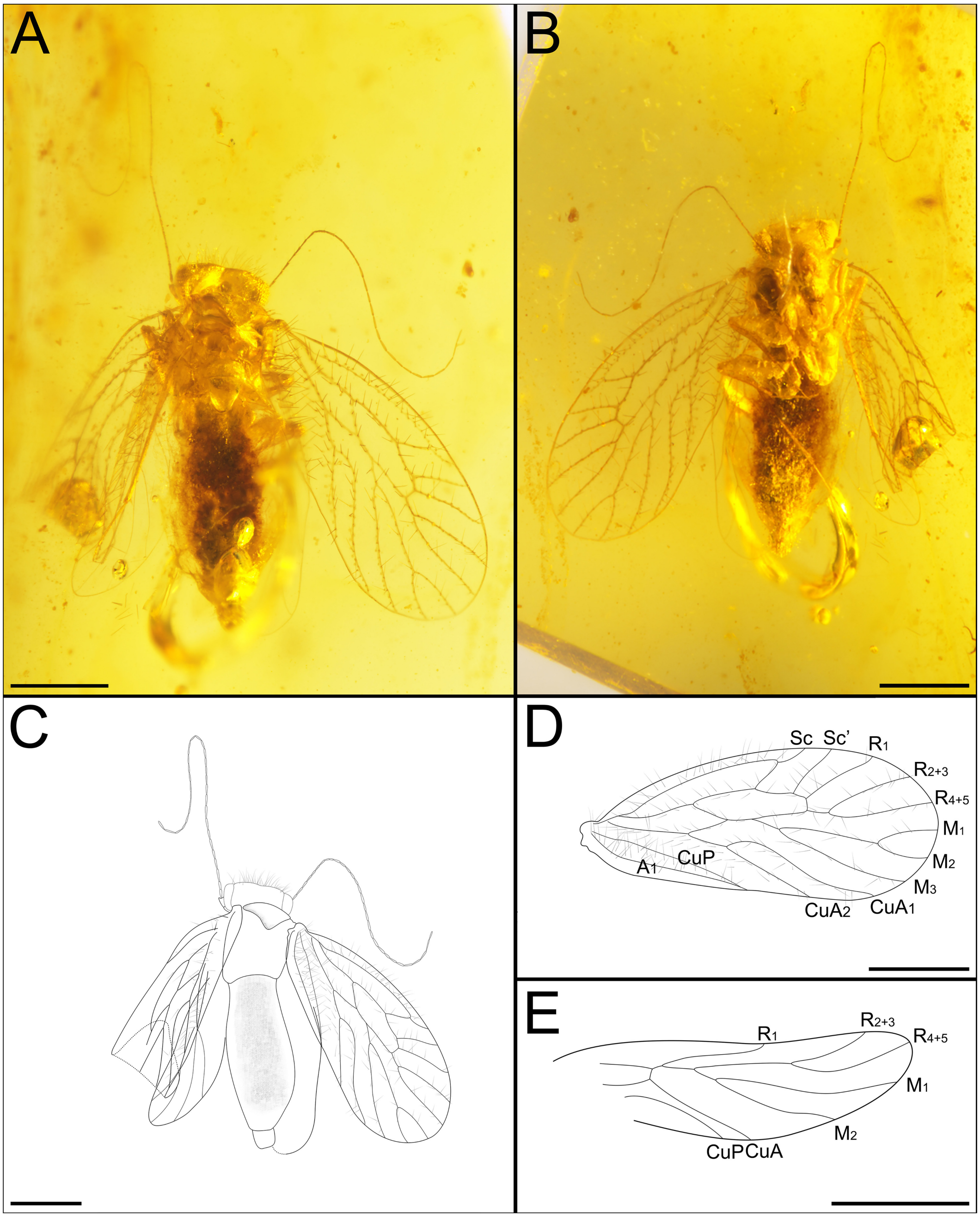

FIGURE 4 | Habitus of *Burmempheria curvatavena* Li, Yoshizawa and Yao, sp. nov. CNU-PSO-2015003. **(A)** Photograph in dorsal view; **(B)** photograph in ventral view; **(C)** line drawing in dorsal view; **(D)** line drawing of forewing; **(E)** line drawing of hind wing. Scale bars:0.5 mm.

Yoshizawa et al. (2006) proposed two autapomorphies of extant Atropetae: (1) external valves of gonapophyses elongated and partially joined together on midline by membrane, composing the ovipositor; (2) spermathecal sac with one or two glandular accessory bodies.

The present analyses recovered the monophyly of Lepidopsocidae + Psoquillidae + Trogiidae, extant members of Atropetae, as recovered by Smithers (1972) and Yoshizawa et al. (2006). The autapomorphies of this clade identified by the present analyses are: forewing Radial cell absent (character 23, state 1); pulvillus broad (character 32, state 2). In this clade, Psoquillidae + Trogiidae formed a monophyletic group. This relationship had already been discussed by Smithers (1972) based on the presence of spermathecal accessory bodies, but Mockford (1993) suggested that this character is an autapomorphy of Atropetae (Yoshizawa et al., 2006). Mockford (1993) and

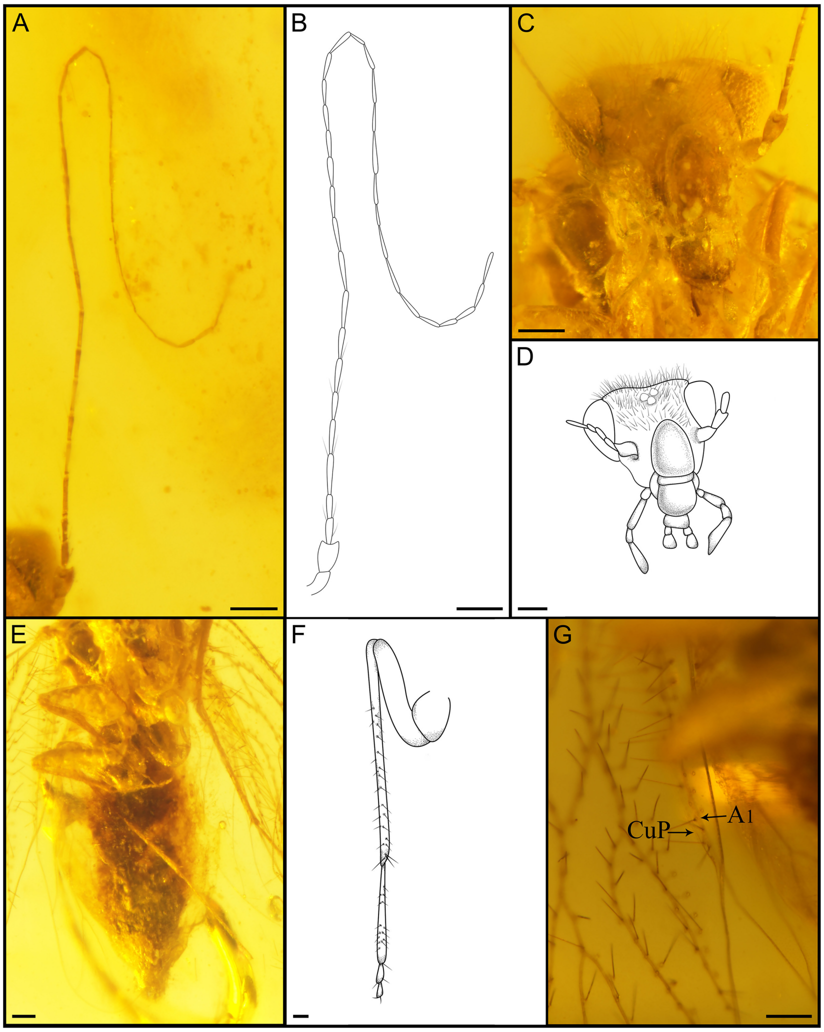

FIGURE 5 | Detailed photograph of *Burmempheria curvatavena* Li, Yoshizawa and Yao, sp. nov. **(A)** Photograph of right antenna; **(B)** line drawing of right antenna; **(C)** photograph of mouthpart; **(D)** line drawing of mouthpart; **(E)** photograph of right hind leg (dorsal view); **(F)** line drawing of right hind leg (dorsal view); **(G)** photograph of CuP and A1 in left forewing. Scale bars:0.1 mm.

Lienhard (1998) proposed two synapomorphies supporting the close relationship between Psoquillidae and Trogiidae: (1) pretarsal claw without preapical tooth; (2) pulvillus distinctly enlarged through its whole length. The autapomorphies of this clade identified by the present analyses are: R1 and Rs not connected by a short crossvein (character 20, state 1).

The current research suggested that Psoquillidae is paraphyletic, and Psoquilla Hagen, 1865 was placed to be the sister taxon of Trogiidae supported by reduced forewing veins (character 16, state 1). Based on Hagen (1856) and Smithers (1972), Psoquilla forewing veins are distinct but much simpler or more reduced than other genera. In Yoshizawa et al. (2006) and de Moya et al. (2021), both analyses are based on a single species of Psoquillidae. According to Yoshizawa et al. (2006), Psoquillidae and Trogiidae are treated as sister taxa, and in de Moya et al. (2021), Psoquillidae was placed as the sister group of Lepidopsocidae. The relationships among Psoquillidae, Lepidopsocidae, and Trogiidae remain unclear while the monophyly of Psoquillidae still requires further studies. The monophyly of Trogiidae is well-supported by an apparent apomorphic character, i.e., reduced forewing (character 9, state 1), as also suggested by a previous study (Mockford, 1993). Mockford (1993) and Yoshizawa et al. (2006) suggested the monophyly of Lepidopsocidae was supported by body covered by scales, which was also recovered by the present analyses.

Based on the differences in the forewing setae arrangement and nodulus condition, Empheriidae and Archaeatropidae have been treated as two different families. However, these families share a lot of similarities in amber deposit (Spain, France, Myanmar), living period, and morphological characters such as number of flagellomeres, shape of maxillary palps, wing shape and venation, and shape of external valves (Baz and Ortuño, 2001). The main differences between them are the rows of forewing veins setae (Empheriidae with two rows of

TABLE 1 | Genera and species of Empheriidae.

Taxa	Locality	Age
Archaeatropos randatae Azar and Nel, 2004 *	Lebanon	Lower Cretaceous
Bcharreglaris amunobi Azar and Nel, 2004 *		
Libanoglaris mouawadi Perrichot et al., 2003 *		
Libanoglaris chehabi Azar and Nel, 2004 *		
Setoglaris reemae Azar and Nel, 2004 *		
Empheropsocus arilloi Baz and Ortuño, 2001	Spain	Lower Cretaceous
Empheropsocus margineglabrus Baz and Ortuño, 2001		
Preempheria antiqua Baz and Ortuño, 2001		
Archaeatropos alavensis Baz and Ortuño, 2000 *		
Proprionoglaris axioperierga Azar et al., 2014 *	France SW	Lower Cretaceous
Proprionoglaris guyoti Perrichot et al., 2003 *		
Prospeleketor albianensis Perrichot et al., 2003 *		
Empherium rasnitsyni Hakim et al., 2021	Siberian	Lower Cretaceous
Burmempheria densuschaetae Li et al., 2020	Myanmar	Upper Cretaceous
Burmempheria raruschaetae Li et al., 2020		
Burmempheria curvatavena Li, Yoshizawa & Yao, sp. nov.		
Latempheria kachinensis Li, Yoshizawa & Yao, sp. nov.		
Archaeatropos perantiqua Cockerell, 1919 *		
Heliadesdakruon morganae Cumming and Le Tirant, 2021 *		
Longiantennum fashengi Liang et al., in press*		
Jerseyempheria grimaldii Azar et al., 2010	New Jersey	Upper Cretaceous
Eoempheria intermedia Nel et al., 2005	France Oise	Lower Eocene
Empheria (*Bebiosis*) *pertinens* Enderlein, 1911	Baltic	Eocene
Empheria (*Bebiosis*) *reticulata* Pictet-Baraban and Hagen, 1856		
Trichempheria villosa Hagen, 1882		

**Represent this genus originally placed in Archaeatropidae.*

setae vs. Archaeatropidae with one row of setae) and forewing nodulus (Empheriidae without nodulus vs. Archaeatropidae with nodulus) (Baz and Ortuño, 2000, 2001; Mockford et al., 2013). However, the forewing veins setae are not stable (Li et al., 2020). For example: *Prospeleketor albianensis* Perrichot et al., 2003 and *Proprionoglaris axioperierga* Azar et al., 2014 have been assigned to Archaeatropidae, but they have two rows of vein setae, and the Empheriidae species: *Preempheria antiqua* Baz and Ortuño, 2001 has one row of vein setae; *Burmempheria* has two rows of vein setae in Sc, A and Cu, but other veins have only one row; *Jerseyempheria grimaldii* Azar et al., 2010 with the setae covering the membrane of forewing. The forewing nodulus is also an unstable character (Wang et al., 2019) and cannot be used to distinguish these two families (Li et al., 2020). Li et al. (2020) mentioned that Empheriidae and Archaeatropidae are presumed to be closely related because of shared morphological conditions in the forewing veins setae and the setose anal area. The present phylogenetic analysis suggests for the first time that Empheriidae and Archaeatropidae form a monophyletic group supported by the membranous region of forewing with setae (character 12, state 1); forewing veins with setae (character 15, state 1). Based on these results, we conclude that Archaeatropidae Baz and Ortuño, 2000 should be treated as a junior synonymy of Empheriidae (Kolbe, 1884). As a result, Empheriidae now contains sixteen genera and twenty-five species in total (including this study) (**Table 1**).

This is the first study to explore the phylogenetics of the atropine families including the fossil taxa. To avoid reduction of tree resolution, we only selected well-preserved fossils and did not include highly autapomorphic genera (e.g., *Jerseyempheria* Azar et al., 2010 with the forewing membrane covered with setae). However, due to the limitations of fossil preservation, some important characters could not be observed from the fossils, and the phylogenetic placement of poorly preserved fossil taxa remains unknown. Further research is still needed to obtain more data using techniques, i.e., CT scanning, to obtain more information and to elucidate their relationship. Over the past 40 years, the phylogeny and taxonomy of Psocodea including their higher level of classification have been studied extensively based on the evidence of extant insects, including morphological and molecular systematics (Smithers, 1972; Yoshizawa, 2002; Perrichot et al., 2003; Yoshizawa and Johnson, 2003, 2006; Johnson et al., 2004, 2018; de Moya et al., 2021), but there are still some disagreement (Yoshizawa and Saigusa, 2001; Misof et al., 2014). The bias of sampling, the homogeneity of evidence, and the instability of taxonomic characteristics may be the important reasons for the above arguments. Therefore, it is important to integrate the fossil evidence and the modern insects to construct a phylogenetic tree in order to elucidate the morphological characteristics, origin, and evolutionary history of these insect groups.

The fossil records of Atropetae are mainly from Mesozoic, and twenty-four genera with twenty-nine species have been recorded during Cretaceous from Lebanon, Spain, France SW, Myanmar, New Jersey, and Siberia (Vishnyakova, 1975; Baz and Ortuño, 2000, 2001; Perrichot et al., 2003; Azar and Nel, 2004, 2011; Azar et al., 2010, 2014, 2017; Hakim et al., 2018, 2021; Wang et al., 2019; Li et al., 2020; Corentin et al., 2021; Cumming and Le Tirant, 2021; Liang and Liu, 2021). Only ten genera with thirteen species are known during Cenozoic from the Baltic region, France Oise, FuShun, and Tanzania (Hagen, 1856, 1865, 1866, 1882; Enderlein, 1911; Nel et al., 2005; Azar et al., 2018). The earliest fossil record was from Lebanon (Cretaceous, Lower Barremian). Most extant species of Atropetae live in tropical and subtropical regions (Smithers, 1972, 1999; New, 1975; Mockford, 1991; Lienhard, 2000). During the Cretaceous and Cenozoic, environment about the locality of the fossil record is mainly under a warm and humid tropical or subtropical climate (Scotese, 2002). Research showed that Myanmar had a tropical forest palaeoenvironment during the Cretaceous (Grimaldi et al., 2002; Shi et al., 2022), which also met their requirements for living environment. Over the 100 million years of evolution, the distributional range of Atropetae is probably mainly restricted to warm and humid areas. The Atropetae insects may be an indication of an ancient environment.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Zoobank, https://zoobank.org/52D5D725-1731-4855-86CB-4C2714781C65, https://zoobank.org/e490780d-ac0e-4bf7-a9f1-5ee8f0b01316, (urn:lsid:zoobank.org:act:8500CE76-8F78-402B-AB7D-376B939FC0A9) and (urn:lsid:zoobank.org:act:89231F37-E4CC-44BA-85F0-CCDE453FB3AA). Further enquires can be directed to the corresponding author(s).

AUTHOR CONTRIBUTIONS

SL, YY, and DR designed the research. SL conceived the study with support from KY, DR, and YY. DR and YY provided the materials. SL and QW took the photographs and prepared the line drawings. SL, KY, and QW performed the morphological analysis. SL and KY conducted the phylogenetic analyses. KY and MB revised the draft. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.907903/full#supplementary-material

Supplementary Figure 1 | The most parsimonious tree obtained by TNT analysis. Phylogeny of Atropetae based on 18 species and 38 characters, with characters being nonadditive, under equal weighting. Analyzed with TNT v1.5. * Representsthe genus originally placed in Archaeatropidae.

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