

A Revised Key to the Living and Fossil Families of Strepsiptera, with the Description of a New Family, *Cretostylopidae*

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ABSTRACT: A new family, *Cretostylopidae* Kathirithamby and Engel, is erected to accommodate the mid-Cretaceous species *Cretostylops engeli* Grimaldi and Kathirithamby. Based on this as well as various other recent works pertaining to the higher classification of Strepsiptera, a revised key is provided to the living and fossil families.

KEY WORDS: Strepsiptera, twisted-winged parasites, *Cretostylops*, fossil, identification key

Recently there has been increased interest in the higher classification of evolution of the twisted-winged parasites (Strepsiptera). Indeed, many new changes have been proposed by a variety of authors, particularly in regard to some new fossil and primitive modern lineages (e.g., Grimaldi *et al.*, 2005; Pohl and Beutel, 2005; Pohl *et al.*, 2005; Bravo *et al.*, 2009). Despite this fervor of activity, there has been no revised means through which to identify this diversity. Accordingly, we provide a revised key to the living and fossil families of Strepsiptera. The key is provided here to permit identification not only of recently proposed families (Pohl and Beutel, 2005; Pohl *et al.*, 2005; Bravo *et al.*, 2009), but also a family newly established herein. It has been long known that the Cretaceous genus *Cretostylops* Grimaldi and Kathirithamby is representative of a distinct group of extinct strepsipterans (e.g., Grimaldi *et al.*, 2005; Bravo *et al.*, 2009), but the group has never been formally established under the ICZN. Thus, we herein establish the family and incorporate this group into the newly expanded key. The family includes only the species *Cretostylops engeli* Grimaldi and Kathirithamby, from the mid-Cretaceous deposits of northern Myanmar (Grimaldi *et al.*, 2005).

A few additional changes are incorporated herein. Protoelencholacidae was erected by Pohl & Beutel (2005) to include the fossil *Protoelencholax schleei* Kinzelbach (1979), but the differences given – slender mandibles with medially-crossing, blade-like apices and two tarsomeres – are typical characters of Elenchidae and do not sufficiently distinguish the group. We therefore retain this species within Elenchidae. Also, based on the results of a recent molecular analysis, Callipharixenidae was placed in the Halictophagidae and Lychnocolacidae was recognized as a family distinct from the Myrmecolacidae (McMahon *et al.*, 2011). These alterations of the higher classification are also incorporated herein.

Throughout, groups known only as fossils are denoted with a dagger (†) and other families that are also recorded from the fossil record are mentioned as such. The current classification of the order is summarized in Table 1.

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Table 1. Hierarchical classification of Strepsiptera.

Order Strepsiptera Kirby
Family †Protoxenidae Pohl <i>et al.</i>
Family †Cretostylopidae Kathirithamby & Engel
Suborder Mengenillidia Kinzelbach
Family †Mengeidae Pierce
Family Bahiixenidae Bravo <i>et al.</i>
Family Mengenillidae Hofeneder
Suborder Stylopidia Kinzelbach
Family Corioxenidae Kinzelbach (+1 fossil species)
Infraorder Stylopiiformia Kinzelbach
Family Myrmecolacidae Saunders (+13 fossil species)
Family Lychnocolacidae Bohart
Family Stylopidae Kirby (+2 fossil species)
Family Xenidae Saunders
Family Bohartillidae Kinzelbach (+3 fossil species)
Family Elenchidae Perkins (+1 fossil species)
Family Halictophagidae Perkins

Key to Families of Strepsiptera
(Adult males, living & fossil)

1. Tarsi 5 segmented, pretarsus with pair of strong claws 2
- Tarsi 2–5 segmented; pretarsus with neither claws nor sensory spots; or tarsi 5-segmented and pretarsus with a pair of very weak claws, or a single claw and with sensory spots 6
- 2(1). Antenna 8 segmented; mandibles large and robust, triangular shaped, with broad base and of generalized chewing structure. 3
- Antenna 6–7 segmented; mandibles, if present, small, narrow, and blade-like. 5
- 3(2). Galeal lobe at base of maxillary palp present †Protoxenidae
- Galeal lobe at base of maxillary palp absent 4
- 4(3). Protrochanter and profemur free †Cretostylopidae, n. fam.
- Protrochanter and profemur fused (Host: unknown). Bahiixenidae
- 5(2). Prementum free, with short palps; hind wing CuA₁ short, extending about to middle of wing; front branch of MA absent; antenna 7-segmented, with flabella on antennomeres III and IV †Mengeidae
- Prementum fused to hypopharynx; hind wing CuA₁ extending almost to edge of wing; MA strongly developed with anterior branch; antenna 6-segmented, with flabella on antennomeres III to IV or III to V (Host: *Zygentoma*: Lepismatidae) Mengenillidae
- 6(1). Mandibles absent; tarsi 4–5 segmented, pretarsus with a pair of claws, or a single claw, or tarsi 4 segmented and pretarsus without claws; antenna 5–7 segmented, with flabella on antennomeres III–IV or III–V (Host: Hemiptera: Cydnidae, Blissidae, Pentatomidae, Lygaeidae, Coreidae) (also known from fossils) Corioxenidae
- Mandibles present, narrow and blade-like; tarsi 2–4 segmented, pretarsus without claws; antenna 4–7 segmented, with flabella on antennomeres only on III or IV, or III & IV, or III to V, or III, V, & VI, or III to VI. 7

- 7(6). Tarsi 3 segmented (Host: Hemiptera: Cercopidae, Cicadellidae, Coreidae, Delphacidae, Eurybrachyidae, Flatidae, Fulgoridae, Issidae, Membracidae, Pentatomidae, Tettigometridae; Diptera: Tephritidae; Orthoptera: Tridactylidae; Blattaria: Blattellidae) Halictophagidae
 —. Tarsi 2 or 4 segmented 8
- 8(7). Tarsi 2 segmented; antenna 4 segmented (Host: Hemiptera: Delphacidae, Dictyopharidae Eurybrachidae, Flatidae, Fulgoridae, Ricaniidae) . . . Elenchidae
 —. Tarsi 4 segmented; antenna 5–7 segmented 9
- 9(8). Antennae 7 segmented, with flabella on antennomeres III, V, and VI; maxillary base five times longer than palpus (Host: unknown) (also known from fossils) Bohartillidae
 —. Antennae 4–7 segmented, with flabellum on antennomere III only; maxillary base equal to, or smaller than palpus 10
- 10(9). Antenna 4 or 6 segmented, with flattened flabella 11
 —. Antenna 7 segmented, with rounded flabella 12
- 11(10). Antenna 6 segmented, metathorax with spoon-shaped sclerite (Host: Hymenoptera: Andrenidae, Colletidae, Halictidae) (also known from fossils) Stylopidae
 —. Antenna 4 segmented, metathorax with no spoon-shaped sclerite (Host: Hymenoptera: Masaridae, Mutillidae, Sphecidae, Vespidae) Xenidae
- 12(10). Wing venation with CuA_1 and CuA_2 present (Host: unknown)
 Lychnocolacidae
 —. Wing venation with only CuA_1 (Host: Males – Hymenoptera: Formicidae: Dolichoderinae, Ecitoninae, Formicinae, Myrmicinae, Pseudomyrmecinae, Ponerinae / Females – Orthoptera, Mantodea) (also known from fossils) Myrmecolacidae

Systematic Paleontology

Cretostylopidae Kathirithamby & Engel, new family

TYPE GENUS: *Cretostylops* Grimaldi and Kathirithamby in Grimaldi *et al.* (2005).

DESCRIPTION: **Male.** Body size small (ca. 1.5 mm, much smaller than the massive *Protoxenos* Pohl *et al.* which is ca. 7 mm); antenna 8-segmented, with 6 flabella on antennomeres III–VIII (a plesiomorphic condition for Strepsiptera, similar to that of *Protoxenos*); bases of antennae situated between compound eyes; ommatidia small, not separated by microtrichia; mandibles robust, sclerotized, large, and triangular (a distinctive plesiomorphy shared with *Protoxenos*, and unlike the mandibles in *Bahiaxenos* which are large but not as robust as other Recent Strepsiptera in which they are narrow, small, and blade-like); maxillary lobe lacking galeal lobe (as in all other Strepsiptera except *Protoxenos*); labrum reduced (also present in *Protoxenos* but absent in all other strepsipterans except *Mengea* Grote and the Australian *Mengenilla* Hofeneder); tarsi long and pentamerous; pretarsus with a pair of claws, setae absent (present in *Protoxenos* and all basal extant groups such as Bahiaxenidae and Mengenillidae); pseudohalters (forewings) large; hind wings with well-developed R_1 and R_4 , with pterostigma-like thickening; protrochanter and profemur free (unlike all extant Strepsiptera).

Female. Unknown.

COMMENTS: The earliest known Strepsiptera and the first described from the Mesozoic is *C. engeli* (Grimaldi *et al.*, 2005; Grimaldi and Engel, 2005), preserved in mid-Cretaceous amber from Myanmar. All phylogenetic analyses which included both fossil and modern families recover the extinct genus *Protoxenos*, in middle Eocene Baltic amber, as sister to all other Strepsiptera, with *Cretostylops* the next lineage to diverge (Grimaldi *et al.*, 2005; Pohl and Beutel, 2005; Bravo *et al.*, 2009; Hünefeld *et al.*, 2011). Although *Cretostylops* is older (99 Ma) than *Protoxenos* (45 Ma), the latter is clearly supported as the most basal group and must have been an ancient relic lineage even by the Paleogene.

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