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The Tethepomyiidae, a new family of enigmatic Cretaceous Diptera

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ABSTRACT

Two new species and a new genus of unusual Diptera are described in amber from the late Early Cretaceous (c. 110 myo) of northern Spain: *Tethepomyia buruhandi*, n. sp. and *Tethepomima holomma* n. gen., n. sp. These and *Tethepomyia thauma* Grimaldi and Cumming, 1999 (mid-Cretaceous: New Jersey, USA) are placed into the new family **Tethepomyiidae**, characterized by very large eyes, reduced mouthparts, a highly reduced antennal flagellum, and greatly reduced venation. Extreme specialization obscures relationships, but available evidence indicates these are nematocerous flies. A prior proposal that they belong to the brachyceran family Eremochaetidae, known from the Late Mesozoic of central Asia, is discussed and refuted.

KEY WORDS: Tethepomyiidae, Eremochaetidae, Álava amber, Cretaceous, morphological reduction.

INTRODUCTION

An enigmatic, gracile fly merely 1.6 mm in length, *Tethepomyia thauma* Grimaldi and Cumming, was described on the basis of a single specimen preserved in 90 myo amber from New Jersey (Grimaldi and Cumming, 1999). The relationships of this fly were entirely obscured by numerous autapomorphic features, including highly reduced venation, lack of tibial spurs and macrosetae, vestigial mouthparts, and – most significantly – a flagellum reduced to a single U-shaped article. Despite the reduced antenna, it was surmised that *Tethepomyia* was nematocerous, based on the structure of the male genitalia, which are somewhat flattened and have well-developed but simple gonocoxae and gonostyli. Here we report two additional species related to *T. thauma*, from Cretaceous amber of Álava, northern Spain. One species is extremely similar to *T. thauma*; the other species has a distinctively more plesiomorphic venation, which provides more information on the relationships of this enigmatic group.

The Álava outcrop is in the Sierra de Cantabria, near the village of Peñacerrada, approximately 30 km south of Vitoria-Gasteiz. It occurs in the Escucha Formation, (previously cited as Nograro Fm.) which is well dated to upper Aptian - middle Albian (ca. 110 myo). The Escucha Formation amber is abundant and highly fossiliferous, with some 22 orders of hexapods and 17 families of Diptera found thus far. The stratigraphy, taphonomy, and diversity of organismal inclusions are given in Delclòs et al. (2007). This amber deposit is of exceptional paleoentomological significance since it is the only other diverse assemblage of Lower Cretaceous insects in amber besides those from Lebanon and possibly Myanmar, an Albian or Cenomanian age of the latter being controversial. All amber fossils are deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz.

SYSTEMATIC PALAEONTOLOGY

Order: Diptera Linnaeus, 1758

Family Tethepomyiidae fam. nov.

Diagnosis. Small nematocerous flies with head spherical or nearly so, eyes very large (holoptic in males, females unknown); antennae highly reduced (all but scape, pedicel, and basal flagellomere lost); mouthparts highly reduced; wing venation highly reduced to 3 or fewer branches of R, one branch of M, and a forked CuA with a long stem present or entirely lost; mesothorax short and compact, with few or no macrosetae; abdomen long and slender; male genitalia large, not dorso- or lateroflexed (projected posteriad), with simple gonostyli and gonocoxae; legs with tibial spurs or macrosetae very small or missing. Known only in Cretaceous amber from New Jersey, USA and Álava, Spain.

Type Genus. *Tethepomyia* Grimaldi and Cumming, 1999.

GENUS: ***Tethepomyia*** Grimaldi and Cumming, 1999

Tethepomyia Grimaldi and Cumming, 1999: 6. By original designation. Type species: *T. thauma* Grimaldi and Cumming, 1999: 6.

Tethepomyia buruhandi sp. nov.

Figures 1-2

Etymology. From Basque, *buruhandi*, meaning "big headed."

Holotype. Male, MCNA 8821, from near Peñacerrada, Álava, Spain, Escucha Formation, Lower Cretaceous. It is preserved in a small piece of amber with a phlebotomine psychodid.

Diagnosis. Like *Tethopomyia thauma***,** with flagellum highly reduced to a single, U-shaped flagellomere; mouthparts vestigial; eyes large; venation highly reduced; legs without spurs or macrosetae. Distinguished from *T. thauma* by the larger eyes, occupying virtually entire head in dorsal and lateral view; antennal pedicel smaller, diameter only slightly more than that of reduced flagellum. Male genitalia much more narrow, dorsally with narrow,

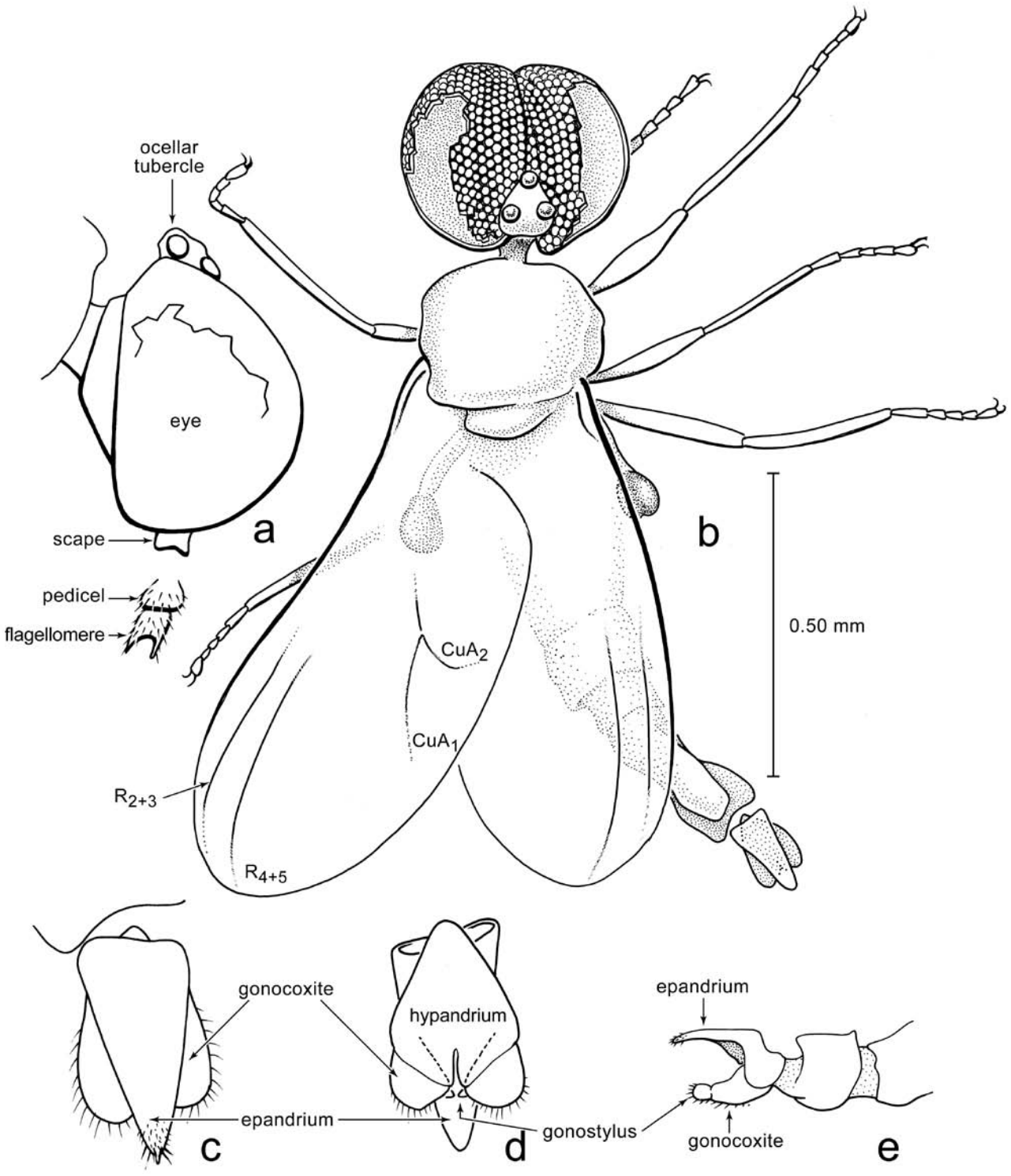

Figure 1. *Tethepomyia buruhandi*, sp. nov. a. Lateral view of head, with pedicel and basal flagellomere detached from base. b. Dorsal habitus, showing venation. c-e: Male genitalia. c. Dorsal view. d. Ventral view. e. Lateral view.

apically pointed epandrium (tIX); gonocoxae not distantly separated, nearly touching medially; gonostylus with apical tooth. Wing with venation less incomplete, with remnants of R2+3 and R4+5 and a short fork of CuA1 + CuA2.

Description. (Male only) Body length 1.56 mm; wing length 1.00 mm. HEAD: Large, spherical, occupied almost entirely by eyes in dorsal or lateral view (except for ocellar triangle, dorsally); eyes extensively holoptic, entire dorsal margins in contact except where separated by ocellar triangle; no differentiation of dorsal and ventral facets. Ocelli on small turbercle, raised slightly more than diameter of ocellus; no ocellar setae present; ocelli large, ca. 30 µm diameter. Mouthparts vestigial. Antennal scape pedestal-like; pedicel cup-shaped, diameter only slightly greater than flagellomere; flagellum reduced to single, U-shaped segment. Gena collar-like. THORAX: Mesonotum compact, 0.27 mm long, 0.38 mm wide; devoid of setae; scutellum small, length less than ¼ that of notum, without even apical setae. Legs virtually undifferentiated, without large setae, spines, or spurs; tibiae long, 1.3-1.6x length of tarsi; basitarsomere of each leg ca. twice the length of distal tarsomeres; pretarsal claws and pulvilli well developed, empodium pulvilliform. Wing completely hyaline; basal venation, if present, very obscure. No fine setulae on margin of wing. Vein C appears evanescent; a long vein (R2+3) incomplete, occuring on apical half (base evanescent); R4+5 parallel to this, with similar reduction; fork of veins CuA_1 + CuA_2 widely divergent, evanescent basally and apically (not meeting anal margin of wing, base of stem incomplete); CuA2 strongly curved toward anal lobe; anal lobe of wing well developed. Halter long, equal in length to notum; knob bulbous and pigmented. ABDOMEN: Long and thin. Male genitalia observable dorsally, ventrally, and laterally: Epandrium a long, triangular sclerite in dorsal view, length slightly less than 2x the width, with minute denticle at tip; gonocoxae large, well separated; gonostyli folded inwards, approximately one-third size of gonocoxae, with sclerotized tooth at apex; hypandrium with very narrow median notch on posterior margin.

Figure 2. *Tethepomyia buruhandi*, sp. nov. Photograph of the Holotype MCNA 8821. Scale bar 0.5 mm

Comments. The very close relationship of these two highly reduced dipterans is unquestionable, and indicates a distinctive taxon uniquely shared between the New Jersey and Álava amber faunas. Besides the features given above, other features of *T. buruhandi* sp. nov. shared with *T. thauma* are: tibiae long and slender, 1.3-1.6x the length of the tarsi, without large setae, spines, or spurs; scutum virtually bare; scutellum very small; wing with well developed anal lobe but not alula; and the abdomen long and slender. Each specimen is virtually the same size, indicating that the slightly less reduced venation of *T. buruhandi* sp. nov. is not due to a difference in size (small species often having extensive reduction in venation). Several features of the specialized, U-shaped basal flagellomere in *Tethepomyia* spp. indicate that the apical flagellomeres are naturally absent, not just lost as a result of preservation. These features are that apical flagellomeres are absent from both antennae of each specimen, there are no nearby remains of disarticulated flagellomeres, and there is no socket on the basal flagellomere into which flagellomere two would insert.

GENUS: ***Tethepomima*** gen. nov.

Type Species: *T. holomma*, sp. nov. Monotypic.

Etymology. Stem from *Tethepomyia*, and *–mima*, from the Greek for mimic.

Diagnosis. Similar to Tethepomyia in general body shape and proportions: head large, round, with huge eyes, mesothorax compact, halteres long, abdomen slender. Differs from Tethepomyia by the following features: male eyes extensively holoptic (including the postocciput), dorsal ommatidia slightly larger than ventral ones; antennal articles smaller, possibly with a minute flagellum or flagellomere; venation less incomplete, particularly the presence of veins R, Rs, basal cells of R, and presence of veins M and CuA. Margin of wing with fine setulae. Mesoscutum, mesoscutellum and legs with macrosetae; tibiae each with minute apical spur.

Comments. This species is clearly the basal one of the three, as based on the setation of the thorax, presence of tibial spurs, and the less incomplete venation.

Tethepomima holomma, sp. nov.

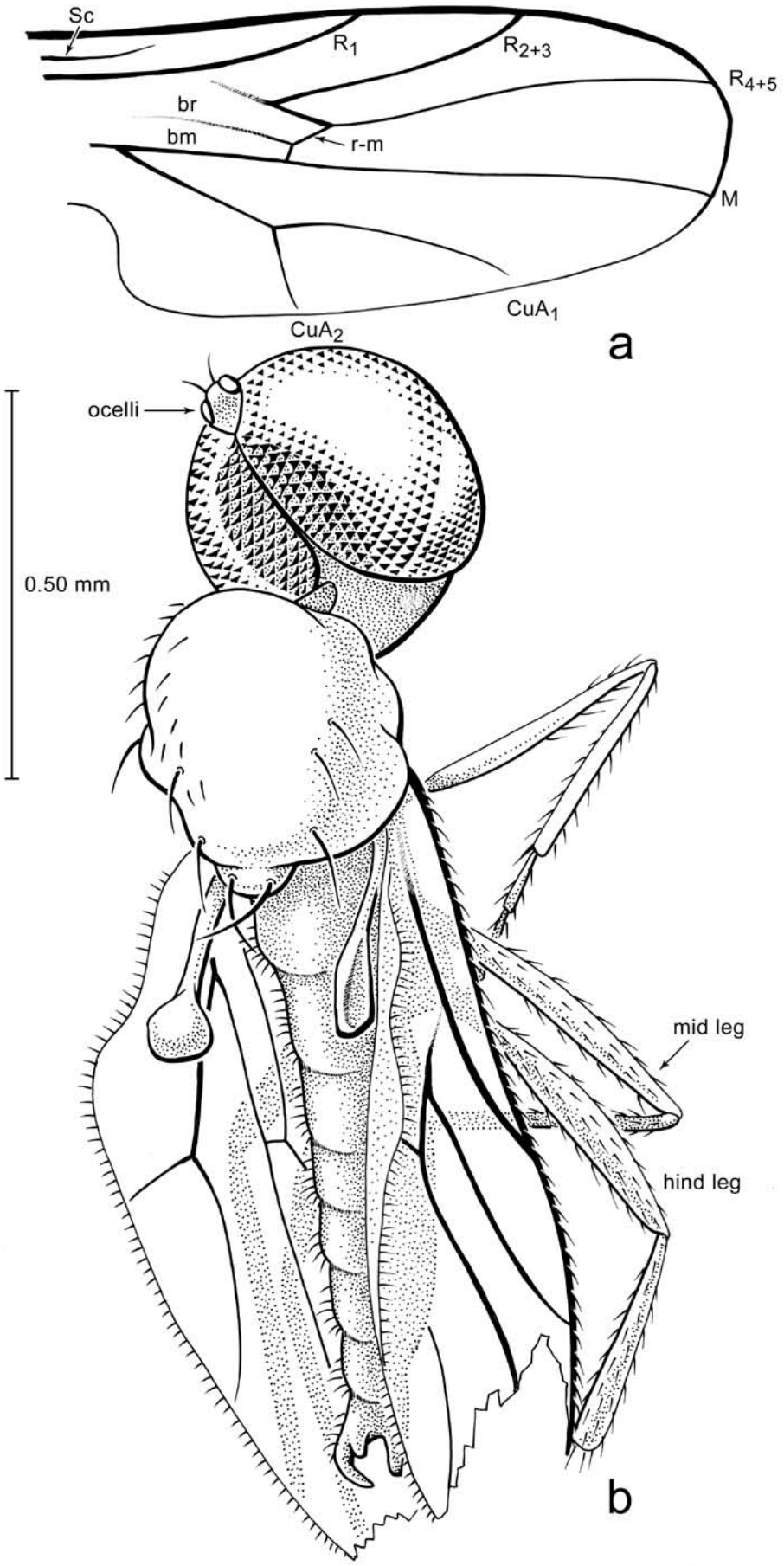

Figure 3. *Tethepomima holomma*, sp. nov. a. Wing, reconstructed from both wings. b. Dorsal habitus, oblique view.

Figure 3-4

Etymology. "All eyes," from the Greek *holos* for whole; and *omma,* eye.

Holotype. Male, MCNA 9915. From same locality as *T. buruhandi*. Specimen is in a chip of amber barely larger than the fly itself, 2 x 1 x 1 mm, embedded in epoxy and trimmed to a square 12 x 12 x 1.5 mm. The left half of the head is lost at the surface, and apices of the wings and some of the legs are lost. Otherwise, the fly is largely complete. Observation of microscopic details, such as the antennae and pretarsal pulvilli, are largely obscured by an occluding suspension of dark orange particles. Observing the venation requires intense oblique reflected and transmitted fiber optic light, as well as constant tilting of the specimen at various angles. Basal parts of the venation are particularly obscure, but the R veins can be confidently viewed, as is a forked CuA1-CuA2. Although size and preservation of the antennae make them difficult to observe, they seem to have a very small, fine, aristate style. Bases of the antennae (pedicel, basal flagellomere) are smaller than in *Tethepomyia*.

Diagnosis. As for genus.

Description. (Male only) A minute fly, body length 1.50 mm, wing 0.85 mm. HEAD: Large, spherical, occupied entirely by large, holoptic eyes. Holoptic condition extensive: occupying most of face and postocciput, with exception of small, raised ocellar tubercle on vertex. Postoccipital portion of eyes slightly concave. Dorsal 2/3 of eye with ommatidia slightly larger than ommatidia in ventral 1/3. Ocelli present, large, nearly contiguous; ocellar tubercle with pair of small setae. Mouthparts very small or vestigial. Antenna difficult to observe, but with cup-shaped pedicel and basal flagellomere, possibly with minute arista-like style (any segmentation is obscure). THORAX: Mesothorax compact, approximately long as is wide; scutellum very small, with pair of cruciate setae. Scutum with two pairs of small dorsocentral setae, pair of small notopleural setae, sparse and scattered acrostichals. Legs long and slender, with sparse macrosetae; each tibia apparently with very small apical spur. Halter with long, slender stem and round knob. Wing (see reconstructed venation): fairly broad, base wide, with well developed anal lobe. Vein Sc incomplete, apically evanescent, short (ca. 1/6th wing length); R1 short, apex reaches middle of wing; stem of Rs evanescent, apparently originating on distal half of R. Veins R2+3 and R4+5 simple. Cells br and bm present, divided by evanescent vein. Crossvein r-m short, oblique. M1 lost, M2 the only longitudinal median vein, virtually linear. CuA connected directly to stem of M; with asymmetrical fork (branch of CuA1 almost three times the length of CuA2). If CuP and/or A veins present, not apparent. Margin of wing with fine setulae. ABDOMEN: Slender, long, narrow, apex not reaching apex of wings. Genitalia with generalized gonocoxae and gonostyli; other details not apparent.

Figure 4. *Tethepomima holomma*, sp. nov. Photograph of the Holotype MCNA 9915. Scale bar 0.5 mm

DISCUSSION

The phylogenetic position of the Tethepomyiidae is perplexing, since the great modifications of the antennae and wings makes it difficult to definitively decide whether these flies are even nematocerous or Brachycera. Fortunately, the less reduced venation of *Tethepomima* and to some extent *T. buruhandi* allows some inference. Cells br and bm are widespread in nematocerous and basal Brachycera flies, but structure of the br and bm cells in *Tethepomima* is most similar to that in some empidoids, such as *Symballophthalmus* and *Micrempis*, including the way in which the R veins are connected to the br cell. However, the forked CuA vein (CuA1 + CuA2) that occurs in *Tethepomima* and *Tethepomyia buruhandi* is perhaps the most significant feature: such a forked CuA is found repeatedly in nematocerous flies and never in Brachycera. (We are following the vein nomenclature in the Manual of Nearctic Diptera, volume 1, in our identification of the posterior fork as CuA1–CuA2, although we acknowledge that some paleoentomologists interpret CuA1 as M3+4). Moreover, the typical (but not universal) brachyceran feature of a cup cell is missing in Tethepomyiidae, which is formed by the apical convergence of veins CuA2 and A1. The male genitalia of the two species of *Tethepomyia* are best preserved, revealing a simple, plate-like epandrium (tIX), not the capsule found in Brachycera. Gonocoxites and gonostyli are simple and large, and not integrated into tIX (or even reduced) as is typical amongst Brachycera. Moreover, a

sclerotized tooth at the apex of the gonostylus, observed in *T. buruhandi*, appears repeatedly in various nematocerous flies. Lastly, the male genitalia are directed posteriad, not dorso- or ventroflexed as in many Brachycera. All these features indicate that the Tethepomyiidae is a group of nematocerous flies.

Mostovski (1999) stated that "eremochaetids from Alavese and New Jersey ambers (Grimaldi and Cumming, 1999) may be allocated to a new subfamily of their own." Without referring to particular specimens, he presumably meant the tethepomyiids described here and previously (Grimaldi and Cumming, 1999), since these are the only Diptera in these deposits that have a general habitus similar to the family Eremochaetidae. Eremochaetidae is an extinct family of seven genera and approximately 10 species of brachyceran flies, known entirely as compression fossils from the Late Jurassic and Early Cretaceous of eastern and central Asia (Ussatchev, 1968; Kovalev, 1986, 1989; Ren and Guo, 1995; Mostovski, 1997). Eremochaetidae, indeed, are very similar to *Tethepomyia* and *Tethepomima*, with a significant list of similarities: a spherical head with very large eyes; small to highly reduced antennae; small, compact, thorax; long, slender abdomen; and legs with minute or no tibial spurs.

There are, however, also significant differences between the two families. First, eremochaetids are nearly an order of magnitude larger in size (up to 15 mm, instead of 1.5mm body length), but this is arguably a bias of preservation in rock versus amber. In eremochaetids the apex of the abdomen extends well beyond the apex of the wings, unlike *T. holomma* and *T. buruhandi*. Also, eremochaetids have an antennal flagellum that is either a thick, segmented style (e.g., *Pareremochaetus minor* Ussatchev) or, more commonly, a minute arista. The possibility that the flagellum of *T. holomma* may be in the form of a minute arista or style adds to Mostovski's argument, but otherwise the antennal reduction in tethepomyiids is significantly different. Also, there occurs remarkable convergence with Brachycera in the antennal structure of some extinct nematocerans (e.g., Archizelmiridae: Grimaldi et al., 2003). By far the most substantial basis for evaluating the identity of tethepomyids involves the wing venation of *T. holomma*, and in this respect the family differs completely with Eremochaetidae. The latter family has a complete wing venation composed of: a long Sc (vs. short, incomplete); long R veins that are Żto ¾ the wing length (vs. ½ the length); vein R4+5 that usually has a small terminal fork (vs. none); the discal cell is always present, and sometimes an additonal, smaller cell adjacent to the discal (m3?) (vs. both cells absent); three M veins present (vs. one); a large cup cell (vs. none); a slender wing base with the anal lobe lost (vs. broad and with anal lobe); and CuA2 is lost, let alone it being forked with CuA1 as in tethepomyiids. In short, the venation of eremochaetids is typical of lower Brachycera, and that of the Tethepomyidae is not. It could be argued that the diminutive size of tethepomyiids is responsible for the evolution of extreme venational reduction, as repeatedly occurs in insects. However, this argument fails since there is virtually no difference in size between *T. holomma*, which has a relatively complete venation, and *T. thauma* which has extremely reduced venation. Other, but minor, features inconsistent between the two families regard structure of the legs and ocelli. In those Eremochaetidae where the legs have been sufficiently preserved, the hind femur is significantly (ca. 2x) thicker than the tibia, and ocelli were either not reported, not observed, are minute, or all of these. Unfortunately, no female tethepomyiids have yet been found in amber, as this might finally resolve the issue since Eremochaetidae have a very distinctive sting-like, aculeate oviscape (Kovalev, 1986; Mostovski, 1997). This feature has led some to hypothesize that eremochaetids were endoparasitoids, since other flies with similar oviscapes (i.e., Cryptochaetidae) have such a life cycle.

While a relationship of Tethepomyiidae with the extinct family of basal Brachycera, the Eremochaetidae, is an intriguing hypothesis, we feel that almost all available evidence contradicts this placement and even indicates these are wholly unrelated families. The extent of their morphological convergence, nonetheless, is remarkable. It is hoped that further new material will provide more detailed information on the relationships of this intriguing extinct lineage of flies.

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