Brachyceran Diptera (Insecta) in Cretaceous ambers, Part IV, Significant New Orthorrhaphous Taxa

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Abstract
Thirteen species of basal Brachycera (11 described as new) are reported, belonging to nine families and three infraorders. They are preserved in amber from the Early Cretaceous (Neocomian) of Lebanon, Albian of northern Spain, upper Albian to lower Cenomanian of northern Myanmar, and Late Cretaceous of New Jersey USA (Turonian) and Alberta, Canada (Campanian). Taxa are as follows, with significance as noted: In Stratiomyomorpha: Stratiomyidae (Cretaceogaster pygmaeus Teskey [2 new specimens in Canadian amber], Lysistrata emerita Grimaldi & Arillo, gen. et sp. n. [stem-group species of the family in Spanish amber]), and Xylomyidae (Cretoxyla azari Grimaldi & Cumming, gen. et sp. n. [in Lebanese amber], and an undescribed species from Spain). In Tabanomorpha: Tabanidae (Cratothorax newyorkensis Grimaldi, sp. n., in New Jersey amber). In Muscomorpha: Acroceridae (Schlingeromyia minuta Grimaldi & Hauser, gen. et sp. n. and Burmacyrta rasmithi Grimaldi & Hauser gen. et sp. n., in Burmese amber, the only definitive species of the family from the Cretaceous); Mythicomyiidae (Microburmyia analvena Grimaldi & Cumming gen. et sp. n. and M. veanalvena Grimaldi & Cumming, sp. n., stem-group species of the family, both in Burmese amber); Apsilocephalidae or near (therevoid family-group) (Kumaromyia burmitica Grimaldi & Hauser, gen. et sp. n.)
[in Burmese amber]); Apystomyiidae (*Hilarimorphites* burmanica Grimaldi & Cumming, sp. n. [in Burmese amber], whose closest relatives are from the Late Jurassic of Kazakhstan, the Late Cretaceous of New Jersey, and Recent of California). Lastly, two species belonging to families incertae sedis, both in Burmese amber: Tethepomyiidae (*Tethepomyia* zigrasi Grimaldi & Arillo sp. n., the aculeate oviscapt of which indicates this family was probably parasitoidal and related to Eremochaetidae); and unplaced to family is *Myanmyia asteformia* Grimaldi, gen. et sp. n., a minute fly with highly reduced venation. These new taxa significantly expand the Mesozoic fossil record of rare and phylogenetically significant taxa of lower Brachycera.

**Keywords**

amber, fossils, flies, Lebanon, Myanmar, New Jersey, Spain

**Introduction**

This is the fourth paper in a series devoted to the Cretaceous record of brachyceran flies preserved in amber, the original work being a treatment of orthorrhaphans and Cyclorrhapha (Grimaldi and Cumming 1999), and the second and third being treatments of the enigmatic families Tethepomyiidae (Grimaldi and Arillo 2008) and Chimeromyiidae (Grimaldi et al. 2009). The present paper deals specifically with additional records and taxa of orthorrhaphan (“basal”) Brachycera, while separate papers will deal with the empidoids and Cyclorrhapha. Rhagionidae will also require separate study, given their confusing Mesozoic diversity and relationships. Updates to the original 1999 monograph are necessary since additional Brachycera have been uncovered in all of the major Cretaceous amber deposits dealt with then (i.e., New Jersey, western Canada, Lebanon), but, most importantly, diverse Brachycera have been discovered in amber from the Early Cretaceous (Albian) of northern Spain (Alonso et al. 2000; Delclòs et al. 2007; Peñalver and Delclòs 2010) and the Late Albian to Early Cenomanian of northern Myanmar (Grimaldi et al. 2002; Cruikshank and Ko 2003).

**Materials and methods**

Specimens were prepared according to the protocols described in Nascimbene and Silverstein (2000) and, for the Spanish amber, in Corral et al. (1999). After rough pieces were screened for inclusions, preliminary preparation to view the inclusion was done by grinding and polishing one or more flat surfaces onto the piece using emory papers of decreasing grit sizes on a wet flat lapidary wheel. Then each piece was embedded in epoxy under vacuum in order to impregnate cracks within the amber, which improved transparency and strengthened the piece for trimming (using a water-fed diamond saw with a very thin blade) and more grinding and polishing. Eventually, depending on the size and number of inclusions, the preparations were several millimeters in thickness, such that it could be mounted between a microscope slide and coverslip using a drop of glycerin on each of the two opposing surfaces. The inclusions were examined with
a stereomicroscope and with compound microscopy at 40 – 400× using both reflected and transmitted light.

**Collection repositories of specimens are the following:**

| Code | Repository                                      |
|------|------------------------------------------------|
| AMNH | American Museum of Natural History, Entomology Section, New York. |
| AZ   | Azar Collection, presently housed in Musée national d’Histoire naturelle, Paris. |
| KU   | University of Kansas Division of Entomology, Natural History Museum, Lawrence. |
| MCNA | Museo de Ciencias Naturales, Álava, Spain. |
| NHML | Natural History Museum, London. |
| RTMP | Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada. |

It is a pleasure for the senior author to dedicate this paper to Kumar Krishna, world authority on the Isoptera, close colleague and friend.

**Infraorder Stratiomyomorpha**

This lineage comprises three living families, the Xylomyiidae (cosmopolitan; approximately 134 species in four genera), Stratiomyidae (cosmopolitan; 2651 species in 375 genera as of the year 2000 [Woodley 2001]), and Pantophthalmidae (Neotropical; approximately 20 species of very large flies in two genera). Xylomyids and stratiomyids are closely related based on the shortened vein R₁, Rs branching off of R distally, and the stem of Rs very short, as well as the larval cuticle with calcareous “warts” and pupariation taking place within the last larval cuticle. Pantophthalmids appear to be the sister group to the other two families (Sinclair et al. 1994; Yeates 2002; Wiegmann et al. 2011). Pantophthalmids have no fossil record, and the other two families have very limited Mesozoic fossil records, reviewed below. A fourth family of the infraorder is the extinct Zhangsolvidae, originally erected by Nagatomi and Yang (1998) for *Zhangsolva cupressa* from the Early Cretaceous Laiyang Formation in China (Zhang et al. 1993). The original description of *Zhangsolva* included obvious errors, and the antenna probably has no more than eight flagellomeres (the groundplan of Brachyera); some artifacts were also reported as venational features in the original report. There are two well preserved zhangsolvid species in Early Cretaceous limestone from the Crato Formation of Brazil, *C. macrorrhyncha* (Mazzarolo and Amorim, 2000), and *Cratomyoides cretacicus* Wilkommen (in Martill et al. 2007). Both of these species have a long, jutting proboscis and a venation very similar to that *Zhangsolva; Cratomyoides* is separated from *Cratomyia* on the basis of minor features and probably should be synonymized with the latter genus. Based on the long proboscis, hovering-type of venation, and phylogenetic position, the three species of Zhangsolvidae probably fed from flowers (Grimaldi and Engel 2005).
Family Stratiomyidae

Genus Cretaceogaster
http://species-id.net/wiki/Cretaceogaster

*Cretaceogaster* Teskey 1971: 1660. Type species: *C. pygmaeus* Teskey 1971: 1660; Woodley 1986 (redescription, placement); Grimaldi and Cumming 1999: 17–19 (redescription, new specimens).

*Cretaceogaster pygmaeus* Teskey 1971: 1660.

**Remarks.** We were able to study two additional specimens of this very primitive genus of stratiomyid, both in Canadian amber collected by Ted Pike from Grassy Lake, Alberta (Campanian) (Pike 1995), housed in the RTMP.

RTMP 96.9.1117: Amber is a typical clear, dark yellow with reddish flow lines; it also contains a small spider. The piece is a cylindrical runnel 12 × 4 × 2 mm, with the fly preserved near the middle, which was embedded in epoxy at the AMNH and trimmed to 9 × 13 × 4 mm (including epoxy) for better observation. The fly is laterally very flattened, especially the thorax, and is a male (though details of the genitalia are not observable). Unfortunately, the apex of the mid tibia cannot be observed in detail, so the apparent absence of tibial spurs is uncertain. Wing is slightly distended in length, but otherwise the venation is very similar to *C. pygmaeus*.

RTMP 96.9.1230: Fly is also preserved in a cylindrical runnel of amber, 7 × 3 (diam.) mm, and embedded in epoxy for careful trimming. The fly is lying at the rounded end of the runnel, with its dorsal surface against the surface of the flow. The thorax is partly decayed and wing venation is obscured. The antenna and mouthparts are visible in ventral view. Specimen is a male, but its genitalic details are also not observable. Mid tibia appears to have a small apical spur, contrary to the original description of the species but in agreement with Woodley (1986: 380).

*Lysistrata* Grimaldi & Arillo, gen. n.
urn:lsid:zoobank.org:act:C038F6C9-1BFF-49D2-A756-A6235259B6A9
http://species-id.net/wiki/Lysistrata

**Diagnosis.** Antennal flagellum submoniliform, with approximately 7 short flagellomeres tapered in width apicad; articulation between basal 3 flagellomeres faint. Protibia lacking spurs; mesotibia with two short apical spurs (c. 50 µm length). Metatibia probably with one pair of short apical spurs. Vein Rs branches from R₁ in the distal third of vein R. Stem of R₄₊₅ straight, R₄ curved basally, long and subparallel to R₅. Cell d long and narrow, length approximately 3.5× the width; cell m₁ absent.

**Type species.** *Lysistrata emerita*, sp. n., by present designation.
Etymology. From the Greek, Λυσιστράτη, meaning “army disbander”, after the comedy by Aristophanes and in reference to the common name for Stratiomyidae, or “soldier flies”. Feminine.

Discussion. Lysistrata is clearly within the Stratiomyomorpha, and appears closely allied with Stratiomyidae on the basis of the radial branching. The presence of two minute spurs on the mesotibia, and probably a short pair on the metatibia is indicative of either Stratiomyidae or Xylomyidae. A few Recent stratiomyids have a minute apical spur on the mesotibia, whereas xylomyids have either a 0–2–2 or 0–2–1 tibial spur formula. Pantophthalmids have one or two spurs on the mesotibia only, but are distinct from the other two families by the longer branches of R₁ and Rs.

The Recent and primitive genus Parhadrestia James (consisting of two species from Chile) shares some similarities with Lysistrata, both of them possessing a long R₄ vein curved only at the base and with the main branch only slightly divergent from R₁. The genus Montsecia Mostovski, 1999, preserved as a compression in Early Cretaceous (Barremian) limestone of Montsec, Lérida Province, Spain (originally and incorrectly placed in the subfamily Beridinae) also has the fork of R₄+R₅ quite long. This long fork may be a plesiomorphic feature, seen for example in Rhagionidae and Spaniidae.

Lysistrata differs plesiomorphically from Parhadrestia by the following: antenna multi-articulate; wing longer, narrower; R₂+₃ slightly longer and gradually sloped to C; apex of R₂+₃ not close to the apex of R₁; R₃ and M₁ slightly divergent instead of parallel; M₁, M₂, and CuA₁ not as divergent (a condition shared with Montsecia); cell d much longer, its length approximately 3× the width (vs. 2× the width in Montsecia and 1.5× the width in Parhadrestia; in most Recent stratiomyids cell d is quite small); CuA₂ more sloped toward CuP (e.g., apex of cell cup acute, instead of truncate [similar to Montsecia], although an acute cell cup is considered apomorphic by Woodley [2001]). In Montsecia the base of M is weak, whereas it is well developed in Lysistrata. Lysistrata has two apomorphic features: small female abdominal segments 6 and 7, which telescope within the proximal ones (in the basal Recent subfamilies Parhadrestiinae, Chiromyzinae and Beridinae segments 6 and 7 are large [Woodley 2001]); also, vein M₃ is lost. Loss of this vein occurs in all Parhadrestiinae and Pachygastrinae, and is frequently absent in Chiromyzinae and Beridinae (Woodley 2001). Absence of M₃ may actually be a ground-plan feature of Stratiomyidae.

The oldest fossil stratiomyiid is Montsecia martinezdelclosi Mostovski (1999), from the same outcrop that yielded several larvae believed to be stratiomyiids (Whalley and Jarzembski 1985). According to Mostovski (1999), several undescribed stratiomyiids are known from Jurassic and Cretaceous outcrops of Kazakhstan and Russia, although none has as yet been described. Gigantoberis liaoningensis, described as a stratiomyiid by Huang and Lin (2007) from the Early Cretaceous of Liaoning, China, was shown by Zhang (2009) not to belong to this family, which Huang acknowledges (pers. comm. to AA, 2010). The only other Cretaceous stratiomyiids are Cretaceogaster pygmaeus (Teskey 1971; Grimaldi and Cumming 1999; herein vide supra), an incomplete and undescribed species in Turonian-aged amber from New Jersey USA (Grimaldi and Cumming 1999), and the very well-preserved Lysistrata emerita, described below and which is very basal in the family. Diverse
Lysistrata emerita Grimaldi & Arillo, sp. n.
urn:lsid:zoobank.org:act:FD339789-7504-41CB-832A-23238FC6675A
http://species-id.net/wiki/Lysistrata_emerita

Fig. 1

Diagnosis. As for the genus.

Description. Body length 5.75 mm. Head length 0.60 mm. Specimen well preserved, but only visible in lateral view. Head slight distorted, with right antenna slightly separated from base. Eyes bare, large, covering most of head; facets not differentiated. Ocellar triangle not visible. Antenna submoniliform, with approximately 7 short flagellomeres tapered in width distad (articulations between 3 basal flagellomeres faint, number of articles difficult to discern); length of antenna approximately equal to length of head; length of flagellum 3× that of scape + pedicel combined. Distal flagellomere distinctly longer and narrower than more basal ones. Palpi reduced, segmentation not discernable; labellum well developed. Thorax: Mesonotum short and compact, finely pilose dorsally, without macrosetae. Scutellum without spines. Surface of notum slightly metallic and foveolate. All legs preserved; protibia lacking spurs; mesotibia with two apical spurs (50

Figure 1. a, b Lysistrata emerita Grimaldi & Arillo, gen. et sp. n (Stratiomyidae) in Albian amber from Spain. Holotype, MCNA 12698 a lateral view b Antenna (scale bar 0.25 mm).
µm long); probably one short apical spur on metatibiae. Length of hind basitarsomere equal to that of tarsomeres 2–5. Wing length 3.05 mm, width 0.75 mm; hyaline, vein Sc straight, length approximately 0.45× wing length, complete. Lengths of costal section of wing between apices of R_{2+3} and R_{1} equal to that between R_{1} and Sc. R_{2,3} arising distant from r-m. R_{4,5} straight, R_{4} curved at base, long and subparallel to R_{3}. Veins M_{1} and M_{2} separated at discal cell. Cell m_{3} absent, vein M_{3} either absent or fused to CuA_{1}. Abdomen elongate; basal 4 or 5 segments large and wide; apical 5 segments narrow and telescoping. Cercus composed of 2 segments, basal segment longer than apical one.

**Type.** Holotype, female, MCNA 12698, SPAIN: Alava, Peñascerrada I (Moraza), Escucha Formation, Lower Cretaceous (Albian). Deposited in MCNA. Specimen is well preserved in a clear piece of amber 10 × 7 × 1.5 mm, partially missing the left side of the thorax and the left wing; the amber is embedded in epoxy 15 × 13 × 2 mm. An empidoid fly (Microphorinae) is present as a syn inclusion.

**Etymology.** From the Latin noun, *Emeritus*, a name given to retired Roman soldiers, used here in reference to this long-retired (i.e., extinct) species.

**Family Xylomyiidae**

*Cretoxyla* Grimaldi & Cumming, gen. n.

urn:lsid:zoobank.org:act:EB99B611-9DD4-4B20-A808-02847EC2188D

http://species-id.net/wiki/Cretoxyla

**Diagnosis.** Antenna thick, greatest width (in middle) 0.25× total length, with apparently 7 flagellomeres; protibia without apical spur; most distinctive features are in venation, which distinguishes this genus from other Mesozoic xylomyids by: vein M (separating cells br and bm) weak; cell m_{3} very small, width and length approximately half that of cell d (these are of equivalent size in other xylomyids, or m_{3} is slightly smaller), and, very distinctively, vein R_{2+3} is uniquely lost.

**Type species.** *Cretoxyla azari* sp. n., by present designation.

**Etymology.** From *Cretaceous*, and *Xylomyidae*.

**Discussion.** The closed wing cell m_{3} is a feature also seen in some Xylophagidae. *Cretoxyla*, however, apomorphically has no protibial spur (as in Stratiomyomorpha) and plesiomorphically does not have a reduced alula (a greatly reduced alula occurs in the Xylophagidae). The extent of vein C, particularly whether it extends only to the apex of M_{1} or M_{2} (Woodley 1986: 1377), unfortunately cannot be checked since the apical quarter of the wing is lost. Vein C is definitely not circumambient. Other features that are important for xylomyid relationships that cannot be observed in the incomplete fossil are the number of palpal segments (1 vs. 2), presence of denticles on the ventral surface of the hind femur (e.g., *Solva* Walker), and various male and female genitalic structures.

The oldest fossil record of Xylomyiidae is *Xylymyia [sic] sheherbakovii* Mostovski from the Upper Jurassic (Karabastau Formation) of Kazakhstan (Mostovski 1999). Zhang and Zhang (1993) indicated that *Mesosolva* Hong and *Prosolva* Hong, also
described as xylomyids from the Upper Jurassic of China, belong in another lower brachyceran family. Undescribed Cretaceous xylomyids are from the Upper Cretaceous amber of Siberia (Zherikhin and Sukacheva 1973), and an incomplete specimen of an undescribed species in Spanish amber (vide infra), so Cretoxyla is the oldest Cretaceous xylomyid (Early Cretaceous, Neocomian). Tertiary fossil xylomyids are Solva inornata Melander, 1949 and Xylomya moratula Cockerell, 1914 in late Eocene shale from Florissant, Colorado; and Solva nana Loew, 1850 in mid-Eocene Baltic amber.

Cretoxyla azari Grimaldi & Cumming, sp. n.
urn:lsid:zoobank.org:act:0B1DC31D-17E2-4756-BDB2-E24C5E066E05
http://species-id.net/wiki/Cretoxyla_azari
Fig. 2

Diagnosis. As for genus.

Description. Head: Largely preserved, visible in oblique dorsal and ventral views. Head slightly flattened dorsoventrally, wider than deep, but exact proportions unclear since head seems somewhat distorted. Eyes large, bare, facets not differentiated; dorsal margins of eyes widely separated, by distance approximately 3× width of ocellar triangle. Gena/postocciput with fine pilosity; frons bare. Antenna large and thick; length equal to length of head, thickest portion of antenna near middle (width 0.25 × length of antenna). Flagellomeres difficult to discern, apparently 7, all but distal 2 are wider than long; flagellomere “2” [which may be 2 flagellomeres – if sulcus is present it is very obscure] twice the length of other flagellomeres; apical flagellomere small and conical. Mouthparts slightly prognathous, elements separated but difficult to discern; pair of stiff, stylate maxillae apparent, other elements probably include a labrum or hypopharynx, the labium and/or palps (segmentation of possible palps cannot be discerned).

Thorax: Pronotum fairly large, collar-like; mesonotum large, relatively flat; mesonotum, apical 2/3 of mesoscutellum, and anepimeron with homogeneous vestiture of fine, stiff setulae, each setula having a slightly raised, papilla-like base; row of such setulae just above wing base. Only fore leg preserved sufficiently; without spines or spurs even at apex of tibia. Empodium pulvilliform. Halter slender. Wing: Distal quarter lost at surface of amber. Sc complete, meeting C slightly beyond level of crossvein r-m. Vein h in line with short m-cu. Vein R1 straight. Vein R2+3 lost. Cells br and bm virtually equal in size, bisected by weak vein M. Cell m3 spindle-shaped, very small, approximately half the length and width of discal cell; vein M3+CuA1 incomplete (not reaching wing margin) and long, length only slightly less than length of cell m3. Cell cup very large, considerably thicker than and extended well beyond apical levels of cells br and bm. Vein A1 complete, A2 not apparent; alula present, but not particularly large.

Abdomen: Poorly preserved, genitalia lost.

Type. Holotype, sex unknown, Lebanon (Early Cretaceous, Neocomian): “Hammana/Mdeiru, Aptien inférieur,” in Azar Collection no. 391, temporarily deposited in Musee National d’histoire Naturelle, Paris. The specimen is partially preserved, missing
the right side of the body, most of the legs, and the right wing at the surface of the amber. It is mounted in a shallow glass well in Canada balsam on a glass slide.

**Etymology.** Patronym, for Dany Azar, for his extensive contributions to the paleontology of Lebanese amber.

**Xylomyidae(?) genus indet.**

Fig. 3

**Description.** *Head:* Lost. *Thorax:* Partially preserved, relatively broad (width of mesonotum equal to length, 1.40 mm), mesoscutellum of moderate size. Notum foveolate and scutellum covered only with numerous fine setulae, no macrosetae. Left wing 3.57 mm long, it and halter entirely preserved; right wing partially preserved. Vein C ends either at apex of R₃ or R₅; Sc long, meets C beyond midpoint of wing length, approximately at same level as crossvein r-m. R₁ parallel and very close to Sc, with slightly sclerotized, pterostigmatic membrane where they diverge slightly at apex. Base of Rs (before fork of R₂₃ and R₄₅) short, Rs connected to R₁ quite distal, at 0.42 complete length of wing. Veins R₃ and R₅ forked, branches of fork relatively straight (not curved), with R₅ distinctively ending at apex of wing rather than below it. Cell d small, distinctively short (length 2.5× greatest width); closed cells m₃ and cup present, cell m₃ triangular, short branches of M₃+CuA₁ and A₁+CuA₂ present. Alula relatively small. Halter relatively short and stout. *LEG:* [Presumably] hind leg without macrosetae on it; presence of an empodium difficult to discern, but pulvilli well developed. *Abdomen:* Relatively broad, ending short of wing apex.

**Specimen.** MCNA 8833, Spain: Álava: Peñacerrada I, Escucha Formation, Lower Cretaceous (Albian). Specimen lacks a head, and the thorax and abdomen are only partially preserved.
Discussion. Because of the incomplete preservation, a precise diagnosis and family placement of the specimen is not possible, so we did not provide a name and formal description. There are genera of lower Brachycera in several families that have a venation similar to this fossil, including the closed cell m₃. A distinctive feature of the fossil is vein R₅ ending at the apex of the wing. This is rarely seen in the lower Brachycera, occurring, for example, in Xylomyiidae and Apsilocephala Kröber, 1914 (Apsilocephali-
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Unlike *Apsilocephala*, which has the branches of R₄ and R₅ curved, these branches in the fossil are straight. Also, *Apsilocephala* and most therevids usually have a longer, more slender abdomen (although see *Kumaromyia, vide infra*), and usually have bristle-like setae on the mesonotum. These features, plus the short branch of Rs and its distal connection to R₁ indicate that the fossil is in the Stratiomyomorpha, not the Asiloidea.

Infraorder Tabanomorpha

Family Tabanidae

Genus *Cratotabanus*

http://species-id.net/wiki/Cratotabanus

*Cratotabanus* Martins-Neto and Santos, 1994: 291. Type species: *C. stenomyomorphus* Martins-Neto and Santos, 1994. Crato Formation (Aptian), Early Cretaceous of Brazil.

**Diagnosis.** *Cratotabanus* is distinguished from modern tabanids by veins M₁, M₂, and M₃ long, with lengths of M₁ approximately the same as that of cell d (vs. 0.5 – 0.7× length of cell d in Recent Tabanidae); R₅ only slightly deviated from the path of vein R₄₊₅ in most Recent tabanids, excepting *Chrysops* Meigen 1803, R₅ curved strongly downward). Distinguished from some Cretaceous Tabanidae, as follows: *Eotabanoid* Mostovski et al. 2003 and Yixian Formation genera with longer R₁ (reaching well past level of apex of cell d); fork of R₄₊₅ in *Eotabanoid, Palaepangonius* Ren, 1998, and *Eopangonius* Ren 1998 much longer (about equal in length to vein M₁).

*Cratotabanus newjerseyensis* Grimaldi, sp. n.

urn:lsid:zoobank.org:act:B8FD8A73-669D-44EB-B923-464378B6AB94

http://species-id.net/wiki/Cratotabanus_newjerseyensis

Fig. 4

**Diagnosis.** Venation differs from congener by *C. stenomyomorphus* having vein R₄ not strongly upcurved (vs. strongly upcurved) and R₃ slightly downcurved (vs. nearly in line with R₄₊₅).

**Description.** AMNH NJ-1862 (holotype): Body length 1.0 cm, wing length 8.0 mm. Most of left lateral view and some of dorsal, right lateral, and frontal view of face observable. Specimen apparently female. **Head:** Eyes bare, large, not dichoptic, no differentiation of facets nor apparent color patterns. Details of frons and face not entirely observable (e.g., presence of frontal callus and subcallus unlikely; development of ocelli not discernable). Antenna with scape and pedicel not observable but apparently short (not projected); flagellomere I apically narrowed to 0.5 × basal width, with 3 faint annuli; remaining 6 flagellomeres stylate, tapered apicad, articles of approximately equal
lengths [best seen in frontal view]. Proboscis robust, palps barely discernable (but apparently short, length 0.4 × that of proboscis), labellum well developed; entire proboscis fairly long, length = 0.75 × depth of head. Thorax: Standard proportions for Tabanidae; legs without discernable spurs (although apices of hind tibiae not observable). Metathoracic spiracle also not observable [e.g., presence of postspiracular scale]. Wing: Completely hyaline, no patterning. Base of $R_{2-5}$ nearly perpendicular to $R_1$, not at a sharp, acute angle. Fork of $R_{4-5}$ widely divergent and encompassing entire wing tip, base of $R_4$ perpendicular to $R_3$, then strongly and concavely curved to meet $C$; base of $R_4$ without a small appendix. $M_1$, $M_2$, $M_3$ nearly parallel; $M_3$ and $CuA_1$ convergent (not parallel); $CuA_1$ and $A_1$ meeting just before wing margin. $A_2$ extended nearly to wing margin; alula very large. Abdomen: Details (e.g., segmentation of cerci) not observable.

Specimen. AMNH NJ-1081 (paratype): Thorax + abdomen length 8.2 mm, wing length 8.5 mm (from base of basicosta to wing tip). Wing: Basicosta present as a thick, scale-like lobe at base of vein $C$. $C$ thickened proximally, circumambient. Short cross-vein $h$ present, where costal thickening is narrowed. $Sc$ long, 0.6 × length of wing, straight and parallel to vein $C$. Veins $R$ and base of $R_1$ also straight, parallel, and close to $Sc$; apices of $Sc$ and $R_1$ diverging apically. Dark, heavily sclerotized pterostigma cov-
ers and surrounds R₁, vein C, and extends to tip of R₂,₃. \(R_{2,3}\) straight, turned slightly upward at apex. Stem of \(R₃\) and \(R₄\) straight, base of \(R₄\) nearly perpendicular to this stem, then curved upward and meeting C anterior to tip of wing; \(R₃\) nearly in line with stem of \(R₁+R₃\). Cell d large, length ca. 2.7 \times \) the width; with veins \(M₁\), \(M₂\) and \(M₃\) each deriving directly from apical wall of cell. M veins slightly divergent, long; \(M₁\) slightly longer than cell d, \(M₃\) ca. 0.6 \times \) length of cell d. Crossveins r-m and m-cu in line with each other. Veins \(CuA₂\) and \(A₁\) meet slightly before wing margin, forming long, complete cua cell with very short vein \(CuA₂+A₁\). Vein \(A₂\) well developed, concave to \(A₁\), evanescent apically; anal lobe and anal cell well developed. Alula present but partially obscure. Abdomen: Short, broad, tergites short, typical of tabanids.

**Types.** Holotype (sex unknown), AMNH NJ-1862, New Jersey (USA): Middlesex Co., Sayreville, White Oaks [Old Crossman's] pits (Turonian), collected by Stephen Swolensky. Observation of the fly was optimized by embedding the amber in epoxy under vacuum and trimming very close to surfaces of the fly, but the specimen is not well preserved, being occluded with a reddish, crazed layer over most of the body and by similar internal fractures in the piece, as well as by a suspension of fine particles in the amber. Piece is irregular in shape, 10 \times \) 13 mm in largest dimensions. Study of the specimen might benefit from microtomography.

Paratype (sex unknown), AMNH NJ-1081, in Late Cretaceous (Turonian) amber from Crossman’s Pits, Sayreville, New Jersey. Fly is partially preserved: besides the entire right wing and a very small portion of left wing, only the dorsal surfaces of the abdomen and thorax remain; the head and legs are entirely lost. The amber piece is triangular and approximately 19 \times \) 8 \times \) 5 mm, embedded in epoxy but trimmed and polished so as to expose a dorsal view of the fly. The amber itself is light yellow and turbid, with a thick suspension of organic particles that obscures much of the fly. AMNH NJ-1081 differs from NJ-1862 by the following minor venational details: \(R₁\) slightly longer, Rs branches from \(R₁\) at a more acute angle, proximal end of cell d slightly more shallow V-shaped; \(A₂\) slightly shorter. Both specimens are also very similar in body shape and size.

**Etymology.** “from New Jersey,” in reference to provenance.

**Discussion.** These are the only tabanids known to be preserved in Cretaceous amber. Other tabanids in amber are from the Miocene of the Dominican Republic and the Eocene Baltic amber (Evenhuis 1994).

Ren (1998) described three genera of putative, compression-fossilized tabanids with long proboscides from the Early Cretaceous Yixian Formation of China. Grimaldi (1999) discussed the characters on which his assignment was made, and concluded that these fossils may not be tabanids. For example, features of *Palaepangonius eupterus* Ren that are inconsistent with Tabanidae are the short, upturned \(R_{2,3}\), very long veins \(R₃\) and \(R₄\) (half this length and much more divergent in true Tabanidae), and veins \(A₁\) and \(CuA₂\) that do not fuse but meet the wing margin independently (Fig. 4c). These do appear to be tabanomorphs, but may be stem-group taxa to Recent Tabanidae, Athericidae, Pelecorhynchidae, and possibly even Rhagionidae (some fossil rhagionids had long, piercing mouthparts). Another early compression fossil, *Baissomyia redita*, from the Early Cretaceous Zaza Formation of Russia, was attributed to the Tabanidae.
essentially on the basis of body shape and styletiform mouthparts (Mostovski et al. 2003), since the antennae and most of the wing (and, thus, most features defining the family) were not preserved. *Eotabanoid lordi*, from the Early Cretaceous of England, is probably a tabanid, but it too plesiomorphically has long R₄ and R₅ veins, which are nearly symmetrical (in true tabanids R₄ is typically much more curved) (Mostovski et al. 2003) (Fig. 4c). Besides the specimens in New Jersey amber described herein, the only other definitive Tabanidae from the Cretaceous is *Cratotabanus stenomyomorphus* from the Aptian-aged Crato limestone of Brazil (Martins-Neto and Kucera-Santos 1994). Venation of *C. stenomyomorphus* and *C. newjerseyensis* are extremely similar. Another species of the genus from the Crato Formation is as yet undescribed (Martins-Neto 2003). Diverse Tabanidae occur in Tertiary rocks and amber (summarized by Evenhuis, 1994), but generic assignments of those species described prior to 1950 need to be assessed. Cretaceous fossils assigned to the Tabanidae include the following:

*Baisomyia redita* Mostovski, Jarzembowski & Coram, 2003: Zaza Formation, Baissa, Transbaikalia, Russia.

*Eotabanoid lordi* Mostovski, Jarzembowski & Coram, 2003: Durlston Formation (Berriasian), Purbeck Group, Dorset UK.

“Allomyia”₁ [sensu Ren] ruderails Ren, 1998: Yixian Formation, China.

*Eopangonius pletus* Ren, 1998: Yixian Formation, China.

*Palaeopangonius eupterus* Ren, 1998: Yixian Formation, China.

*Cratotabanus stenomyomorphus* Martins-Neto & Santos, 1994: Crato Formation (Aptian), Ceara, Brazil.

“Cratotabanus sp. n.”: Crato Formation (Aptian), Ceara, Brazil (in Martins-Neto 2003: pg. 31, ex: Grimaldi 1990).

*Cratotabanus newjerseyensis* sp.n.: Raritan Formation amber (Turonian), New Jersey, USA (herein).

**Infraorder Muscomorpha**

**Superfamily Nemestrinoidea**

**Family Acroceridae**

Acroceridae has been hypothesized to be closely related either to the family Nemestrinidae (Woodley 1989), or as the basal family of the Heterodactyla with the Nemestrinidae as the basal family of the Muscomorpha (Yeates 2002). Both of these families have larvae that are ectoparasitoids on other terrestrial arthropods (in the case of Acroceridae, on spiders). Relationships presented in Wiegmann et al. (2011) are extremely unusual, with Nemestrinidae close to the Tabanomorpha and Acroceridae close to Stratiomyomorpha. Nemestrinidae

₁ Allomyia Ren, 1998 is a junior primary homonym of *Allomyia*, Banks 1916 (Trichoptera) and requires a replacement name. See the thorough and very entertaining discussion by O’Hara (2011) on homonym-chasing by cyber-nomenclaturists and the extravagant case of *Allomyia*. 
in particular is an ancient lineage with a distinctive wing venation, the oldest of which are Early Jurassic, and they were quite diverse by the Late Jurassic (Evenhuis 1994). An equivalent age of Acroceridae is very plausible, but Bayesian estimates of divergence between the Acroceridae and Nemestrinidae in the Triassic (Winterton et al. 2007) are almost certainly too old. The two new Burmese amber genera described below are very significant records for the family since these are the only acrocerids known from the Cretaceous, and also the best-preserved Mesozoic ones. The only other Mesozoic species of an acrocerid is from the Late Jurassic sediments of Karatau (Ussatchov 1968; Mostovski 1998), Archocyrtus gibbosus Ussatchev (Juracyrtus kovalevi Nartshuk 1996, from the same outcrops, is very similar and may even be conspecific [Hauser and Winterton 2007]). There are five acrocerid species preserved in Eocene Baltic amber. In the monophyletic subfamily Philopotinae (Winterton et al. 2007) are Archoteraphis hennigi Hauser and Winterton 2007 (closely related to the African genus Africateraphis Schlinger 1968), Eulonchiella eocenica Meunier 1912 (which is closely related to the Recent South African genus Thyllis Erichson 1840), and Prophilopota succini Hennig 1966. Other Baltic amber species are Glaesoncodes completinervis Hennig 1968 and Villalites electrica Hennig 1966. Ogcodes exotica, in Miocene Dominican amber, is closely related to several Asian species of the genus (Grimaldi 1995).

Schlingeromyia Grimaldi & Hauser, gen. n.
urn:lsid:zoobank.org:act:A659E121-9307-4454-B910-A586A82613E4
http://species-id.net/wiki/Schlingeromyia

Diagnosis. A minute, distinctive acrocerid with medial margins of male eyes contiguous above and below antennae, hind and ventral margins of eye strongly emarginate; antennae minute, in middle of head; proboscis vestigial; eyes bare, thorax with very sparse, fine setulae; postpronotal lobes of moderate size, slightly protruding; abdomen devoid of microtrichia and glabrous (possibly reflective). Mediolobus (i.e., “pulvilliform empodium”) and pulvilli pad-like. Venation distinct: All veins sclerotized, none faint; C ends at apex of R4+5; Sc short; R1 and Rs fork at ca. 0.4× length of wing; cells br and bm continuous, not bissected (vein M extremely faint or lost from this area); two closed radial cells (r4+5 and d), plus cell m3 present; R4+5 ends near apex of wing, without an apical fork of R4-R5 encompassing apex of wing.

Type species. S. minuta, sp. n., by present designation.

Etymology. Patronym in honor of Evert Schlinger, Emeritus Professor of entomology at the University of California, Berkeley, who has devoted his career to the study of Acroceridae and who also has been a very generous patron of systematic entomology. Feminine, following the Greek myia, for fly.

Discussion. This is a very distinctive, minute acrocerid – in body size quite the opposite of its generic namesake – which is unique for the venation, genitalia, and virtually bare body. Most acrocerids have long, fine pile on the thorax and abdomen, and many have it on the eyes and calypters. Vein Sc is very short in the fossil, and cells br and bm are contiguous. In addition, apparent retention of freely articulated gonostyli...
in the male genitalia appears to be a significant feature of the genus, since loss of articulated gonostyli through fusion with the gonocoxites is considered an apomorphy of the remainder of the family (Sinclair et al. 1994). The broad, pad-like structure between the pulvilli, called the empodium in homeodactylous flies, is actually a median outgrowth of the pulvilli as based on the detailed but overlooked work of Röder (1986). The true empodium is a bristle-like distal extension of the unguitractor plate. Thus, we are calling the pad-like empodium a mediolobus. Presence of a true (setiform) empodium is considered a synapomorphy of the Heterodactyla (Woodly 1989; Yeates 2002).

Winterton et al. (2007) recently analyzed acrocerid relationships based on sequences, and concluded that the subfamily Acrocerinae is diphylectic, and the subfamilies Panopinae and Philopotinae are monophyletic. Philopotines are particularly distinctive for the hump-backed notum and postpronotal lobes that are so enlarged as to form a collar dorsally over the cervical region. Although the Baltic amber *Archaeterphis hennigi* superficially resembles *Schlingeromyia* in small body size and eye shape (Hauser and Winterton, 2007), the relatively complete venation of the latter, structure of male genitalia, and pretarsal structure indicate a much more basal position for the Burmese amber species. Relationships of *Schlingeromyia* to any Recent generic-group or subfamily is obscure and may reflect a stem-group position.

*Schlingeromyia minuta* Grimaldi & Hauser, sp. n.
urn:lsid:zoobank.org:act:4881BDDC-D10C-47FE-91B1-5BA12EBE2B64
http://species-id.net/wiki/Schlingeromyia_minuta

*Fig. 5*

**Diagnosis.** As for the genus.

**Description.** Body length 3.0 mm, wing length 2.1 mm. *Head*: Large, spherical. Eyes very large, occupying most of head capsule. Eyes bare, without interfacial setulae; no dorso-ventral or frontal differentiation of facets. Entire mesal margins of eyes above antennae are contiguous, portion of mesal eye margin below antenna also contiguous. Posterior margin of eye strongly emarginate; ventral margin of eye slightly less so. Antenna minute, length approximately equal to diameter of 2–3 eye facets; consists of small oval pedicel and minute apical style. Mouthparts vestigial. Postocciput with scattered, fine setulae.

*Thorax*: Scutum strongly arched, very large, length of (meso)thorax 1.25 mm (nearly half the body length). Scutellum small. Position of cervical region near ventral surface of thorax. Pair of well-developed postpronotal lobes dorsal to cervical region, posterior surface of lobe slightly concave. Scutum with sparse, short setulae; scutellum with slightly thicker setulae. Legs slender, mesotibia with short pair of apical spurs; apices of tarsomeres with pair of short, thick setae. Length of basitarsomere approximately equal to that of remaining, distal tarsomeres; hind tibia expanded in width apically to approximately twice the proximal width. Pretarsus with claws large; mediolobus and pulvilli large, pad-like. Wing short and slender, length 2.10 mm, greatest width 0.75 mm; membrane with fine, faint pleating/wrinkling over
apical and posterior regions, but not in closed cells [best seen in oblique views]. Calypter large, ovoid, greatest diameter 0.58 mm. All veins sclerotized, none faint. C ends at apex of R_{4,5}; Sc short, meets C slightly distal to level of where R_{1} and Rs fork. R_{1} and Rs fork at ca. 0.4x length of wing; stem of Rs short, approximately 0.2 × total length of Rs. Rs surrounds large r_{4,5} cell, near middle of which R_{2+3} branches off to meet C. Vein R_{4,5} branches off of apex of cell r_{4,5}; apex meets C slightly posterior to wing apex; M_{1} also short, branching subapically off of cell r_{4,5}. Tip of wing not encompassed by an apical fork of R_{5} R_{6}. Cell d bounded by M_{1} and M_{2}; slender (ca. 0.3 × thickness of cell r_{4,5}). Cell m_{3} slender, trapezoidal, with proximal end slightly opened. Cells br and bm continuous, not bisected (vein M extremely faint or lost from this area). A_{1} slender, meeting CuA shortly before wing margin. A_{2} not apparent; anal lobe of wing well developed. Calypter large, hemispherical, greatest diameter 0.25 × length of wing. Abdomen: Smaller than thorax, with six tergites visible (tergite I small, tI and tII virtu-
ally obscured in dorsal view under postnotum). Tergites entirely bare of microtrichia and setulae; glabrous [probably reflective], with cuticular microsculpture of minute hexagonal cells present. Spiracles not visible near lateral margins of tergites [in pleural membrane?]. Tergites VII-VIII apparently small [not discernable]. Two pairs of male genitalic appendages present: slender dorsal pair (probably gonostyli), thicker ventral pair (gonocoxites), plus terminal, central, membranous appendage, the phallus.

**Type.** Holotype, Male, AMNH Bu332a, in Burmese amber. Paratype, AMNH Bu332b, in same piece of amber. Both specimens are entirely preserved, though slightly obscured by debris and a few small fractures. The specimens occur in a runnel-shaped piece of dark but transparent amber, 16 × 7 mm, which has been embedded in epoxy. The piece also contains 1 Coleoptera, 1 Hymenoptera (Serpitidae), and 6 other Diptera (Cecidomyiidae, Empidoidea), as well as twisted strands of spider webs. Interestingly, acrocerids are parasitoids of spiders.

**Etymology.** Latin, adjective, in reference to the very small size of the species.

*Burmacyrtus* Grimaldi & Hauser, gen. n
urn:lsid:zoobank.org:act:622EFA4E-5D9E-4244-8213-D20654E1AE15
http://species-id.net/wiki/Burmacyrtus

**Diagnosis.** A small, primitive acrocerid in Burmese amber easily separated from *Schlingeromyia* based on the well developed mouthparts; long, fine antennal stylus; dense, fine pilosity on thorax and abdominal tergites; absence of a mediolobus on the pretarsus; absence of tibial spurs; wing apex rounded; and by the venation: Vein C circumambient, cells br and bm completely separated, absence of cells r_{4,5} and m_{3}, presence of a very large cell d, vein R_{4} present but vestigial (not connected to R_{3}), veins CuA_{1} and CuA_{2} each present, vein A_{1} vestigial (cell cup not present).

**Type species.** *B. rusmithi* sp. n., by present designation.

**Etymology.** Combination derived from Burma (the pre-junta name for Myanmar) and *Cyrtus*, nominal genus of Cyrtidae, a formerly used name of Acroceridae.

**Discussion.** Derived acrocerid features that *Burmacyrtus* shares with *Schlingeromyia* and Recent acrocerids are the following: spherical head with large, holoptic eyes in male; apex of antennal flagellum with simple stylus; presence of a distinct cervical region; wing membrane with fine wrinkling and devoid of microtrichia; and with a large calypter. Apomorphic features in *Burmacyrtus* that are lacking in *Schlingeromyia* are fine, dense pilosity; a broadly rounded wing apex; long, fine stylus; and lack (loss) of a mediolobus. The wing shape of *Burmacyrtus* is similar to that of some Recent acrocerine genera such as *Turbopsebius* Schlinger, 1972, but the latter genus has cell r_{4,5} present, veins CuA_{1}+M_{3} fused, and a complete vein A_{1}, among other features. Like *Schlingeromyia*, *Burmacyrtus* is also very basal in the Acroceridae. Some of the derived features in wing venation of the two species in Burmese amber may be due to the very small body size.
**Burmacyrtus rusmithi** Grimaldi & Hauser, sp. n.
urn:lsid:zoobank.org:act:17FA87A4-457F-4BB0-AC59-03ECEBF4CAA4
http://species-id.net/wiki/Burmacyrtus_rusmithi
Fig. 6

**Diagnosis.** As for genus.

**Description.** Wing length approximately 1.4 mm, body length approximately 2.0 mm. *Head:* Rounded, spherical. Male eyes bare of setulae, frontally holoptic [dorsum of head not visible], occupying most of head capsule, ventromesal margins of eyes diverging around clypeus; facets in ventral portion of eye not differentiated in size; posteroventral margin of eye with shallow emargination. Basal portion of flagellum small, ovoid; stylus long and very slender, length c. 2 × that of basal portion; apex of stylus with pair of minute setulae. Labellum well developed; palps not evident. Postocciput with dense, fine pilosity. *Thorax:* Cervical region elongate, but not comprised of elongate postpronotal lobe (which protrudes slightly from anterior surface of scutum); cervical region connected anteroventrally to thorax. Thorax deep. Dorsal surface of mesoscutum and scutellum with dense, fine pilosity. Legs slender, metatibia longest; without spines, bristle, or tibial spurs; tibial and tarsal setulae not in regular rows. Apical portions of tibiae not distinctly broadened. Pretarsal claws large; pulvilli large, mediolobus absent [if setiform empodium present, not visible]. Wing short, with broadly rounded apex and narrow base; surface
devoid of microtrichia, with fine wrinkling throughout. Vein C circumambient, though thinner past apex of M₁; small hump in C midway along length of Sc. Sc complete, length ca. 0.4 × that of wing (a thin, faint, incomplete, and apparently spurious vein runs parallel and very close to Sc). Vein R₁ short, length approximately 0.5 × length of stem of R; R₂ and C thickened where they meet. Stem of Rs short, length approximately 0.5 × that of R₁; Rs and where it meets M thickened. R₁, apparently a vestigial fork (R₂ incomplete, not connected to R₁. Cells r₄₋₅ and m₃ absent; cell d present, large; length of cell d 0.3 × that of wing. Cells br and bm present, separated by well developed basal portion of M. Veins M₁, M₂, M₃ present, originating from apex of cell d. Veins Cu₄₁ and Cu₄₂ present, originating from apex of cell bm. Vein A present, but short and vestigial (cell cup absent). Alula and calypter well developed, each with fine wrinkling; calypter approximately 2 × diameter of alula. Halter apparently dark.

Abdomen: larger than thorax; sternites well developed, glabrous, without setulae or punctures. Tergites large, with dense, file pilosity; each setula situated in minute puncture. Male genitalia: epandrium well developed, shallow; cerci slender and apically pointed; everted, distal portion of phallus bulbous; subapical portion flanked by pair of flat, setulose lobes. Spiracles not visible.

Type. Holotype, Male, AMNH Bu-RS1, in Burmese amber. The holotype is in excellent condition, though only the ventral and lateral portions are visible (the dorsal surface is obscured by the depth and curvature of the amber). The amber is clear yellow and the fly lies on an internal surface plane that contains bubbles and stellate trichomes. The original piece was drop-shaped, 10 × 16 mm, and contained a small spider, cecidomyiid midge, and berothid lacewing. These inclusions were separated from the fly.

Etymology. Patronym, for Dr. R.D.A. (Ru) Smith, who generously donated the specimen to the AMNH from his personal collection.

Superfamily Asiloidea

Family Mythicomyiidae

*Microburmyia* Grimaldi & Cumming, gen. n.

urn:lsid:zoobank.org:act:7C83B2CC-BD8F-4BDA-A19D-E61110619770

http://species-id.net/wiki/Microburmyia

Diagnosis. R₁ long, apex reaching to 2/3 length of wing; R₁ branching off of the stem of R quite distad, R₂+₃ long, branching off of Rs in the distal half of the wing; cells br and bm large, length nearly half that of wing; M₁₊₂ forked; vein A₁ either incomplete or absent. Mesoscutum strongly arched; it and abdominal tergites devoid of bristle-like setae or long pilosity; apical tibial spurs lacking. Body size minute, ca. 1.0 mm in length.

Type species. *M. analvena*, sp. n. By present designation

Etymology. Derived from micro- (L.), minute; -burn-, Burma; and -myia (Gr.), fly, in reference to the minute body size and provenance of this brachyceran. Feminine.

Discussion. The family placement of the two new species in this genus is not entirely certain, particularly since in mythicomyiids vein R₂₊₃ is typically short and its
apex fused with $R_1$. The genus is placed in the Mythicomyiidae since the venation bears a resemblance to the Baltic amber genus *Carmenelectra* Evenhuis (Evenhuis 2002), though differing from that Baltic amber genus by $R_1$ branching off of the stem of $R$ quite distal (vs. near the base of the wing), $R_{2,3}$ branching off of $Rs$ in the distal half of the wing (vs. in the basal half), and by crossveins $r-m$ and $cu-m$ being in line (vs. stepped). Other features of *Microburmyia* that are consistent with mythicomyiids are the strongly arched scutum, structure of apical antennal articles (with minute stylus in *M. analvena*, ovoid first flagellomere in *M. veanalvena*), incomplete Sc vein, palpi minute or absent, and the minute body size. *Microburmyia* is plesiomorphic with respect to all other known mythicomyiids (cf., Evenhuis 2002).

Mythicomyiidae are traditionally (e.g., Hall 1981) and phylogenetically (e.g., Yeates 1994; Woodley 1989; Woodley et al. 2009) placed as the sister group to the Bombyliidae s.s., often classified as a subfamily, but also as a separate family (e.g., Evenhuis 2002). There is strong morphological and molecular support for Bombyliidae + Mythicomyiidae being the sister group to the rest of Asiloidea (Woodley 1989; Yeates 2002; Wiegmann et al. 2011) or the sister group to the rest of Asiloidea and Eremoneura (Sinclair et al. 1994; Trautwein et al. 2010). With the exception of an unforked $R_{4,5}$ and short or vestigial anal vein in *Microburmyia*, it is very interesting that its venation is intermediate between that of the Hilarimorphidae and the more specialized venation of mythicomyiines. This would lend support to the hypothesis that Hilarimorphidae is the sister group to the Bombyliidae (Woodley 1989; Yeates 1994; Woodley et al. 2009). Another hypothesis places the Hilarimorphidae (sometimes including the enigmatic and monotypic genus *Apystomyia* Melander 1950) as the sister group to the Eremoneura (Yeates, 2002) (see also discussion under Apystomyidae, *vide infra*). Oddly, the recent total-evidence phylogeny of flies placed the Hilarimorphidae (excluding *Apystomyia*) as sister group to the Acroceridae (Wiegmann et al. 2011), for which there is very limited molecular and no morphological support, although this result does suggest a position of Hilarimorphidae distant from Eremoneura.

Lastly, it is interesting to note that the fossil record of Bombyliidae s.s., exclusive of mythicomyiines, is entirely Tertiary. Bombyliidae is a large, cosmopolitan family (ca. 4,500 species) of flies that are most diverse in xeric ecosystems, where they are important pollinators of herbaceous plants. Their fossil record in sedimentary matrices and in amber (Baltic, Dominican) is quite diverse for North America and Europe (Evenhuis 1994), suggesting that the bombyliids s.s. radiated rapidly in the early Tertiary.

*Microburmyia analvena* Grimaldi & Cumming, sp. n.

urn:lsid:zoobank.org:act:E64C24A4-F610-4034-AC24-D65721D5BEF5

http://species-id.net/wiki/Microburmyia_analvena

Fig. 7a, b

**Diagnosis.** Distinguished from *M. veanalvena* sp. n. (below) by longer wing; presence of an anal vein; fringe of fine (vs. thick) setae on posterior wing margin; antennal style very fine, with very small article between it and basal flagellomere.
Description. A minute fly, body length c. 1.1 mm, thorax length 0.5 mm, wing length 1.15 mm. Head: Short, somewhat flattened anteroposteriad. Cervical region long. Eyes bare, large, well separated; no dorsoventral differentiation of facets; with small, shal-

Figure 7. Microburmyia Grimaldi & Cumming, gen. n. (Bombyliidae: Mythicomyiinae), in Burmese amber a, b M. analvena Grimaldi and Cumming sp. n. Holotype, KU-Bu079 (a lateral view, with detail of antenna b dorsal view, as preserved) c – e M. venanalvena Grimaldi and Cumming, sp. n., Holotype AMNH Bu1552 c, d left and right wings, showing variation in vein proportions. e, antenna.
low emargination on posterior margin. Proboscis short [palps not visible]. Antenna with basal flagellomere drop-shaped, with sparse setulae; apical style 0.6 × length of basal flagellomere, very thin, with two articles. Three ocelli present. Postocciput expansive, concave. Thorax: Mesoscutum dorsally arched, devoid of setae or setulae; thorax deep in lateral view; mesoscutellum triangular in shape (nearly equilateral), posterior end tilted upward. Coxae of moderate size; legs slender; devoid of setae, tibiae without apical spurs. Pretarsus with large pulvilli; empodium probably setiform. Halter with slender stem, large knob. Wing long, length slightly greater than length of body, wing L/W = 2.72. Costa either without spinules or spinules minute; C reaching slightly beyond apex of Rs. Posterior margin of wing with fringe of short, fine setae, including alula (setae longer in this area). Vein Sc with apex apparently evanescent, not reaching C. R-R1 nearly straight; R23 2.0 × length of R1; R4+5 straight, ends at apex of wing; proximal portion of R4+5 joined to r-m to form distal margin of cell br. Cells br and bm large, br is 0.33× length of wing, W/L cell br = 0.3; cell bm narrower and shorter. Base of M straight, with short apical fork. Crossvein bm-cu slightly shorter than r-m, not in line with each other. CuA1 and CuA2 short, curved slightly toward each other. Vein A1 present, incomplete (reaching to 0.6× distance between vein base and wing margin), apex of vein blunt, not evanescent. Anal lobe and alula small. Abdomen: Short, 1.3 × length of mesothorax, apparently devoid of setae and setulae. Tergites I – V with shallow, median keel; epandrium with pair of large ventral lobes.

Type. Holotype, male: Myanmar: Kachin (northern Myanmar), in Burmese amber, KU Bu079 (Univ. Kansas, Division of Entomology, Natural History Museum). The amber piece containing the holotype is a very transparent, deep amber color, 14 × 7 × 5 mm, which also contains 2 scelionid wasps. The minute holotype is at the surface of a fractured corner.

Etymology. in reference to the presence of an anal vein (i.e., the Latin noun vena), albeit incomplete.

**Microburmyia veanalvena** Grimaldi & Cumming, sp. n.
urn:lsid:zoobank.org:act:440657CB-BAD8-4D35-8F8A-1D03B5752FB0
http://species-id.net/wiki/Microburmyia_veanalvena
Fig. 7c-e

Diagnosis. cf. *M. analvena* (above), distinguished by the absence of an anal vein; posterior fringe of setae long, thick; basal flagellomere and style setulose, style with one article, oval.

Description. A minute fly, wing length 0.85 mm. Head: Short, somewhat flattened anteroposteriad. Cervical region with connection anteroventrally on thorax; not visible dorsally. Eyes bare, large, well separated; no dorsoventral differentiation of facets [presence of emargination on posterior margin not visible]. Proboscis short [palps not visible]. Antenna with basal flagellomere ovoid, having dense setulae (longer apicad); apical style 0.6 × length of basal flagellomere, thick (nearly 0.5 × thickness of basal flagellomere), one articulated, setulose. Three ocelli present. Postocciput expansive, concave. Thorax: Mesoscutum dorsally arched, devoid of setae
or setulae; thorax deep in lateral view; mesoscutellum triangular in shape (nearly equilateral). Legs slender; devoid of setae, tibiae without apical spurs. Pretarsus with large pulvilli; empodium probably setiform. Halter with slender stem, large knob. Wing W/L = 0.43. Costa either without spinules or spinules minute; C reaching slightly beyond apex of R₄+₅. Posterior margin of wing with fringe of long, thick setae (visible only on left wing), but margin of alula bare. Vein Sc extremely faint, evanescent. R-R₁ nearly straight; R₂₋₃ 2.0 × length of R₁; R₄₋₅ straight, ends at apex of wing; proximal portion of R₄₋₅ joined to r-m to form distal margin of cell br. Cells br and bm large, br is 0.42 × length of wing, W/L cell br = 0.27; cell bm slightly narrower and shorter. Base of M straight, with short apical fork. Length crossvein bm-cu approximately equal to that of r-m, in line with each other. CuA₁ and CuA₂ short, straight and diverging. Vein A₁ absent. Anal lobe differentiated, alula small.

Abdomen: Very broad anteriorly, devoid of setae and setulae on tergites. Tergites I – V apparently without shallow, median keel [difficult to discern with preservation]; epandrium with 5–6 long, thick setae on posterior surface, length of setae approximately equal to length of epandrium.

Type. Holotype, Male: Myanmar: Kachin (northern Myanmar), latest Albian to earliest Cenomanian. AMNH Bu1552. Specimen is displayed with wings and legs outspread, but body is only moderately well preserved, with some details obscured beneath layer of deep reddishness. Dorsal view is better than ventral view.

Etymology. ve- (Latin prefix meaning without), anal vein (L., vena), in reference to this venational character.

Discussion. It could be argued that these two species might warrant separate genera, based on the differences of antennae, wing fringe, epandrial setae, and proportions of the wing. However, other than the presence/absence of the anal vein, the wing venation is very similar between the two species.

Therevidae family group

This asiloid group includes the Recent families Therevidae (cosmopolitan; 1,063 described species), the Scenopinidae (cosmopolitan, approximately 420 described species), the monotypic family Evocoidae from Chile (Yeates et al. 2003, 2006), and the small, relict family Apsilocephalidae. Species in the group are most diverse in and largely adapted to dry habitats. Apsilocephalidae is comprised of Apsilocephala Kröber (one extant and several undescribed ones species from western North America, plus two fossil species [see below]), Burmapsilocephala Gaimari & Mostovski, 2000 (one species in Burmese amber), Cleshtentia White (two species, from Tasmania), and Kaurimyia Winterton and Irwin (one species, from New Zealand) (Yeates et al. 2003; Winterton and Irwin 2008). Monophyly of the family group is not disputed, though hypotheses of relationships among the four families differ slightly (Yeates 2002; Yeates et al. 2003; Wiegmann et al. 2011), and the possibility exists that Therevidae is paraphyletic with respect to Scenopinidae (Woodley 1989; Yeates et al. 2007).
Family Apsilocephalidae, or near

*Kumaromyia* Grimaldi & Hauser, gen. n.
urn:lsid:zoobank.org:act:08C3574B-22B5-4654-99CE-3DE0488EDBA2
http://species-id.net/wiki/Kumaromyia

**Diagnosis.** Body stout, abdomen short (length about equal to that of thorax); eyes large, bare; antenna with 3 flagellomeres, second article and third (style) minute; palp one-segmented; legs and thorax with bristle-like setae, no pilosity except for postoccipital region; hind coxa with small knob on anterior surface; thickness of metatarsi equal that of metatibial base; wing with C ending between apices of R$_5$ and M$_1$; apex of R$_5$ ending slightly subapically; R$_4$ and R$_5$ divergent, not parallel for any part of their lengths, base of R$_5$ not perpendicular to stem of R$_6$+$7$ and R$_5$.

**Etymology.** Patronym in honor of a great colleague and friend to the senior author, Prof. Kumar Krishna. Appropriately, *Kumaromyia* (as presently known) is preserved in amber from Burma, a place of significance in Kumar’s early years.

**Type species.** *K. burmitica*, sp. n., by present designation.

**Discussion.** *Psilocephala electrella* Cockerell, 1920, is a similar species preserved in Burmese amber, but *Kumaromyia burmitica* has a smaller body size (wing width 0.75 mm, vs. 1.5 mm in holotype of *electrella*), and differs venationally, specifically with the apex of R$_5$ meeting C preapically (vs. slightly postapically in *electrella*), M$_1$ and M$_2$ nearly parallel (distinctly divergent in *electrella*), and apex of M$_1$ distinctly curved to meet apex of CuA$_1$ at the wing margin (vs. straight in *electrella*). The holotype and unique specimen of *electrella* (NHML In. 20148) is shown in an excellent photograph in Gaimari and Mostovski (2000: fig. 1), and it was examined by the senior author in 2004. It is very partial, with most of the specimen lost (just portions of the scutum and abdomen, two legs and most of both wings remain), so it is very difficult to determine if the two species may be congeneric.

*Kumaromyia burmitica* Grimaldi & Hauser, sp. n.
urn:lsid:zoobank.org:act:96FE6FDB-D380-47A8-8EDB-2FE979761B72
http://species-id.net/wiki/Kumaromyia_burmitica
Fig. 8

**Diagnosis.** As for the genus.

**Description.** Small fly, total body length ca. 2.70 mm, thorax length 1.0 mm, wing length (estimated) 2.50 mm. *Head:* Large, with large eyes. Eyes bare, hemispherical in lateral view (posterior margin flat), no dorsoventral differentiation of facets; inner margins of eyes parallel, separated by distance approximately equal to width between antennal bases. Frons slightly convex, not protruding anteriad; with numerous fine setulae, without calli. Face (“subcranial cavity”) depressed, dark (sclerotized?), glabrous. Antennal scape and pedicel small, approximately equal in size, devoid of thick setae; basal flagellomere largest antennomere, drop-shaped, with dense setulae (no setae); api-
cal two antennomeres (including apical style) small, fine, with style slightly longer than penultimate antennal article. Maxilla with bases (cardostipites) sclerotized and partially fused, palp 1-segmented. Labellum slightly larger than palps. Postgena well developed, with numerous fine setae (pilosity). Thorax: Deep in lateral view, pleura apparently devoid of fine or bristle-like setae; scutum with at least 8 pairs of setae [dorsal view, including scutellum, obscured]. Scutum with 3 pairs of notopleurals and 5 pairs in supraalar region and some setulae; no cervical/postcervical setae. Legs: With thick, stiff setae, primarily on tibiae; fore tibia slender, hind tibia thickest. Fore leg: Femur with lateral row of ca. 10 fine setae, tibia with anterior row of 4–5 setae, 4 pre-apical setae. Mid leg: Femur apparently devoid of setae, tibia with 3 evenly-spaced setae on dorsal surface, 2 more ventrad, 4 apically. Hind leg: Coxa with small knob on ventral surface [best seen in left coxa]; femur devoid of setae, tibia with dorsal row of 3–4 setae, lateral row of 3 setae, ventral row of 3–4 setae. Basitarsomere on each leg equal in length to (or slightly longer than) combined length of distal tarsomeres. Each tarsomere with ca. 4 short, stiff setae on rim of distal end. Pretarsus with pair of large pulvilli, empodium setiform.

Figure 8. Kumaromyia burmitica Grimaldi & Hauser, gen. et sp. n. (Therevoid family group: ?Apsi-locephalidae), in Burmese amber. Right lateral habitus of holotype AMNH Bu131, as preserved. Below: wing, partially reconstructed.
Wing: Large, length nearly equal to that of body. Crossvein h long (space between Sc and C deep); Sc long, length approximately \( \frac{1}{2} \) that of wing and slightly shorter than length of R1; apex of Sc apparently incomplete (not meeting C). Apices of Sc and R1 without pterostigma surrounding apices. Fork of R and Rs deep, proximal to level of vein h. R\(_{2+3}\) straight, without apical curve. Fork of R\(_{4+5}\) not widely divergent; R\(_5\) in line with stem of R\(_{4+5}\), apex of R\(_5\) ending near apex of wing (not posterior to it); R\(_4\) slightly curved, distinctly shorter than R\(_5\). Cell d slender, greatest width <0.25 × length. Veins M\(_1\) and M\(_2\) slightly divergent, M\(_2\) and M\(_3\) very divergent, all M veins attached to apex of cell d. Apex of M\(_3\) meeting apex of CuA\(_1\) at wing margin. ABDOMEN: Short, only slightly longer than thorax; details (e.g., sternites, genitalia) not observable.

**Type.** Holotype, female, AMNH Bu131: Myanmar: Kachin State, near Myitkyina (mid-Cretaceous: Late Albian – Cenomanian). Specimen is complete, but the right wing (the only one observable) is folded, and most of the dorsal view is obscured, compromising a complete reconstruction of the venation (fig.8). The fly is complete, though slightly compressed and with a slight coating of particulate matter over some areas. Its left side is lying on a rough surface of the amber, which obscures that view. The piece also contains some twisted strands of spider webbing.

**Etymology.** In reference to the country of origin.

**Discussion.** There is little question this fossil belongs to the therevid group, albeit unusually small (within the range in body size of some apsilocephalids and a few genera of Phycinae, such as *Efflatouniella* Kröber, 1927). Therevid-group features include the antennal structure, bristle-like setae on the scutum and on the legs, the small knob on the hind coxa, as well as the venation. Unlike most Therevidae, *Kumaromyia* lacks any pruinosity and pilosity (except for the postgena), although Xestomyzininae and Agaphotinae are also robust and have sparse pilosity. *Kumaromyia* lacks any thick setae that typically encircle the scape and/or pedicel subapically in Therevidae. Also, *Kumaromyia* has R\(_4\) and R\(_5\) above the wing tip, whereas in Therevidae these are above and below the wing tip, respectively. Unlike Apsilocephalidae, *Kumaromyia* has a one-segmented palp, vs. two-segmented in Apsilocephalidae, where the basal segment is distinctively thin and long (oddly, palp segmentation and structure was not described for *Kaurimyia*). The antennal stylus and stout body in *Kumaromyia* is much more similar to that of *Clesthentia*, as the stylus in *Apsilocephala*, *Kaurimyia*, and even *Burmapsilocephala* is long and thin. It is quite possible that *Kumaromyia* is a stem-group taxon for the therevid-family group, not necessarily belonging within Apsilocephalidae or Therevidae.

Fossil Therevidae are scarce, with only five definitive species known, all from the Tertiary. Hauser (2007) and Hauser and Irwin (2005) revised the fossil species:

*Ambradolon grimaldii* Metz and Irwin 2000: Early Miocene Dominican Republic amber
*Arctogephyra agilis* (Meunier 1908): mid-Eocene Baltic amber
*Dasystethos hoffeinsi* Hauser 2007: mid-Eocene Baltic amber
*Kroeberiella pinguis* (Loew 1850): mid-Eocene Baltic amber
*Palaeopherocera scudderii* (Cockerell 1909): uppermost Eocene, Florissant, Colorado, USA

Fossil Apsilocephalidae range from the Cretaceous to early Tertiary:
Apsilocephala pusilla (Hennig 1967): mid-Eocene Baltic amber
Apsilocephala vagabunda (Cockerell 1927): uppermost Eocene, Florissant, Colorado, USA
Burmapsilocephala cockerelli Gaimari and Mostovski 2000: mid-Cretaceous Burmese amber
Undescribed sp.: Early Cretaceous amber, Wealden, UK (Chandler 2010: plate 32, fig. 2).

The position of Psilocephala electrella Cockerell 1920 within the therevoid group is uncertain.

Families Incertae sedis

Family Apystomyiidae

This family contains the sole Recent species Apystomyia elinguis Melander, 1950, from California, one of the world’s most relict and intriguing flies, with a dramatic history of systematic interpretation. Traditionally, Apystomyia has been placed in the Bombyliidae (e.g., Hall 1981), and then was hypothesized to be the sister group to the Eremoneura (Wiegmann et al. 1993). It has been placed in the Hilarimorphidae (Yeates 1994), as well as allied to the Therevidae (Sinclair et al. 1994). Nagatomi and Liu (1994) concluded that the male and female terminalia differ markedly from Hilarimorphidae, with the female terminalia similar to those of the Cyclorrhapha, and they erected the Apystomyiidae for this species. Soon thereafter, Nagatomi (1996) indicated that Apystomyia is allied to the proratine Scenopinidae. More recently, Yeates (2002), in his morphological analysis of basal Brachycera relationships, hypothesized the Hilarimorphidae (including Apystomyia) as being the sister group to the Eremoneura. However, Trautwein et al. (2010) considered Apystomyia to be the sister group to the Cyclorrhapha based on molecular evidence. Lastly, the comprehensive total-evidence study by Wiegmann et al. (2011) proposed a sister-group relationship of Apystomyia to the Cyclorrhapha, separate from Hilarimorphidae (which was placed near Bombyliidae).

Genus Hilarimorphites

Hilarimorphites Grimaldi & Cumming, 1999: 21. Type species: H. yeatesi Grimaldi and Cumming. By original designation.

Hilarimorphites burmanica Grimaldi & Cumming, sp. n.
urn:lsid:zoobank.org:act:BAEACD0A-8879-4761-95DB-4AF8297CADA0
http://species-id.net/wiki/Hilarimorphites_burmanica

Fig. 9

Diagnosis. Distinguished from the 4 other species in the genus (known only in New Jersey amber) by venation: vein C ending just slightly beyond apex of R₄ (not
at apex of R₅); Sc long, distally incomplete (more so than in *H. superba* Grimaldi and Cumming 1999, the only other species with this trait); veins CuA₂ and A₁ not joined before meeting wing margin (anal cell open distally). Distinguished from *Apystomimus* by the larger (normal-sized) wings, with an open cup (anal) cell. Also, basal flagellomere is more elongate and triangular in *H. burmanica*, and the antennal stylus longer than in the other species of *Hilarimorphites*.

**Description.** Based on a virtually complete, well-preserved female. Body length (excluding antennae) 1.40 mm; thorax length 0.50 mm; wing length 0.95 mm. *Head:* Antenna with first flagellomere an elongate triangle in lateral view; apical antennal article(s) form a thin style, with possibly a minute apical article. Eyes large, glabrous. Frons with sparse, scattered setae. Proboscis with broad, flat labellum (palps not vis-

*Figure 9. Hilarimorphites burmanica* Grimaldi & Cumming, sp. n. (Apystomyiiidae) in Burmese amber, as preserved. Holotype, AMNH 098.
ible). Thorax: Notum dome-shaped, with sparse, fine, stiff setae; scutellum with 2 pairs of erect setae. Legs very slender, of moderate length, without distinctive spines or tibial spurs. Wing: typical of Hilarimorphites, except as given in diagnosis above [also, anal lobe may be less developed than in other species, but this area slightly folded under and obscured]. Halter of moderate length, knob slender. Abdomen: Slender, tergites unmodified, cerci and genitalia not fully visible.

Type. Holotype female, AMNH Bu-098, in amber from Myanmar: Kachin, Tanai Village (on Ledo Rd. ca. 105 km Myitkyna). Amber is a deep, clear yellow, 15 × 10 × 5 mm, and was embedded in epoxy and trimmed to a wedge shape in order to maximize a full lateral view of the fly and its venation. The piece also contains a male chironomid and a thrips (Thysanoptera).

Etymology. From Burma (Myanmar).

Discussion. Hilarimorphites was known only from Turonian-aged amber of central New Jersey, USA, and besides the new species in Burmese amber a very similar taxon is also now known from the Upper Jurassic of Kazakhstan. Mostovski (1999) described Apystomimus zaitzevi, preserved as a compression from the Karabastau Formation (Upper Jurassic) of the famous Karatau-Mikhailova Lagerstätte. That well-preserved specimen has a venation indistinguishable from that of Hilarimorphites Grimaldi & Cumming, 1999. Apystomimus differs from that genus by having small, brachypterous wings (ca. 0.5× length of the body) and very long cerci (nearly 0.5× length of wing; Hilarimorphites has very small cerci typical of lower Brachycera). Since these are autapomorphic features of Apystomimus, it could be appropriate to synonymize one of the genera (although Apystomimus is more aptly named, Hilarimorphites has date precedence by two months). Hilarimorphites was originally placed in the Hilarimorphidae, and Mostovski placed Apystomimus in Asilomorpha family-incertae sedis (but near the extant genus Apystomyia). Recent Hilarimorpha lack the discal cell, they have the cup cell closed, and lack a well-developed anal lobe while retaining a vestige of the anal vein, so the venation of the fossils is far more easily derived from Apystomyia. Thus, we agree that Hilarimorphites and Apystomima should both be classified in Apystomyiidae.

The wing of Hilarimorphites differs from that of Apystomyia by the following: slightly shorter R1 and R2+3 veins; fork of R4+R5 less divergent, the branches slightly longer; cells br and bm significantly larger; cell cup significantly larger, with veins CuA2 and CuP meeting just before or at the wing margin, or not all (vs. CuA2+CuP with a long stem in Apystomyia); anal lobe of wing not protruding; and cell d much shorter, its length ca. 3× the width in Hilarimorphites (vs. 5× the width in Apystomyia).

Hilarimorphites burmanica is intermediate in age between the previously known fossils, and greatly extends the geographic range. An extinct clade or grade of Apystomyiidae occurred minimally throughout Laurasia from the Upper Jurassic to the Upper Cretaceous, which is an age that is consistent with its hypothesized sister-group relationship near Eremoneura (Grimaldi and Cumming, 1999; Grimaldi and Engel, 2005; Wiegmann et al., 2011). Oddly, there are no other fossils as yet known of the family, not even from prolific and diverse Tertiary deposits like Baltic amber.
Family Tethepomyiidae

**Diagnosis.** Small flies 1.5 mm in total body length, with venation and other features of the wing reduced. Vein CuA₁-CuA₂ comprised of short fork; vein M simple; vein A either absent or reduced to vestige at base of wings. Eyes very large, extensively holoptic in males. Cervical region long, head well separated from thorax; mesonotum compact, scutellum very short.

This is a highly specialized family of Diptera known only in amber from the Cretaceous of New Jersey, USA (Grimaldi and Cumming, 1999), Spain (Grimaldi and Arillo 2008), and now Myanmar (herein), comprised of two genera, *Tethepomyia* Grimaldi & Cumming and *Tethepomima* Grimaldi & Arillo. Discovery of the female of a new species in Burmese amber reveals the oviscapt to be a highly specialized, aculeus-type possibly used for parasitizing insect hosts. A few structures of tethepomyiids are similar to that of the Cretaceous brachyceran family Eremochaetidae (Ussatchev 1968; Kovalev 1986, 1989; Ren and Guo 1995; Mostovski 1997), which are discussed by (Grimaldi and Arillo, 2008: p. 264). The aculeate oviscapt is now known to be another shared similarity (below). Either the highly reduced venation of tethepomyiids is a result of miniaturization, or these two families are unrelated and share remarkably convergent features. Tethepomyiidae were originally considered to possibly be nematoceran (Grimaldi and Cumming 1999), but we are including the family in this report since the oviscapt reveals a likely close relationship with Eremochaetidae, which are definitive Brachycera.

**Genus Tethepomyia**

http://species-id.net/wiki/Tethepomyia

*Tethepomyia* Grimaldi and Cumming 1999: 6. By original designation.

**Diagnosis** (emended). Distinguished from *Tethepomima* by the following: Most or all of antennal flagellum lost; mesonotum bare, devoid of setae or setulae; apical tibial spurs absent; costal vein incomplete, not reaching to apex of Rs; costal spinules and fringe of fine setae on posterior margin of wing lost; alula and anal lobe lost; veins R₂+₃ and R₄+₅ lost (Rs simple, unbranched), crossvein r-m lost.

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

*Tethepomyia zigrasi* Grimaldi & Arillo, sp. n.

urn:lsid:zoobank.org:act:1D051ABF-34FA-461F-8583-F3E6CB322FCF  
http://species-id.net/wiki/Tethepomyia_zigrasi  
Fig. 10

**Diagnosis.** Distinguished from the other two species of the genus, which are known only from males (*T. thauma* Grimaldi and Cumming: New Jersey amber; and *T. brurubandi* Grimaldi and Arillo: Spanish amber), by the following: thickened costal and
Description. Body length (tip of basal flagellomere to posterior-most surface of tergite VIII) 2.15 mm. HEAD: Hemispherical in female; eyes very large, covering most of head, only small strip of gena exposed [view of face and frons not visible]. Dorsal eyes facets approximately 0.5× diameter of ventral facet; eye completely bare, no interfacetal setulae. No setae apparent on gena or frons. Ocelli possibly on small tubercles – small, digitate lobes in this area [but details obscure]. Antenna with large, crescent-shaped basal flagellomere; pedicel apparently small [indistinct]. Proboscis and palps not visible [ventral surface of head covered with bubble]. Posterior surface of head evenly and shallowly concave. Cervical region long; head not adpressed to pronotum.

Thorax: Small and short, L = 0.55 mm, with scutum arched, posterior half long and sloped; scutum and scutellum devoid of acrostichals or setae. Scutellum short, length
ca. 0.20 × that of scutum; posterior margin flat and slightly concave, not acute. Legs bare, devoid of setae or setulae; with femora slightly swollen in middle. Fore and mid coxae adjacent, hind tibia with coxal-trochanteral articulation facing anteriad (hind legs apparently held forward). Tibiae long and slender (slightly shorter than respective femur). Metatibia slightly bowed, as if to fit tightly against ventral surface of femur. Tarsi short, with basitarsomere only slightly longer than tarsomere 2 (most tarsomeres obscured by layer of air). Halter long; knob large, length of stem approximately 2.2 × greatest diameter of knob; stem without setae. Forewing with reduced venation; veins extremely light (particularly M and Cu); microtrichia of forewing either absent or so microscopic as to not be visible; no costal spines or fringe of fine setulae on posterior margin of wing. Vein C short, extended to only ca. 0.6 × length of wing, sclerotized, swollen towards apex; apex of R₁ fused with swollen portion of C. Rs thick, width slightly increased apicad; vein incomplete, not reaching wing margin/tip. Vein M faint, complete, tip evanescent and not reaching wing margin. Vein CuA faint, with short fork CuA₁–CuA₂ (length of fork 0.7 × length of stem); branches of fork curved towards anal region. What appears as deep fold (CuP?) parallel and posterior to stem of CuA. Faint, short vein A at base of posterior portion of wing; anal lobe and alula not present.

Abdomen: Tergites and sternites well developed, sclerotized; segments I – VI short (I longest), tergite VII long, sclerotized, length approximately equal to that of tII through tVI, with deeply incised membranous region basally, dorsal and lateral surfaces concave. Sternite VII very large, lobe-like, suspended beneath abdomen; apex pointed, bearing three short, sharp spines. Base of tVII apparently articulating with apex of tVI; tVII+VIII formed into a curved, sclerotized, sharp ovipositor-like structure, with a small, sharp, sclerotized spine at tip. Spine at tip of abdomen/oviscapt (sts IX) apparently interdigitating between three spines of sVII.

Type. Holotype, Female: Myanmar, Kachin State, Early Cenomanian. Specimen is in excellent condition and is in the private collection of James Zigras.

Etymology. Patronym for James Zigras, for allowing preparation and study of this remarkable specimen.

Discussion. Tethepomyia zigrasi sp. n. appears to be a sister group to T. buruhandi + thauuma, from Spanish and New Jersey ambers, respectively. Tethepomyia zigrasi retains the bases of M, Rs, and Cu, which the other two species have lost. It shares with buruhandi and thauuma many losses: of the antennal stylus, tibial spurs, crossvein r-m, veins R₂₃ and R₄₅, costal vestiture, fringe of marginal setulae on the wing, as well as the reduction of vein C.

With little question the oviscapt of T. zigrasi is a hypodermic-like (“aculeus”) structure, probably used for injecting its eggs into hosts. It was probably a parasitoid. An oviscapt of similar specialization has sporadically evolved in Diptera. It occurs in a few Phoridae (e.g., Apocephalus), all Pipunculidae, and within the Schizophora in some Conopidae (e.g., Stylogaster), most Tephritoidea, all Cryptochaetidae, and probably other families. The trait appears to have evolved most often in parasitoid groups (all those listed above except tephritoids). Most tephritoids inject their eggs into fruits or stems, though a few (like Pyrgotidae) are parasitoids. Fine structure of the injecting
oviscapt reveals its convergent development: what is labelled as the “ovipositor” in Pipunculidae (Hardy, 1989: pg 747) is probably a sclerotized, spine-like derivative of the cercus. In Cryptochaetidae the syringe-like oviscapt is sternite VIII; in Tephritoidea the oviscapt is a telescoping structure composed of segments 7–9. Interestingly, Thethepomyia has a suite of other convergent features similar to those of parasitoid families. Like Pipunculidae, Thethepomyiidae possess large eyes; like Pipunculidae and Cryptochaetidae the family has large pulvilli; and like Cryptochaetidae the basal flagellomere is enlarged and the arista minute to lost. These are probably functionally correlated features.

Unplaced to Family

_Myanmyia_ Grimaldi, gen. n.
urn:lsid:zoobank.org:act:7090815B-8878-487D-9980-78581DB36111
http://species-id.net/wiki/Myanmyia

**Diagnosis.** Distinctive small flies (body length less than 1.5 mm) with antennal stylus arista-like and terminal, having a single article; face without ptilinal suture; median margins of eyes very close on frons; maxillary palpus two-segmented; mesonotum with dorsocentral and scutellar setae; wing venation highly reduced, with R_2+3_ and R_4+5_ each unbranched, M unbranched and evanescent at both ends, Cu simple; female with pair of long, digitate, unsegmented cerci.

**Etymology.** From Myanmar, country of origin, and —_myia_, a common suffix referring to the feminine Greek word for fly.

**Type species.** _M_. _asteiformia_ sp. n. By present designation.

**Discussion.** This is a perplexing little fly. Chaetotaxy of the thorax, the wing venation, and even body shape are strikingly similar to acalypttrate flies in the Asteiidae. Convergent wing features of the two groups include short R_1_ and R_2+3_ veins; a straight R_4+5_ that meets the tip of the wing, and even microtrichia that are arranged in rows. However, _Myanmyia_ is not even a cyclorrhaphan, by virtue of the terminal (versus dorsal) arista-like stylus, lack of a ptilinum, and presence of two-segmented (vs. 1-segmented) palpi. With the exception of a few very basal Recent and extinct Platypezidae, almost all other Cyclorrhapha have a dorsal arista. Two-segmented palpi exclude _Myanmyia_ from the Eremoneura (the apparent basal segment of the two segmented palpi seen in some Phoridae is probably a palpifer [Cumming and Wood 2009]). While some empidoids (e.g., Cretaceous _Nemedina_ genus-group species [Grimaldi and Cumming 1999]) have short R veins and faint M and Cu veins, the branching pattern for these flies differs significantly at the base from that of _Myanmyia_.
Myanmyia asteiformia Grimaldi, sp. n.
urn:lsid:zoobank.org:act:3BD4F73D-375A-4B7F-8637-5449BC695495
http://species-id.net/wiki/Myanmyia_asteiformia
Fig. 11

Diagnosis. As for genus.

Description. Body size small, length 1.35 mm (excluding antennae and cerci), slender. Wing length 1.05 mm. Head: Slightly wider than thorax [possibly preservational, as head is slightly compressed]. Antenna with cup-like pedicel, distal edge rimmed with fine, stiff setae; basal flagellomere drop-shaped, width approximately equal to length; arista-

Figure 11. a-d Myanmyia asteiformia Grimaldi, gen. et sp. n. (unplaced to family), in Burmese amber (holotype, AMNH Bu1616) a Anteroventral detail of head b dorsal habitus, as preserved c pretarsus. d apex of abdomen, ventral view.
like stylus terminal, setulose, 1-articled (no small basal articles), length approximately 3 ×
length of basal flagellomere. Eyes large (occupying virtually entire lateral surface of head),
bare, with slight dorsoventral differentiation of facets (dorsal facets ca. 2 × diameter of
ventral ones); inner margins of eyes (on frons) very close, width of separation equal to
c. 3 facet diameters. Ptilinal suture absent. Maxillary palp 2-segmented, with apical
segment clavate and basal segment slender. Labrum long, very slender; hypopharynx (?)
styllet-like; labellum small. Gena very shallow or barely developed (not apparent). Postoc-
ciput broad, concave. Thorax: Slender, with the following dorsal setae (per side): 1 post-
pronotal, 4 supra-alar/notopleurals, 3 postsutural dorsocentrals (posterior one largest), 2
pairs scutellars [pleura not visible]. Legs of moderate length, setulose, without distinctive
spines/spurs. Pretarsus with claws well developed, but no pulvilli. Wing: Long, slender,
W/L = 0.33; membrane microtrichia arranged in oblique rows (between R veins) and
longitudinal rows (portions of space between R4+5 and M). Vein C slightly beyond apex
of R4+5, no humeral or subcostal breaks; with long, sparse spinules. Sc short, very faint
[best seen when tilting specimen]. Base of vein R thick, R5 short (length 0.3 × length of
wing); R2+3 unbranched, meeting C at ⅓ the length of wing. R4+5 straight, extended to
tip of wing, unbranched. Vein M simple, unbranched, very lightly sclerotized; both ends
evanescant. Sc. Vein A thick, heavily sclerotized strip along alular edge of wing. Anal
lobe and alula not developed. Halter: with large, darkened knob, stem approximately same
length as knob or slightly longer. Abdomen: Tergites I—VII well developed, with sparse
setulae, without macrosetae; sternites II, III, IV large, bare; segment V is tubular; VI, VII
ring-like; terminal segment bearing pair of long, finger-like, one-segmented cerci. Pres-
ence/absence of abdominal muscle plaques not visible.

Type. Holotype, female, AMNH Bu1616, in amber from northern Myanmar:
Kachin State, Tanai Village, 105 km NW Myitkyina. The holotype is the sole inclu-
sion in a clear amber-colored piece 9 × 6 × 2 mm. Ventral surface of the thorax and the
abdomen are compressed, and a crack through the thorax obscures some details. The
left wing of the unique specimen is well preserved, but venation is optimally observed
by tilting and observing the piece at various oblique angles. Right wing is twisted, but
in oblique view additional details of venation are visible.

Etymology. L., for like, and Asteia (type genus of the Asteiidae, a family of Schiz-
ophoran flies) and Latin –formia, meaning like, in reference to the similarity of the
unrelated two taxa in body shape, size, and wing venation.

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