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# New eremoneuran flies (Diptera: Eremoneura) from Cretaceous Charentese amber

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## Abstract

A new genus and two new species of Eremoneura are described from mid-Cretaceous amber of the Charentes region, in south-western France. *Chimeromyia vulloi* **sp. nov.**, from early Cenomanian amber of Fouras, is the first record of Chimeromyiidae from France. It extends the geographical distribution of this family, which was hitherto known only from Cretaceous ambers of Lebanon, Spain, and Myanmar. A key to all known species of *Chimeromyia* is provided. Additionally, a specimen from latest Albian–earliest Cenomanian amber from Archingeay, which was studied using synchrotron imaging, is described as *Francomyina incomparabilis* **gen. et sp. nov.**, and is left unassigned to family within Eremoneura. The affinities of both new species are discussed.

**Keywords:** Brachycera, Chimeromyiidae, *Chimeromyia*, Albian–Cenomanian, French amber

## Introduction

Eremoneura is a monophyletic group of flies comprising the Empidoidea and Cyclorrhapha (Grimaldi & Cumming, 1999), which is well supported by molecular and morphological analyses (Yeates *et al*., 2007; Wiegmann *et al*., 2011). The group is recorded as early as in the Jurassic but remains infrequent until the early Cretaceous (Grimaldi & Engel, 2005). Among Eremoneura, the family Chimeromyiidae was erected by Grimaldi *et al*. (2009) to include the monospecific genus *Chimeromyina* Arillo & Grimaldi, from Albian Spanish amber, and *Chimeromyia* Grimaldi & Cumming, a chimeric genus described a decade earlier from Lebanese amber and left as family *incertae sedis* at the time (Grimaldi & Cumming, 1999). *Chimeromyia* appears widely distributed during the Cretaceous, with seven species known from the Barremian of Lebanon, the Albian of Spain, and the early Cenomanian of Myanmar, while *Chimeromyina* is known from a single species in Albian Spanish amber (Grimaldi *et al*., 2009). The affinities of Chimeromyiidae within Eremoneura remain unclear, but the family seems closer to Empidoidea than to Cyclorrapha (Grimaldi *et al*., 2009).

Eremoneurans are frequent in mid-Cretaceous Charentese amber of south-western France, composing about one quarter of all dipteran inclusions (V. Perrichot, pers. data). However, the group is largely dominated by a single dolichopodid taxon, *Microphorites deploegi* Nel, Perrichot, Daugeron & Néraudeau (Nel *et al*., 2004), which represents 90% of all eremoneuran individuals. Here we describe two new Eremoneura from Charentese amber, including the first Chimeromyiidae from France and one new genus left unassigned to family.

## Material and methods

The amber specimens studied herein derive from the lignitic layers of two deposits from the department of Charente-Maritime, in south-western France: one from the 'lithological subunit A1sl-A' in the Font-de-Benon quarry, near the village of Archingeay, which is dated as latest Albian–earliest Cenomanian (Néraudeau *et al*., 2002; Dejax & Masure, 2005; Peyrot *et al*., 2019); and one from the 'subunit B2ms' exposed occasionally on the "Plage de la Vierge", at Fouras, which is early Cenomanian in age (Néraudeau *et al*., 2003). The location, geology, and stratigraphy of these localities have been summarized in Perrichot *et al*. (2010: figs. 1, 2).

Both amber pieces were polished using thin silicon carbide papers on a Buehler Metaserv 3000 polisher. Specimens were examined and photographed under transmitted and incident lights using a Leica MZ APO

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stereomicroscope equipped with a Canon 5D Mark II digital camera. All photographs are digitally stacked composites of several individual focal planes, which were obtained using Helicon Focus 6.7 (Helicon Soft Ltd.). Specimen IGR.ARC-168 is preserved in a piece of particularly turbid amber and was thus additionally imaged using phase contrast synchrotron microtomography (PPC-SRμCT). The imaging was performed on beamline ID19 of the European Synchrotron Radiation Facility (ESRF, Grenoble, France) following the local tomography protocol detailed by Lak *et al*. (2008), and using a multilayer monochromator with an energy of 25 keV, an isotropic voxel size of 1.4 μm, propagation distance of 50 mm, and 1000 projections for the habitus; and an energy of 20 keV, voxel size of 0.28 μm, propagation distance of 15 mm, and 2048 projections for the genitalia. Each tomography was obtained using a 180º continuous scan and 0.5 sec of exposure time. The scanning data were reconstructed using a filtered back-projection algorithm adapted for local tomography applications with PyHST software (ESRF) and adapted ring artifacts correction protocols. The specimen was segmented in three dimensions using region-growing techniques with VGStudioMax (Volume Graphics, Heidelberg, Germany). Figures were composed with Adobe Illustrator CC2018 and Photoshop CC2018 software.

Both specimens are housed in the amber collection of the Geological Department and Museum of the University of Rennes 1, France (IGR). The synchrotron microtomographic data (stacks of slices, segmentation, animations, pictures and 3D volume model) will be made available at the ESRF palaeontological online database (http://paleo.esrf.eu) upon publication.

The terminology for description generally follows Grimaldi *et al*. (2009), except Cumming & Wood (2017) for the wing venation system, with the following abbreviations: $A_1$, first branch of anal vein; ar, arista; bm, basal medial cell; bm-cu, basal medial-cubital crossvein; bm-m, basal medial crossvein; br, basal radial cell; CuA, anterior branch of cubital vein; CuA+CuP, anterior branch + posterior branch of cubital vein; cup, posterior cubital cell; $M_1$, first branch of media; m-cu, medial-cubital crossvein; ptstg, pterostigma; $R_1$, first branch of radius; $R_{2+3}$, second branch + third branch of radius; r-m, radial-medial crossvein; Sc, subcostal vein.

## Systematic palaeontology

**Order Diptera Linnaeus, 1758**
**Infraorder Eremoneura Lameere, 1906**
**Family Chimeromyiidae Grimaldi & Cumming, 2009**
**Genus *Chimeromyia* Grimaldi & Cumming, 1999**

***Chimeromyia vulloi* sp. nov.**
(Figs 1, 2)

**Holotype.** IGR.FRS-16, male (?). Specimen complete, although left side is partly covered by bubbles within the amber matrix. Deposited in the Geological Department and Museum of the University of Rennes 1, France.

**Locality and horizon.** Charentese amber; Lower Cenomanian, lithological subunit B2ms from the 'Plage de la Vierge' at Fouras, Charente-Maritime department, south-western France.

**Etymology.** The specific epithet is a patronym honoring Dr Romain Vullo (Géosciences Rennes), a colleague and friend who collected and donated the amber piece.

**Diagnosis.** Vein M tubular, not reaching wing margin; $R_{2+3}$ gradually tapered toward C and abruptly curved; crossveins r-m and bm-m not aligned and separated by a short M abscissa; $M_2$ absent; anal lobe barely evident, no alula; two pairs of scutellar setae (posterior pair cruciate); arista dorsal. One row of long, thin, stiff setae on external surface of mid-coxa and mid-femora.

**Description.** Male (?). Body length 0.97 mm, without apparent color patterns.

*Head*: eyes dichoptic, without interfacetal setulae, occupying most of lateral surface of head, no differentiation of facets. Two pairs of ocellar setae, the anterior pair slightly posterior to anterior ocellus, the posterior pair apparently slightly behind posterior ocelli; ocellar triangle not particularly tuberculate. Frons apparently glabrous. One pair of long, vertical, inner setae present, plus at least two smaller postoculars. Antenna with pedicel cup-shaped; basal flagellomere setulose, lobe-like; rest of flagellum aristate, having two small basal articles and a long, fine, setulose terminal article. Clypeus large, with two facial setae. Palpus and labellum small; details not visible.

*Legs*: simple, without distinctive setation or spines, except for row of long, thin stiff setae on external surface of mid-coxa and mid-femora.

*Thorax*: mesoscutum with one row of acrostichal setulae; two long rows of dorsocentrals flanking acrostichals (dorsocentrals slightly larger than acrostichals); each postpronotal lobe with erect seta. Mesoscutellum with two pairs of setae, first pair thinner and smaller than second, apical pair; both pairs slightly erect.

*Wing*: rounded at apex, base narrow, with anal lobe not visible. Sc incomplete, tapering apically; C ending at apex of $R_5$; $R_1$ short, apex reaching to basal third of C; $R_{2+3}$ present and broadly curved toward C; fork of $R_4$ and $R_5$ widely divergent (approximately 70°). Vein $M_1$ tubular, tapering apically, not reaching wing margin; $M_2$ absent; crossveins r-m and bm-m not aligned, separated by a short

**FIGURE 1.** *Chimeromyia vulloi* **sp. nov.** (holotype IGR.FRS-16). Habitus in oblique dorsal view. Scale bar = 0.5 mm.

M abscissa. $M_4$ sclerotized, not reaching wing margin. Veins CuA+CuP and $A_1$ not apparent.

*Abdomen*: ovoid, tapered apicad. Terminalia hidden by a bubble.

**Family *incertae sedis***
**Genus *Francomyina* gen. nov.**

**Type species.** *Francomyina incomparabilis* **sp. nov.**

**Etymology.** Derived from the country of origin of the type specimen, and with the same termination as for the genus *Chimeromyina,* with which it shares some similarities.

**Diagnosis.** Eyes holoptic. Pterostigma present distally of fork of $R_1$ and Rs; crossvein bm-m slightly longer than m-cu and than r-m; fork of $M_1$+$M_2$ equidistant from r-m + bm-cu joint and wing apex; $M_4$ and CuA (+CuP?) reaching wing margin. Male terminalia with surstyli simple.

***Francomyina incomparabilis* sp. nov.**
(Figs 3, 4)

**Holotype.** IGR.ARC-168, male. Specimen with preservation average, in a piece of turbid amber, and missing right portions of eye, antenna, and thorax, as well as base of right wing and apex of left wing. Deposited in the Geological Department and Museum of the University of Rennes 1, France.

**Etymology.** Derived from 'incomparable', for the difficulty to compare this specimen with Chimeromyiidae.

**Diagnosis.** As for the genus.

**Locality and horizon.** Charentese amber; Uppermost Albian / Lowermost Cenomanian, lithological subunit A1sl-A from the 'Font-de-Benon' quarry near Archingeay, Charente-Maritime, south-western France.

**Description.** Body 1.37 mm long from head to apex of abdomen.

*Head*: wider than long. Eyes large, bare, holoptic, facets not differentiated. Ocellar triangle on small, slightly raised tubercle, setae no visible. Antenna with arista inserted apically, at least two aristomeres present, first aristomere slightly longer than second one, third one hypothetically longer than preceding ones. Mouthparts not visible.

*Thorax*: 0.35 mm long, rather stout and large in dorsal view, slightly wider than head, conspicuously convex in lateral view, setae not visible. Legs short, apparently simple, with no distinctive setation or spines.

*Wing*: about 1.20 mm long, approximately half as broad as long; vein C extending to apex of $M_1$; Sc present but incomplete; $R_1$ curved, $R_{2+3}$ parallel to $R_1$, slightly curved only apically, $R_4$ and $R_5$ subequal in length; crossvein bm-m slightly longer than r-m or m-cu; $M_1$ subequal to $M_1$+$M_2$; $M_4$ and CuA(+CuP?) reaching wing margin; anal vein not visible.

Abdomen lacking distinctive bristles (possibly not visible by preservation). Male terminalia with surstyli simple and basally fused with sclerotized epandrium.

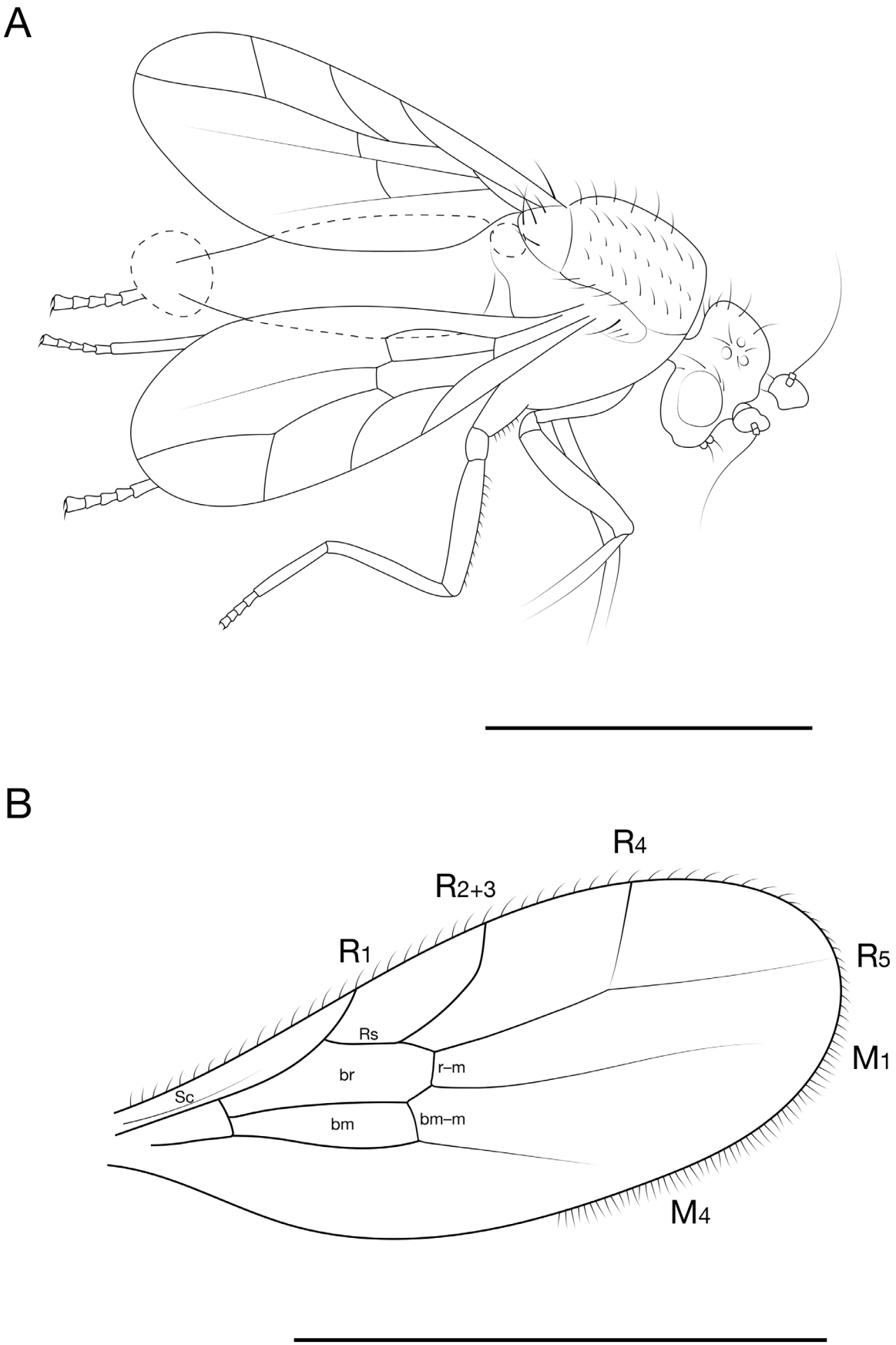


**FIGURE 2.** *Chimeromyia vulloi* **sp. nov.** (holotype IGR.FRS-16). **A**, Line drawing of habitus in oblique dorsal view. **B**, Line drawing of wing venation (see Material and methods for abbreviations). Scale bars = 0.5 mm.

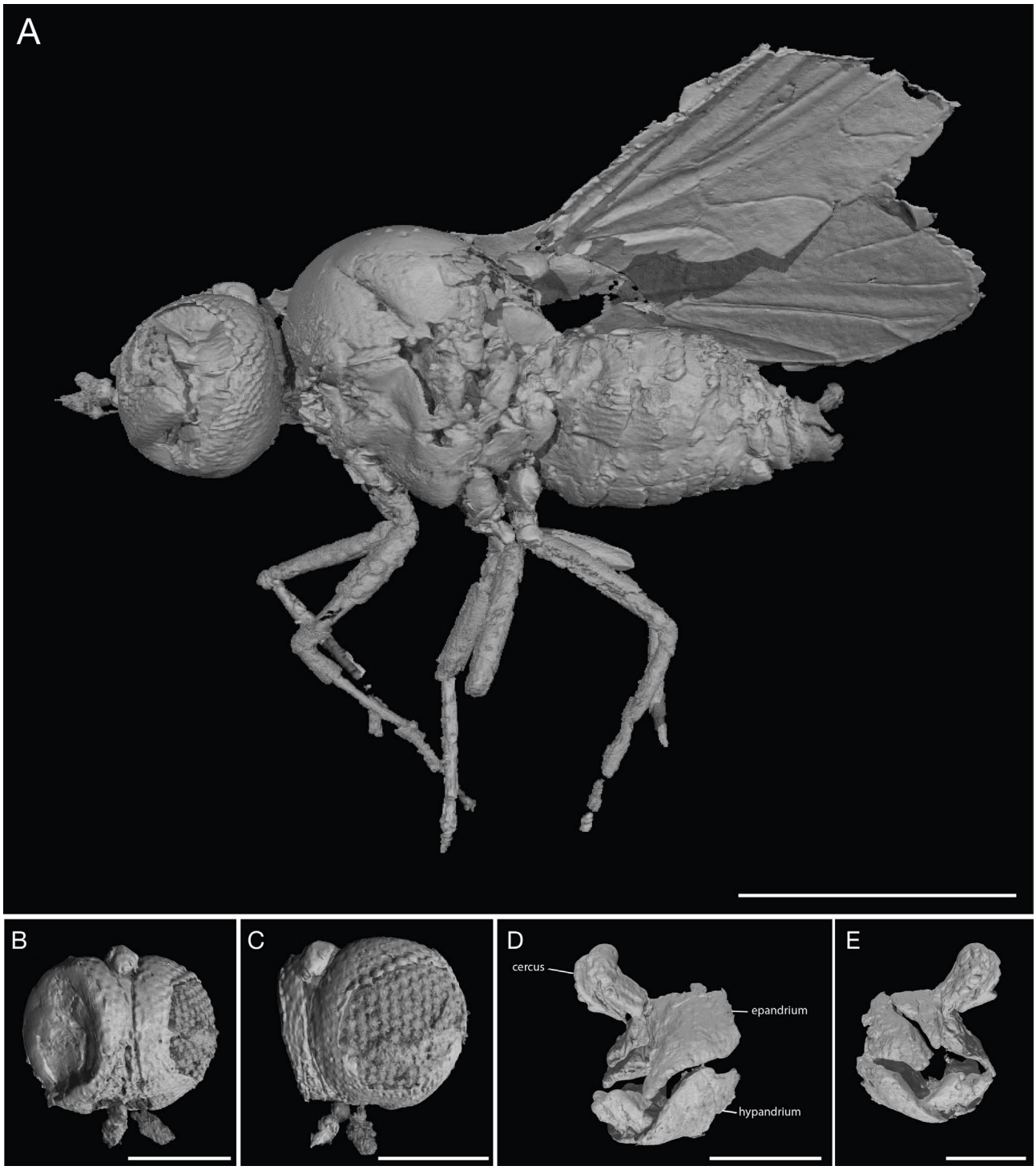


**FIGURE 3.** 3D virtual extraction of *Francomyina incomparabilis* **gen. et sp. nov. (**holotype IGR.ARC-168). **A**, Habitus in left lateral view. **B**, Head in anterodorsal view. **C**, Head in oblique dorsal view. **D**, Genitalia in right oblique posterior view. **E**, Genitalia in left oblique posterior view. Scale bars = 0.5 mm (**A**), 0.25 mm (**B**–**E**).

## Discussion

*Chimeromyia vulloi* **sp. nov.** can be assigned to Chimeromyiidae based on its small size (body length *ca*. 1.00 mm), antennal flagellomeres modified into a long arista with three articles (basal two aristomeres very short), a pair of oral vibrissae, two pairs of long ocellar setae, and a single row of acrostichal setulae. Additionally, the wings of *Chimeromyia vulloi* **sp. nov.** possess all distinctive characters of the family: humeral vein absent; Sc incomplete; Rs divergence very distal from base of wing; $R_{2+3}$ short and usually abruptly upturned; $R_{4+5}$ forked with $R_4$ and $R_5$ widely divergent; crossveins r-m and bm-m present and nearly aligned; anal veins highly reduced or lost.

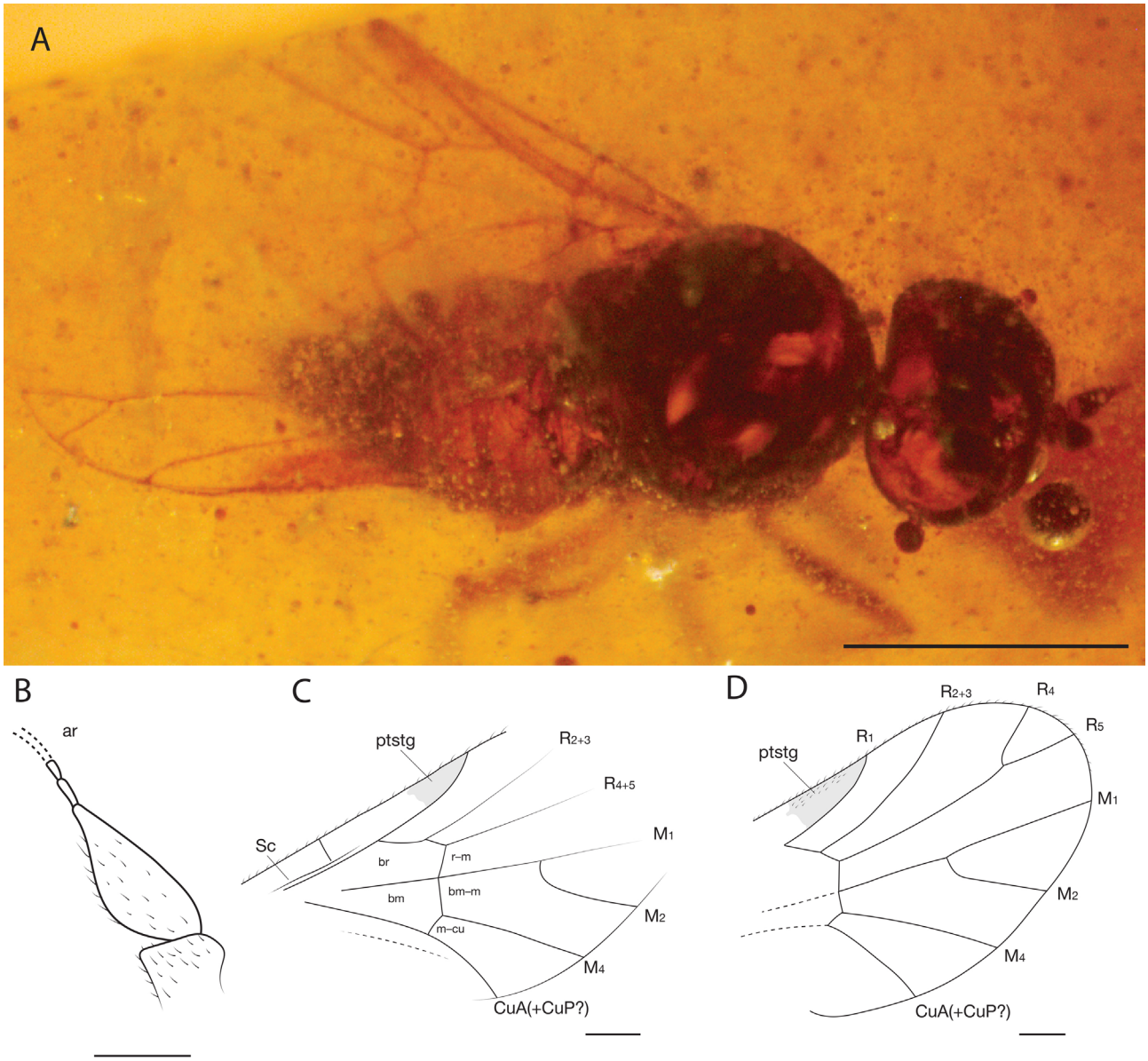


**FIGURE 4.** *Francomyina incomparabilis* **gen. et sp. nov.** (holotype IGR.ARC-168). **A**, Photomicrograph of habitus in oblique dorsal view. **B**, Line drawing of left antenna. **C**, Line drawing of left wing. **D**, Line drawing of right wing. See Material and methods for abbreviations. Scale bars = 0.5 mm (**A**), 0.1 mm (**B**–**D**).

Within Chimeromyiidae, the new species is assignable to the genus *Chimeromyia* based on the following combination of characters as described by Grimaldi *et al*. (2009): vein $M_2$ absent; crossvein dm-m and cell dm lost; CuA(+CuP) and cell cup absent; crossveins r-m and bm-m either in line or separated by a distance no greater than 1/3 the length of either vein; anal vein lost and anal lobe lost or reduced.

The new species differs from the seven other species of *Chimeromyia* by the following combination of characters: vein M tubular, not reaching wing margin; $R_{2+3}$ gradually tapered toward C and abruptly curved; crossveins r-m and bm-m not aligned and separated by a short M abscissa; $M_2$ absent; anal lobe barely evident, no alula; two pairs of scutellar setae (posterior pair cruciate); arista dorsal. Below, we propose a key to the eight species now known in *Chimeromyia*.

### Key to species of *Chimeromyia*

1. Wings with crossveins r-m and bm-m aligned or slightly offset; apical part of $M_2$ present ..... 2
– Wings with crossveins r-m and bm-m not aligned; $M_2$ absent ..... *Chimeromyia vulloi* **sp. nov.** (Albian–Cenomanian Charentese amber)
2. Vein $R_{2+3}$ present; abdomen ovoid ..... 3
– Vein $R_{2+3}$ absent; abdomen elongated ..... *C. burmitica* Grimaldi & Cumming, 2009 (Cenomanian Burmese amber)
3. Second abscissa of Rs sub-equal or shorter than first abscissa ..... 4
– Second abscissa of Rs conspicuously longer than first abscissa ..... *C. reducta*

Grimaldi & Cumming, 1999 (Barremian Lebanese amber)

4. Vein $R_{2+3}$ only slightly curved ..... 5
– Vein $R_{2+3}$ conspicuously curved..... 6
5. Veins r-m and bm-m aligned, both separated from $M_1$ by a gap; metathoracic tibiae without tibial brush..... .....*C. mediobscura* Grimaldi & Cumming, 2009 (Barremian Lebanese amber)
– Veins r-m and bm-m not aligned, both reaching a short abscissa of M; metathoracic tibiae with a tibial brush ..... .....*C. pilitibia* Grimaldi & Cumming, 2009 (Barremian Lebanese amber)
6. Flagellomere 1 short and ovoid, without acute ventral margin..... 7
– Flagellomere 1 broad, with an acute ventral margin.....*C. acuta* Grimaldi & Cumming, 1999 (Barremian Lebanese amber)
7. Vein $R_{2+3}$ slightly curved; $R_{4+5}$ fork close to wing margin.. .....*C. intriguea* Grimaldi & Cumming, 1999 (Barremian Lebanese amber)
– Vein $R_{2+3}$ strongly curved; $R_{4+5}$ fork distant from wing margin..... *C. alava* Arillo & Grimaldi, 2009 (Albian Spanish amber)

*Chimeromyia vulloi* **sp. nov.** extends the distribution of the genus and family to all major Cretaceous amber deposits of Eurasia but Siberian (Taimyr) amber. Chimeromyiidae are still unknown in the Cenozoic, so that they apparently became extinct sometime in the late Cretaceous. But caution is necessary with this kind of assumption: some empidoid taxa have shown a similar, only Cretaceous distribution before more recent, Paleogene or even living representatives were subsequently found, *e.g.*, *Microphorites* Hennig (Dolichopodidae) found in early Paleogene Czech amber and early Eocene French amber (Tkoč *et al*., 2016; Bramuzzo & Nel, 2017); and *Alavesia* Waters & Arillo (Atelestidae) found alive in Namibia and Brazil (Sinclair & Kirk-Spriggs, 2010; Amorim *et al*., 2020).

The placement of *Francomyina* **gen. nov.** is more difficult to assess. It undoubtedly belongs to Eremoneura as it possesses simultaneously Empidoidea and Cyclorrhapha characters, as Chimeromyiidae. But *Francomyina* **gen. nov.** cannot be confidently placed in Chimeromyiidae, as it also displays a mixture of chimeromyiid and non-chimeromyiid features. The vein Sc being incomplete, crossveins r-m and bm-m present and aligned, and the genitalia symmetrical and only slightly dorsoflexed would strengthen its placement in Chimeromyiidae. The holoptic eyes and a pterostigma being present are not diagnostic of the family but are sexual characters that can be present only in some male flies, therefore not excluding Chimeromyiidae. Similarly, the humeral crossvein being present, vein $R_{2+3}$ not abruptly upturned, and $R_4$ and $R_5$ only slightly divergent are likely plesiomorphies and do not exclude Chimeromyiidae either. Still, the simple surstyli would indicate a different family, and with the arista poorly preserved and acrostichal setulae missing, a clear placement of *Francomyina* **gen. nov.** is not possible until further material appears, and it is conservatively left unassigned to family within the Eremoneura. As similarly discussed for Chimeromyiidae by Grimaldi *et al*. (2009), *Francomyina* **gen. nov.** may be considered within Empidoidea because of the frons without a ptinal suture, the distal fork of $R_{4+5}$ present, the short and recurved vein m-cu, and the male terminalia not flexed up under the abdomen. The only support for an affinity of *Francomyina* **gen. nov.** with Cyclorrapha is the surstyli possibly fully articulated with the epandrium.

## Conclusion

*Chimeromyia vulloi* **sp. nov.** adds to the knowledge on the diversity and distribution of the extinct family Chimeromyiidae, but provides no new evidence for the exact affinities of the family within Eremoneura (*i.e*., for Empidoidea *vs* Cyclorrhapha). *Francomyina* **gen. nov.** similarly displays a mixture of empidoid and cyclorrhaphan features and, although it shares some characters with Chimeromyiidae, it cannot be confidently assigned to any eremoneuran family due to the absence of some diagnostic characters, though its morphology and wing venation suggest a closer affinity with Empidoidea than Cyclorrhapha. The discovery of more complete specimens of *Francomyina* **gen. nov.** may help clarifying the relationships within extinct eremoneuran lineages.

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## References

Amorim, D.S., Riccardi, P.R. & Rafael, J.A. (2020) First known extant species of *Alavesia* (Diptera: Atelestidae) in the

Neotropical Region: *Alavesia leukoprosopa*, sp. nov., from the Southern Atlantic Forest, Brazil. *American Museum Novitates*, 3962, 1–12.
https://doi.org/10.1206/3962.1

Bramuzzo, S. & Nel, A. (2017) Youngest representative of the extinct genus *Microphorites* in the Eocene amber of France (Diptera: Dolichopodidae: Microphorinae). *Zootaxa*, 4231 (4), 590–594.
https://doi.org/10.11646/zootaxa.4231.4.11

Cumming, J.M. & Wood, D.M. (2017) 3. Adult morphology and terminology. *In*: Kirk-Spriggs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families.* Suricata 4. South African National Biodiversity Institute, Pretoria, pp. 89–133.

Dejax, J. & Masure, E. (2005) Analyse palynologique de l'argile lignitifère à ambre de l'Albien terminal d'Archingeay (Charente-Maritime, France). *Comptes Rendus Palevol*, 4, 53–65.
https://doi.org/10.1016/j.crpv.2004.12.002

Grimaldi, D. & Cumming, J. (1999) Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History*, 239, 1–124.

Grimaldi, D.A., Cumming, J.M. & Arillo, A. (2009) Chimeromyiidae, a new family of Eremoneuran Diptera from the Cretaceous. *Zootaxa*, 2078 (1), 34–54.
https://doi.org/10.11646/zootaxa.2078.1.2

Grimaldi, D.A. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, New York/Cambridge. 755 pp.

Kirk-Spriggs, A.H. & Sinclair, B.J. (Eds), (2017) *Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera.* Suricata 5. South African National Biodiversity Institute, Pretoria, 1361 pp.

Lak, M., Néraudeau, D., Nel, A., Cloetens, P., Perrichot, V. & Tafforeau, P. (2008) Phase contrast X-ray synchrotron imaging: Opening access to fossil inclusions in opaque amber. *Microscopy and Microanalysis*, 14, 251–259.
https://doi.org/10.1017/S1431927608080264

Lameere, A. (1906) Notes pour la classification des Diptères. *Mémoires de la Société Entomologique de Belgique*, 12, 105–140.

Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.* L. Salvii, Holmiæ [= Stockholm], 824 pp.
https://doi.org/10.5962/bhl.title.542

Nel, A., Perrichot, V., Daugeron, C. & Néraudeau, D. (2004) A new *Microphorites* in the Lower Cretaceous amber of the southwest of France (Diptera: Dolichopodidae, "Microphorinae"). *Annales de la Société Entomologique de France*, 40, 23–29.
https://doi.org/10.1080/00379271.2004.10697401

Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P., Guillocheau, F. & Guyot, T. (2002) Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). *Geobios*, 35, 233–240.
https://doi.org/10.1016/S0016-6995(02)00024-4

Néraudeau, D., Allain, R., Perrichot, V., Videt, B., de Lapparent de Broin, F., Guillocheau, F., Philippe, M., Rage, J.-C. & Vullo, R. (2003) Découverte d'un dépôt paralique à bois fossiles, ambre insectifère et restes d'Iguanodontidae (Dinosauria, Ornithopoda) dans le Cénomanien inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). *Comptes Rendus Palevol*, 2, 221– 230.
https://doi.org/10.1016/S1631-0683(03)00032-0

Perrichot, V., Néraudeau, D. & Tafforeau, P. (2010) Charentese amber. *In*: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 192–207.

Peyrot, D., Barrón, E., Polette, F., Batten, D.J. & Néraudeau, D. (2019) Early Cenomanian palynofloras and inferred resiniferous forests and vegetation types in Charentes (southwestern France). *Cretaceous Research*, 94, 168–189.
https://doi.org/10.1016/j.cretres.2018.10.011

Sinclair, B.J. & Kirk-Spriggs, A.H. (2010) *Alavesia* Waters and Arillo—a Cretaceous-era genus discovered extant on the Brandberg Massif, Namibia (Diptera: Atelestidae). *Systematic Entomology*, 35, 268–276.
https://doi.org/10.1111/j.1365-3113.2009.00506.x

Tkoč, M., Nel, A. & Prokop, J. (2016) Discovery of a new species of the Cretaceous genus *Microphorites* Hennig, 1971 (Diptera: Dolichopodidae *s. lat.*) in Paleogene amber from eastern Moravia (Czech Republic). *Insect Systematic & Evolution*, 47, 181–193.
https://doi.org/10.1163/1876312X-47022139

Wiegmann, B.M., Trautwein, M.D., Winkler, I.S., Barr, N.B., Kim, J.-W., Lambkin, C., Bertone, M.A., Cassel, B.K., Bayless, K.M., Heimberg, A.M., Wheeler, B.M., Peterson, K.J., Pape, T., Sinclair, B.J., Skevington, J.H., Blagoderov, V., Caravas, J., Narayanan Kutty, S., Schmidt-Ott, U., Kampmeier, G.E., Christian Thompson, F., Grimaldi, D.A., Beckenbach, A.T., Courtney, G.W., Friedrich, M., Meier, R. & Yeates, D.K. (2011) Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the USA*, 108, 5690–5695.
https://doi.org/10.1073/pnas.1012675108

Yeates, D.K., Wiegmann, B.M., Courtney, G.W., Meier, R., Lambkin, C. & Pape, T. (2007) Phylogeny and systematics of Diptera: Two decades of progress and prospects. *Zootaxa*, 1668 (1), 565–590.
https://doi.org/10.11646/zootaxa.1668.1.27