Cretaceous Antodicranomyia (Diptera: Limoniidae) and their paleohabitat

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New representatives of the Cretaceous cranefly genus Antodicranomyia (Diptera: Limoniidae) are reported from Albian-Cenomanian Charentese (French) amber. The newly reported specimens allow for an emended diagnosis of the type species A. azari, as well as the description of a new species, Antodicranomyia rubra sp. nov., which is mostly distinguished from the type species by features of its wing venation, antennae, and genitalia. As a rare, extinct genus known only from French amber, Antodicranomyia is compared with its closest relative genera Antocha, Dicranomyia and Antohelia. The evolutionary implications and paleohabitat of Antodicranomyia are discussed. The new discovery adds to the knowledge of the crane flies' diversity and evolution in the mid-Cretaceous.

Limoniidae, or craneflies, are an old lineage of Diptera dating back to the Late Triassic, and currently known by ca. 11,000 extant species1–4. The family is frequently encountered in both modern and fossil entomofauna5–5. The oldest Limoniidae—Architipula youngi Krzemiński, 19921 (representative of Architipulinae, considered as the oldest group of Limoniidae9), is known from Late Triassic of North America1. The family is abundantly documented as soon as in the Early Jurassic (Toarcian) of Europe7–10 and Asia11,12. In the Cretaceous, the Limoniidae comprise lineages known since the Triassic and Jurassic periods, as well as the earliest representatives of genera that are still extant today, such as Helius Lepeletier et Serville13, Dicranopycha Osten Sacken14 or Trichoneura Loew15–22, but also some genera that are documented exclusively from the Cretaceous period, such as Antodicranomyia Perrichot, Nel and Krzemiński23. This genus was hitherto known only by its type species, Antodicranomyia azari Perrichot, Nel and Krzemiński23, which was described based on two males in Albian-Cenomanian amber from the Archingeay deposit in Charentes, south-western France23. Two new specimens of Antodicranomyia are reported herein: a further male of the type species, also from the Archingeay deposit; and a male assignable to a new species from another, slightly younger Charentese amber deposit (Fig. 1). It is the second evidence of the extinct genus Antodicranomyia, still apparently endemic to the mid-Cretaceous Charentese (French) amber.

Results

Systematic palaeontology. Order Diptera Linnaeus24.
Infraorder Tipulomorpha Rohdendorf12.
Family Limoniidae Speiser25.
Subfamily Limoniinae Speiser25.
Genus Antodicranomyia Perrichot, Nel and Krzemiński23.
Type species: Antodicranomyia azari Perrichot, Nel and Krzemiński23: 76, Figs. 1 and 2.
Antodicranomyia azari Perrichot, Nel and Krzemiński23. (Fig. 2).

Emended diagnosis. Wing 3 × as long as wide; tip of Sc distad sc-r 3 × as long as sc-r; r-m nearly oblique to the basal deflection of M1+2; tip of R1+4 straight to weakly upcurved; basal part of R5 slightly arched, twice to three times as long as crossvein r-m; crosvein m-cu aligned with basalmost point of d-cell; vein M1 as long as or slightly longer than d-cell; distance between tips of R5 and R1+4 approximately 2 × to 2.5 × distance between M1 and R5; distance between tips of R1 and R3+4 approximately 1.3 × to 2 × the distance between R1+4 and R3; male genitalia with lobe (branch I = ventral gonostylus) and clasper (branch II = dorsal gonostylus) of gonostyli approximately 2 × as long as wide, shorter than half of gonocoxite, narrowed, slightly broadened distally, bearing apical setae; lobe longer than clasper, armed with one small apical spine, bearing long setae distally on the inner surface and apically.

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Remarks. The following features allowed specimen no. MNHN.F.A30189 (formerly ARC 182.6) to be designated as a paratype of *A. azari*: vein sc-r is one third the tip of Sc, r-m is nearly oblique to the basal deflection of M1+2; crossvein m-cu is aligned with fork of Mb.

Type material. Holotype MNHN.F.A30188 (formerly ARC 186.2), male, paratype MNHN.F.A30189 (formerly ARC 182.6), partial specimen preserved by head and one wing; both in amber from Font-de-Benon quarry (Arc 1 in Fig. 1B), between Archingeay and Les Nouillers, Charente-Maritime department, France. Early-Late Cretaceous, latest Albian-earliest Cenomanian, lithological subunit A1, level A1sl2 sensu Néraudeau et al.26, A1sl-A sensu Perrichot et al.27.

New material examined. Specimen IGR.ARC-259, wing of male.

Type locality & Type horizon. Amber from the same deposit and stratum as the type material.

Additional description. Wing (Fig. 2A, B) with d-cell 0.55 mm long; M3 0.58 mm long. Remarks. The specimen displays a poorly preserved base of right wing and head, and the left wing is the only well visible part.

*Antodicranomyia rubra* sp. nov. (Figs. 3, 4 and 5).
Diagnosis. Wing 3.5 × as long as wide; tip of Sc distad sc-r subequal to sc-r in length; r-m nearly aligned to the basal deflection of M1+2; tip of R3+4 upcurved; basal part of R5 curved, 3 × as long as crossvein r-m; crossvein m-cu before fork of Mb; vein M1 longer than d-cell; distance between tips of R5 and R3+4 approximately twice the distance between M1 and R5; distance between tips of R3+4 and R5; male genitalia with lobe (branch I = ventral gonostylus) and clasper (branch II = dorsal gonostylus) of gonostyli elongate, approximately 7 × as long as wide, narrowed, longer than half the length of gonocoxite; gonocoxite 3 × as long as wide; clasper strongly sclerotized, slightly broadened distally, bearing one thick apical seta-like spine; lobe longer than clasper, armed with two apical setae, pale, not very wide.

Remark. Such features like the rostrum distinctly shorter than head, the male antenna with 13 flagellomeres, the wing with Sc ending beyond the origin of Rs and veins r-r and r-m nearly aligned, the male genitalia with narrow lobe and clasper of gonostyli, additionally with the clasper strongly sclerotized, warrant placement of the new species in the genus *Antodicranomyia* as defined by Perrichot et al.23.

Etymology. The specific name is from the Latin *rubra* meaning red, and refers to ‘La Montée Rouge’ (the red slope), name of the access road to the type locality in Cadeuil.

Type material. Holotype IGR.CDL-23.1, male.
Type locality & Type horizon. Amber from Cadeuil quarry along 'la Montée Rouge' (Cdl 2 in Fig. 1B) at Sainte-Gemme, Charente-Maritime department, France. Late Cretaceous, Early Cenomanian, lithological subunit A2, level A2a sensu Perrichot et al.27.

Description (male). Body (Fig. 4A) pale brown, 4.30 mm long, with dark brown head. Head (Fig. 4A, B) 0.42 mm long, with moderately large, oval, almost holoptic, glabrous eyes; many strong, thick and comparatively short setae on occiput and vertex; rostrum distinctly shorter than head; antenna (Figs. 3A, 4A, B, E) 1.10 mm long, 15-segmented, shorter than head and thorax combined; scape elongate, cylindrical, massive, narrower than other segments of antenna; pedicel short, shorter and wider than scape, approximately as long as wide, widened in midlength; flagellomeres rather short and wide, becoming progressively slender toward antennal tip; flagellomeres 1–7 approximately as long as wide, 8–15 approximately twice as long as wide; last flagellomere longer than penultimate one. Antenna with few moderately elongate setae,
approximately as long as their respective bearing-segments; palpus (Fig. 4B) four-segmented, rather elongate, palpomeres cylindrical, last palpomere short.

Thorax (Fig. 4A, B): wing (Fig. 3D) 4.13 mm long, 1.10 mm wide; vein Sc surpassing midlength of wing and midlength of vein Rs; vein R₁ rather short, ending opposite approximately 0.3 × length of vein R₃+₄; d-cell 0.22 mm long, twice as long as wide; crossvein r-m rather short, as long as one third of basal deflection of R₃; R₁ 1.5 × as long as r-r (R₂); crossvein m-cu before fork of vein Mb on M₁+₂ and M₃+₄; crossvein m-m half the length of basal deflection of M₃; M₃ 0.50 mm long; A₁ and A₂ elongate, almost straight.

Legs (Fig. 4A, C, D) with strong, numerous short setae.

Abdomen (Figs. 3C, 4A, 5C): genitalia (Fig. 5C) 0.66 mm long; gonocoxite 0.43 mm long; lobe 0.22 mm long, clasper 0.20 mm long.

Remark. The specimen is well preserved, although missing apical portions of some legs.

Comparison. The new species differs from A. azari mainly by the male genitalia with more elongate, narrowed clasper and lobe. In A. rubra sp. nov., the clasper is approximately 7 × as long as wide and is longer than half the length of gonocoxite, while in A. azari the clasper is at most 3 × as long as wide, shorter than half the length of gonocoxite. Both species also differ by the wing venation: vein Sc-r is subequal to the tip of Sc in A. rubra sp. nov., one third the tip of Sc in A. azari; r-m is nearly aligned to the basal deflection of M₁+₂ in A. rubra sp. nov., but nearly oblique to the basal deflection of M₁+₂, in A. azari; the tip of R₃+₄ and basal part of R₃ are curved, with basal part of R₃ 3 × as long as r-m in A. rubra sp. nov., vs. tip of R₃+₄ straight or at most weakly upcurved and basal part of R₃ just slightly arched and twice to three times as long as r-m in A. azari. A feature of the wing vein which makes it easy to distinguish between both species is the position of crossvein m-cu: in A. rubra sp. nov. this vein is anteriad fork of Mb, while it is aligned with fork of Mb in A. azari. Moreover, M₃ is distinctly longer than d-cell in the new species, but as long as or only slightly longer than d-cell in A. azari.

Discussion

As reflected by Perrichot et al. in their selection of the genus name, Antodicranomyia shares features with the extant genera Antocha Osten Sacken, and Dicranomyia Stephens. Antocha currently comprises 161 extant species within three subgenera Antocha, Orimargula Mik, and Proantocha Alexander, while only two extinct species left unclassified in subgenus are known. Dicranomyia is represented by over 1150 extant species.
within 25 subgenera (Table 1) including Alexandriaria Garrett33, Caenoglochina Alexander34, or Caenolimonia Alexander35, and the genus has a rather extensive fossil record of almost 30 species. The earliest representatives of Antocha date back to the Cenomanian Burmese amber31, while Dicranomyia first occurs in the Paleocene36. Subgenera such as Dicranomyia, Melanolimonia, or Sivalimnobia are known from the earliest Eocene Mo Clay Formation of Denmark or from Eocene Baltic amber36–38.

As suggested by Perrichot et al.23, Antodicranomyia and Antocha are very similar in their male gonostyli, but Antodicranomyia differs by its long, sclerotized aedeagus and (from almost all subgenera of Antocha) by its narrow lobe of gonostylus. The wide anal area on the wing of Antodicranomyia distinguishes this genus from Caenoglochina. Some species of this subgenus similarly have narrow lobes of gonostylus, however these are broader and apically truncate, in most of Dicranomyia lobe (outer gonostylus) of gonostylus is ballon-like with rostral prolongation, clasper (inner gonostylus) is strongly sclerotized, hooked39. The male genitalia with two elongate gonostyli are characteristic for Antochini, but Antodicranomyia differs from this tribe by its wing venation which is characteristic of the Limoniini. The wing of Antocha is characteristically wide with almost square-shaped anal lobe, in Antodicranomyia anal lobe is well developed, but not so expressive as in Antocha40. The 15-segmented antennae of Antodicranomyia are intermediate between the 14-segmented ones of Limoniini and the 16-segmented ones of Antochini and could suggest a tendency to the reduction of antennal segments within this tribes23.

Based on the reconstructed paleohabitat of the Archingeay and Cadeuil deposits26,27,40–43 Antodicranomyia apparently lived in coastal (estuarine) to back-swamp, warm and moist forests dominated by a variety of conifers (Cheirolepidiaceae, Cupressaceae (taxodioids), Araucariaceae and Podocarpaceae trees) and ferns (mainly Blechnum, Schizaeaceae), with few Ginkgoales, Bennettitales, herbaceous angiosperms, and more or less influenced by marine conditions.

The history of Antodicranomyia somewhat parallels that of Antohelia Kania39. Antodicranomyia shares some features with Antocha and Dicranomyia, two extant genera with a long temporal range (since the mid-Cretaceous for Antocha, the Paleocene for Dicranomyia), while Antodicranomyia is restricted to the mid-Cretaceous French amber (Fig. 6).

Antohelia similarly shares some features with Antocha and Helius, two genera that are known since the Cretaceous16,17,19–21,44,45 and are still living today, while Antohelia is apparently restricted to the Eocene Baltic

| genus            | subgenus has been identified | stratigraphic ranges          |
|------------------|------------------------------|-------------------------------|
| Antodicranomyia  | no subgenus has been identified | Albian-Recent                |
| Antocha          | Antocha Osten Sacken14        | Cenomanian-Recent             |
|                  | Orimargula Mik29             | Recent                        |
|                  | Prosantocha Alexander30       | Recent                        |
|                  | Alexandriaria Garrett15       | Recent                        |
|                  | Caenoglochina Alexander34     | Recent                        |
|                  | Caenolimonia Alexander35      | Lower Miocene-Recent          |
|                  | Cygomy sia Thieschinger42     | Recent                        |
|                  | Dicranomyia Stephens36        | Eocene-Recent                 |
|                  | Doaneomyia Alexander16        | Recent                        |
|                  | Erostrata Savchenko39         | Recent                        |
|                  | Eulimonia Alexander44         | Recent                        |
|                  | Glochina Meigen38             | Recent                        |
|                  | Hesperolimonia Alexander31    | Recent                        |
|                  | Idioglochina Alexander45      | Recent                        |
|                  | Idiopyga Savchenko37          | Recent                        |
|                  | Melanolimonia Alexander33     | Eocene-Recent                 |
|                  | Nealexandriaria Alexander34    | Recent                        |
|                  | Neoglochina Alexander35       | Recent                        |
|                  | Neolimnobia Alexander41       | Recent                        |
|                  | Neolimnobia Alexander42       | Recent                        |
|                  | Nesiomyia Thieschinger47      | Recent                        |
|                  | Numantia Bigot15              | Recent                        |
|                  | Pandamysia Thieschinger49     | Recent                        |
|                  | Peripheriptera Alexander36    | Recent                        |
|                  | Peripheroptera Schiner37      | Recent                        |
|                  | Piosukoglochina Alexander49   | Recent                        |
|                  | Sivalimnobia Alexander47      | Eocene-Recent                 |
|                  | Zalusa Enderlein59            | Recent                        |
|                  | Zelandoglochina Alexander50   | Recent                        |

Table 1. List of subgenera of Antodicranomyia, Antocha and Dicranomyia with information about their extinction.
amber\textsuperscript{18}. Such extinct lineages as *Antodicranomyia* and *Antohelia* uniquely enlighten our knowledge on the past diversity, paleohabitat, and evolutionary history of craneflies. Especially, when it is possible to indicate such features as differentiation of number of antennomeres within *Antodicranomyia*\textsuperscript{15}, in relation to 14-segmented antennae of Limoniini and the 16-segmented ones of Antochini, thus showing the tendency to the reduction of antennal segments\textsuperscript{23}.  

Figure 6. Chronostratigraphic distribution of *Antocha, Antodicranomyia, Antohelia, Dicranomyia, Helius* fossil species with chosen fossil sites localization. Stratigraphic chart according to International Stratigraphic Chart, International Commission of Stratigraphy (v. 2021/05) https://stratigraphy.org/chart (accessed on 16 September 2021).
**Material and methods**

The Charente-Maritime and Charente departments of south-western France comprise several Early-Late Cretaceous deposits of fossil resin known under the collective name Charentese amber (Fig. 1A). The present study is based on inclusions in amber from the Archingeay 1 (Arc 1) and Cadeuil 2 (Cdl 2) deposits, as defined by Perrichot et al. (2010: figs. 1, 2). Now filled up with water forming lakes, both sites are former quarries that each exposed two lignitic, amber-bearing layers within sand and clay beds (Fig. 1B). The geological setting of the deposits have been detailed elsewhere. The amber bed considered herein for Arc 1 was assigned to the lithological subunit A1 and dated as latest Albian or earliest Cenomanian based on palynomorph evidence. Cdl 2 was assigned to the lithological subunit A2 which was similarly dated as Early Cenomanian. A new male specimen of *Antodiscranomymia azari* is reported in amber from the Archingeay deposit (Arc 1), which already yielded the type material of this species described in 2007. And the male of a new species is reported from the Cadeuil deposit (Cdl 2). All specimens newly reported herein are deposited in the Geological Department and Museum of the University of Rennes (IGR), France.

The specimens were examined using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera. The measurements were taken with NIS-Elements D 3.0 software. The length of head was measured as the length of the head capsule. Measurements of the discal cell were taken from the proximal to distal ends of the d-cell; measurements of the vein M3 were taken from the point of connection of vein m-m with vein M3 to the length of the head capsule. Measurements of the vein 3 were taken from the point of connection of vein m-m with vein M3 to the apex of gonocoxite. Drawings and photographs were made by Iwona Kania-Kłosok, with line drawings traced from the photographs. Terminology follows Krzemiński for the wing venation nomenclature, and Ribeiro or Perrichot for the male genitalic nomenclature.

**Data availability**

Requests for materials should be addressed to V.P.

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Author contributions

I.K.-K. conceived and designed the study; led data analysis, made the photographs and drawings, and drafted the manuscript; I.K.-K. and V.F. performed data analysis, made graphical figures, and wrote the manuscript; W.K. performed data analysis and corrected the manuscript.

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Competing interests
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