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The first record of Achilidae (Hemiptera: Fulgoromorpha) in Miocene Dominican amber revealed by synchrotron X-ray tomography

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Abstract

The diversity of planthoppers in the Miocene Dominican amber is considerable but remains underestimated due to the large number of undescribed specimens. Here, we report the first occurrence of the family Achilidae in this amber and provide the first fossil record of the highly diverse tribe Plectoderini, with the description of *Catonia pouilloni* n. sp. The new species is described based on detailed microscopic observations and new X-ray microtomography data. It is diagnosed, and its affinities with other achilids are briefly discussed.

Keywords: Insecta; Auchenorrhyncha; Fulgoroidea; fossil record; micro-computed tomography

1. Introduction

The family Achilidae Stål, 1866 is one of the lesser-known clades within the order Fulgoromorpha Evans, 1946, yet it exhibits remarkable diversity, comprising 521 species of 162 genera (Bourgoin, 2024). Nymphs typically feed on fungi and live on tree barks (O'Brien, 1971), while adults are polyphagous, feeding on the phloem of their various host plants, although the degree of host-specificity remains unclear (O'Brien, 1971; Wilson et al., 1994; Asche, 2015). The family has a worldwide distribution following a latitudinal diversity gradient (Brysz and Szwedo, 2019a), with its highest diversity occurring in tropical and subtropical regions of the Northern Hemisphere.

The Achilidae are currently regarded as the sister group of the Derbidae Spinola, 1839 (Bourgoin, 1993; Urban and Cryan, 2007; Deng et al., 2025). The phylogenetic position of Achilixiidae Muir, 1923 remains debated. This family has been variably treated either as a sub-lineage within Achilidae (Emeljanov, 1991) or as a distinct family (Urban and Cryan, 2007; Bartlett et al., 2018). While some molecular phylogenetic analyses have placed Achilixiidae within Achilidae (Bucher et al., 2023), more recent studies with improved taxon sampling recovered Achilixiidae as monophyletic and distinct from Achilidae (Deng et al., 2025). The Achilidae has been estimated to originate in Late Jurassic (ca. 151 Ma) based on molecular clock anal-

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yses (Deng et al., 2024), whereas fossil-based Bayesian modelling suggests an Early Cretaceous origin (ca. 131 Ma; Boderau et al., 2025).

The classification of Achilidae remains controversial. Following the overview by Bartlett et al. (2014), three subfamilies are currently recognised, encompassing 14 tribes (12 extant and two extinct ones): Achilinae Stål, 1866 (Achilini Stål, 1866; Achillini Emeljanov, 1991), Apatesoninae Metcalf, 1938 (Apatesonini Metcalf, 1938; Ilvini Emeljanov, 1991; Seviini Emeljanov, 1991; Tropiphlepsiini Emeljanov, 1991), and Myconinae Fennah, 1950 (Achiplectini Brysz, Stroiński and Szwedo, 2024; Afrachilini Stroiński, Brysz and Szwedo, 2025; Amphignomini Emeljanov, 1991; Mycarini Emeljanov, 1991; Myconini Fennah, 1950; Niryasaburniini Wang and Bourgoin in Deng et al., 2024; Plectoderini Fennah, 1950; Rhotalini Fennah, 1950; and the fossil tribe Waghildini Szwedo, 2006). The systematic position of Ptychoptilini Emeljanov, 1990, whether within Achilidae or Derbidae, remains uncertain (Emeljanov and Shcherbakov, 2020; Brysz et al., 2022).

The earliest fossil record of Achilidae dates back to the Lower Cretaceous Crato Formation (Hamilton, 1990). To date, 15 genera and 18 species have been described, mostly from mid-Cretaceous Kachin amber and Eocene Baltic amber. *Nabulsitypus wafaai*, described by Kaddumi (2005) from the Early Cretaceous Jordanian amber and tentatively attributed to the Achilidae, is likely *nomen nudum* and warrants re-examination. Although no Miocene species of Achilidae have been formally described, their presence has been reported in the Dominican amber (Szwedo, 2002: p. 44; Brysz and Szwedo, 2019b; Brysz et al., 2022), yet these specimens remain unstudied, unlike those of most other planthopper families.

Here, we report the first confirmed occurrence of Achilidae in the Miocene Dominican amber, represented by *Catonia pouilloni* n. sp., assigned to the tribe Plectoderini, marking its first known fossil record. We discuss the taxonomic affinities of this new species based on morphological evidence derived from classical optical observations and synchrotron-based microtomography.

2. Material and methods

The specimen originates from the La Toca mine, near Santiago de los Caballeros, Santiago Province, Dominican Republic (see map in Penney, 2010: fig. 1). The age of the Dominican amber has long been debated, with estimates ranging widely from 45 to ± 9–15 Ma (Lambert et al., 1985; Schlee, 1990; Landis and Snee, 1991; Grimaldi, 1995; Stach et al., 2019, 2020). However, more recent geological assessments have converged on a late early to early middle Miocene age, approximately 15–20 Ma (see Iturralde-Vinent and MacPhee, 1996, 1999, 2019; Iturralde-Vinent, 2001; Penney, 2010, for review). Accordingly, we adopt a Burdigalian age for the amber from La Toca.

The photographs were taken with an AxioCam MRc 5 camera attached to a Zeiss Discovery V16 stereomicroscope. All the photographs were digitally stacked using Helicon Focus 8 software and processed with Adobe Photoshop CC 2019.

The specimen was scanned at the ANATOMIX beamline at Synchrotron SOLEIL (Saint-Aubin, France) (Weitkamp et al., 2017, 2022). Projection acquisition was performed using a CMOS ORCA Flash 4.0 V2 (Hamamatsu City, Hamamatsu, Japan) in full-frame non-binning mode (2048 × 2048 pixels, physical pixel size 6.5 μm) with a 5× objective lens, resulting in a pixel size of 1.3 μm. The configuration consisted of transmission filters with cumulative thicknesses of 26 μm Au and 100 μm Cu, resulting in an effective mean photon energy around 35 keV. The sample-to-detector distance was set to 1 m. With a 100 ms exposure time, each tomographic scan captured 4000 projection angles, encompassing a 360° acquisition range. The volume reconstruction was performed using PyHST2 software Version 2021c with Paganin correction (Mirone et al., 2014). The volume data segmentation and rendering were performed in ORS Dragonfly (version 2025.1) software, and screenshots of different scene views were exported. The screenshots were post-processed using Pixelmator Pro 3.3.6 Mosaic software.

The systematic framework follows Szwedo (2018) and Bourgoin and Szwedo (2023). Male Terminalia terminology follows Bourgoin (1987). Metatibiotarsal formula (n +(n)/n/n) corresponds to the number of lateral tibial spines + (apical spines of metatibia by groups of spines)/ of the first tarsomere/of the second tarsomere (Mozaffarian et al., 2018). Terminology of the head topological structures follows Stroiński et al. (2025).

Wing venation terminology follows Nel et al. (2012), Bourgoin et al. (2015), adapted by Schubnel et al. (2019) for the postcubitus vein. Venation abbreviations are as follows: C costa; ScP subcostal posterior; RA radius anterior; RP radius posterior; MP media posterior; CuA, first branch of cubitus anterior; CuA, second branch of cubitus anterior; CuP cubitus posterior; PCu postcubitus; A, anal vein. Crossveins are written in lower-case, e.g., *cua-cup* is the crossvein between CuA and CuP.

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Fulgoromorpha Evans, 1946
Superfamily Fulgoroidea Latreille, 1807
Family Achilidae Stål, 1866
Subfamily Myconinae Metcalf, 1938
Tribe Plectoderini Fennah, 1950

Genus *Catonia* Uhler, 1895
Type species: *Catonia intricata* Uhler, 1895 (Island of St. Vincent). The genus is widely distributed from Canada through Central America to Chile (see the list of species

at https://sites.udel.edu/planthoppers/north-america/north-american-achilidae/genus-catonia-uhler-1895/).

Catonia pouilloni Boderau and Nel n. sp.
(Figs. 1–3)

LSID: urn:lsid:zoobank.org:act:6F03DB44-5CD8-427D-8611-21F8E3E7ED7A.

Etymology: The species name honours Jean-Marc Pouillon, who donated the specimen, and is to be treated as a noun in the genitive case.

Holotype: The holotype is included in a 1.4 × 0.2 × 0.9 cm piece of amber. It is complete and well-preserved. It is housed in the amber collection of the Geological Department and Museum of the University of Rennes, France (IGR) under the number IGR.DOM-002.

Diagnosis: Small, 1.46 mm long; body lacking distinct coloration pattern; coryphe as long as broad, greatest width of metope about 1.5 times width at base; coryphe wide reaching two-thirds of length of eyes length; frons and clypeus subequal in length; forewing vein M simple; subcostal cell about, 1/3 length of forewing, wider before its apex; forewing bearing dark spots all other longitudinal veins; hind wing CuA branched.

Age and distribution: Lower Miocene (Burdigalian); Dominican Republic.

Description:

Body. 1.46 mm long (without tegmina), maximum width 0.94 mm across abdomen, dorso-ventrally flattened.

Head. Head with compound eyes with an indentation, slightly narrower than pronotum, ca. 0.90 as wide as pronotum. Coryphe as wide as long in midline. Two carinae present between coryphe and metope, with second apical carina tangent to first, visible from above, but no suture separating coryphe and metope. Anterior margin of coryphe angulate, lateral margin smoothly concave, posterior margin arcuately incised, disc of coryphe depressed, with a strong median carina reaching two-thirds of coryphe length, no sub-horizontal ridge on side of head between eye and anterior margin, coryphe produced before eyes for about one fourth of their length. Metope in mid line 1.1× as long as wide, widest at level of antennal bases, median carina distinct and reaching frontoclypeal suture. Acrometope with shallow depressions. Eumetope bearing a median carina. Clypeus 1.1× longer than eumetope, bearing a median carina almost reaching clypeus apex, lateral carinae extending as prolongations of lateral margins of metope, converging ventrally unfused. Lora visible in ventral view. Rostrum 0.47 mm long, extending beyond base of metacoxae, with apical segment slightly longer than subapical one (ratio 1.1). Base of antenna below compound eye, scape large and rounded, three times wider and longer than pedicel, sensory structures on pedicel not discernable, flagellum about 3.3× longer than pedicel + scape.

Thorax. Pronotum 7.5× shorter than mesonotum, 0.46 mm width, not as long behind eyes as in middle line, anterior margin slightly convex, posterior margin angularly concave, pronotal disc with three distinctly elevated carinae, lateral carinae attaining hind margin, 1.5 times as long as and thinner than median carina, three supernumerary carinae on each side behind eyes, two carinae at each lateral margin between eye and tegula. Mesonotum diamond-shaped, maximum width across midline, distinctly wider than longer, with three subparallel carinae.

Forewings. Tegmina 1.59 mm long, 3× longer than wide, brown patches preserved along wing, costal margin slightly curved, apical margin distinctly convex, anal margin of clavus strongly curved. ScP+R long, forking into ScP+RA and RP at 0.63 mm from forewing base, equal to CuA forking. ScP+RA stem 0.36 mm long, curved towards costal margin and forking into ScP, ScP reaching costal margin obliquely, RA with two terminals. RP with three terminals. Cell C1 closed. Subcostal cell between ScP +RA and RP about 1/3 length of forewing, wider before its apex. Common stem ScP+R+M short. M stem long, almost half of forewing length before *rp-m* crossvein, M simple (more precisely, if anterior branch of M present, appearing as slightly oblique *rp-m* fork and without distal re-emerging from RP). CuA forking in last third of clavus, CuA_1 single and curved upward in basal half, CuA_2 single and situated proximally, *icua* basad of remaining apical veinlets. Clavus 0.89 mm long, more than half of tegmen length. PCu and A_1 fused far after middle of clavus, clavus opened, PCu+A_1 reaching posterior margin of wing slightly basad CuP at apex of clavus.

Hind wings. 1.39 mm long, ScP+RA and RP separating at 0.75 mm from hind wing base; RP stem short, 0.33 mm, forking into two apical branches. ScP+R and M leaving basal cell from same point. M stem long and slightly sinuate, bifurcating into M_{1+2} and M_{3+4} at 0.82 mm from hind wing base, median fold reaching wing margin, *m-cua* basad to *rp-m*. CuA with three terminals, fork of CuA slightly distad to fork of ScP+RA and RP and basad to fork of M. CuP and PCu simple, subparallel to each other, anals veins pattern difficult to establish because of postcubital fold, no crossveins near wing apex.

Legs. Fore and middle legs subequal in length, hind legs significantly longer. All femora similar in shape, flattened. Hind leg 1.1 mm long, hind tibia unispinose (spine in basal half), 1.4× longer than hind femora, teeth gathered in an apical row, lateral ones slightly longer than others. Metatarsi with three tarsomeres, metatarsomeres I 2× longer than metatarsomeres II + III, apical teeth on metatarsomeres I and II equal in length. Metatibiotarsal formula (1 + 1 / 7/ 5).

Male terminalia. Pygofer ventrally symmetrical, dorsal margin slightly shorter than ventral margin in lateral view, unilobed; posterior margin bearing a medioventral process bilobed, each lobe with apical margin roundly convex, extending farther than the medioventral projection. Genital styles tongue-shaped, incurved in their middle portion, broader basally than apically. Anal segment subquadrate in dorsal view; epiproct not exceeding the apical margin of the anal segment; anal tube oval, as long as wide, distinctly exceeding the apical margin of the epiproct. Internal

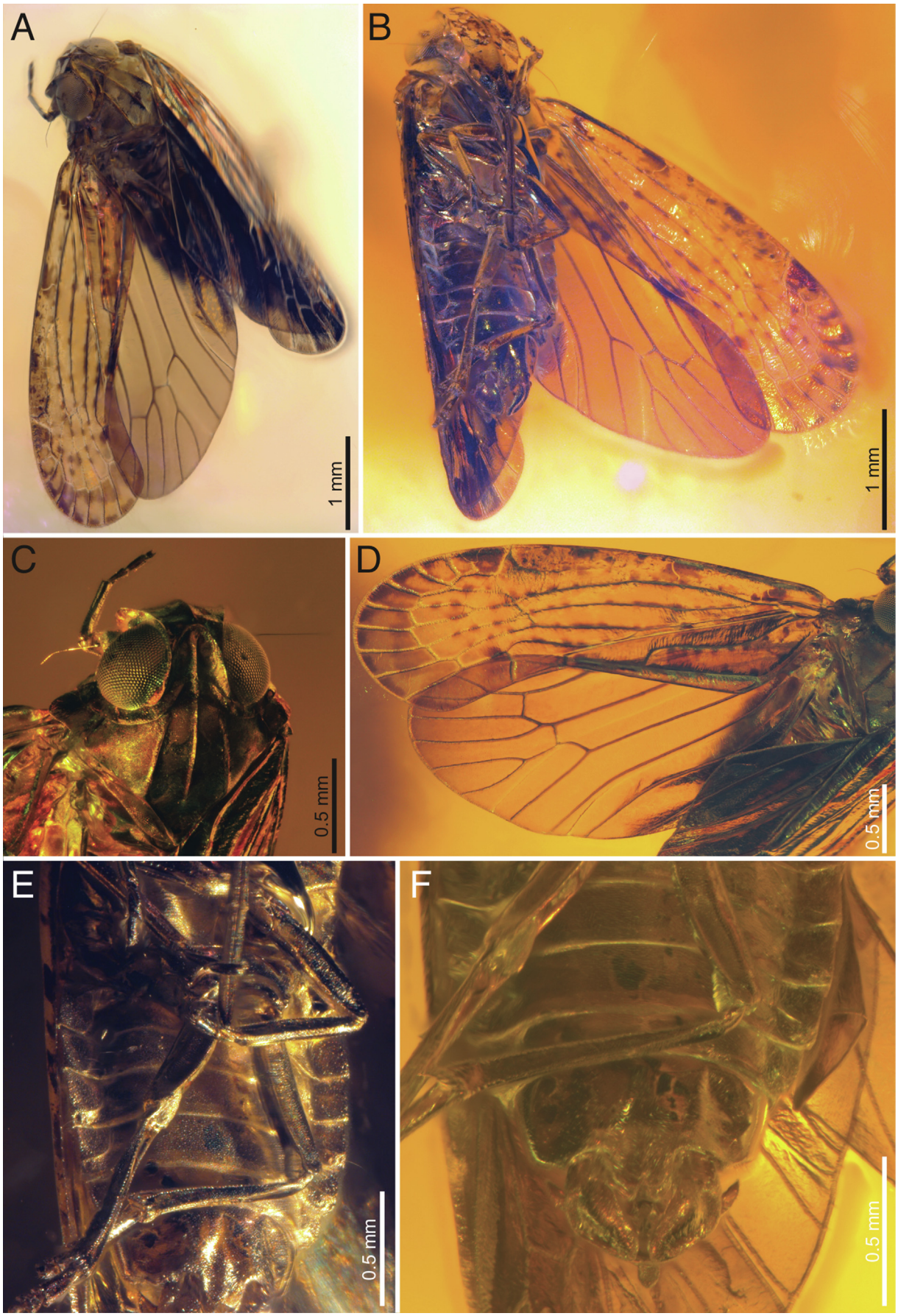
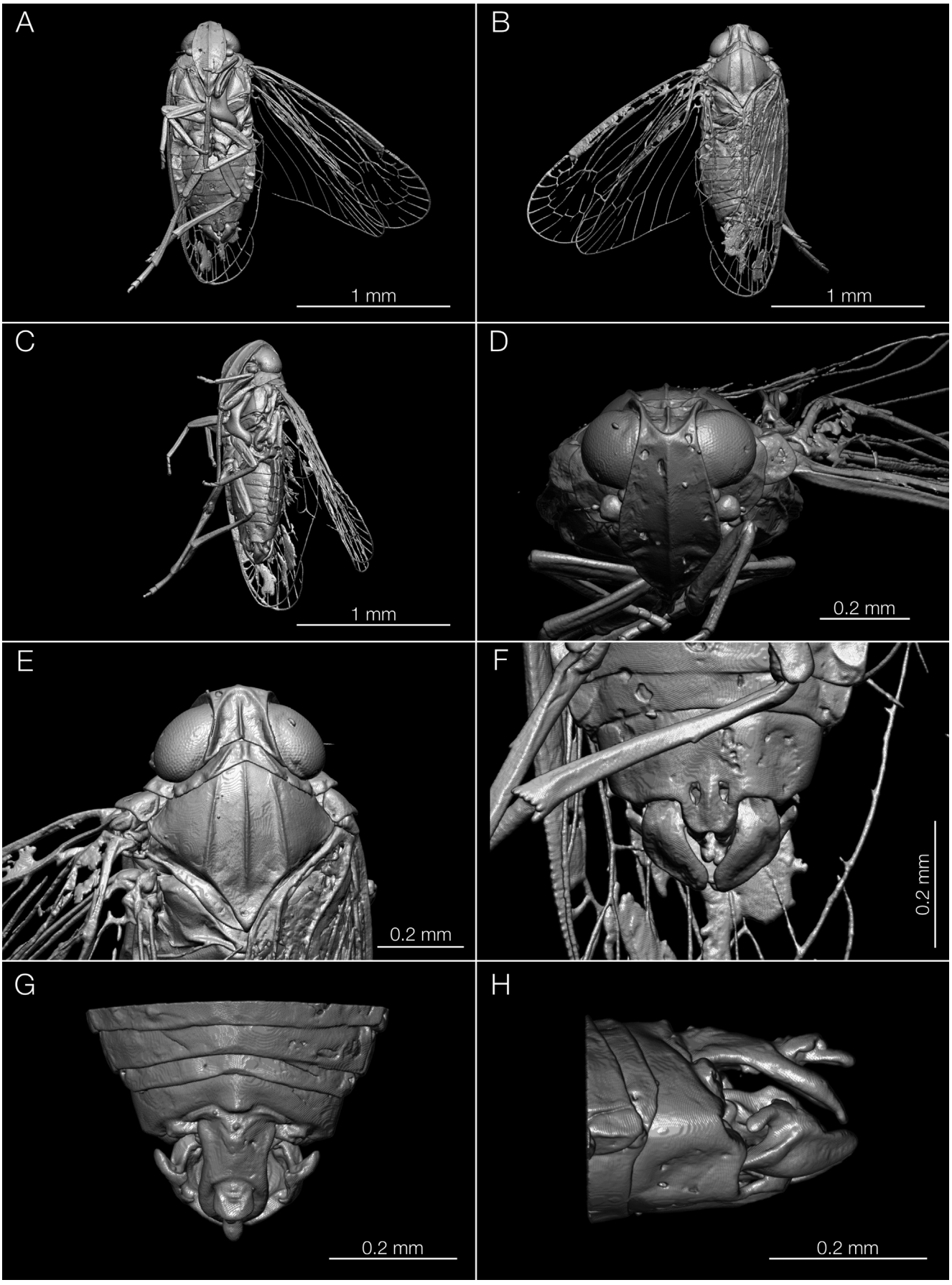


Fig. 1. *Catonia pouilloni* n. sp. (Fulgoromorpha: Achilidae), holotype, IGR.DOM-002. (A) Habitus dorsal view. (B) Habitus ventral view. (C) Head dorsal view. (D) Fore- and hind wings, dorsal view. (E) Legs and abdomen dorsal view. (F) Male genitalia ventral view.


A
1 mm
B
1 mm
C
1 mm
D
0.2 mm
E
0.2 mm
F
0.2 mm
G
0.2 mm
H
0.2 mm

genital structures not preserved and not visible under CT-scan reconstruction.

Locality and horizon: La Toca amber mines, Santiago de Los Caballeros, Santiago Province, Dominican Republic; Lower Miocene (Burdigalian).

4. Discussion

The new fossil can be assigned to the order Fulgoromorpha based on the very short *cua-cup*, the relatively small cells occurring only in the apical part of the forewing and divided by crossveins, and the large media sector (Shcherbakov, 1984; Bucher et al., 2024). Its inclusion within the order Fulgoromorpha is also supported by the transversely wrinkled ambient vein (Bourgoin and Szwedo, 2022) and the configuration of the anal and postcubital vein, with A_1 merging into PCu and PCu distinctly bent at the point of junction with A_1 (Shcherbakov, 1981).

Following the forewing-based key to the families of Auchenorrhyncha Duméril, 1805 proposed by Shcherbakov (1981), the fossil is attributed to the family Achilidae. This assignment is supported by the following combination of characters: fully winged; clavus opened; PCu+A_1 ending at apex of clavus; CuP at very apex curved; clavus without transverse vein; nodal *r-m* at same level as nodal *m-cu*; clavus very long, longer than half wing length; claval plica extending beyond apex of clavus along wing margin. The Achilidae is currently divided into three subfamilies: Achilinae, Myconinae and Apatesoninae (classification history summarised in Brysz and Szwedo, 2019a: fig. 15). Based on the identification keys of Fennah (1950) and Emeljanov (1992) for tribes and genera of Achilidae, affinities with Achilinae, Apatesoninae and most tribes of Myconinae (except Plectoderini Fennah, 1950) can be excluded. This exclusion is supported by the head-to-pronotum proportions, specifically, the head width at coryphe level (ocular distance) exceeding two-thirds of pronotal width.

The new fossil has all the diagnostic characters of the subfamily Myconinae as redefined by Stroiński et al. (2025): coryphe visibly exceeding anterior margin of the eyes. Lora visible in ventral view. Compound eye with an indentation. Metatibial subgenual lateral spine present [in the same paper, Stroiński et al. indicated that the subgenual spine is absent in the Myconinae tribe Plectoderini; our fossil has only one lateral spine]. Tegmina at rest folded flat. Tegmina overlapping [probable but unknown]. Postcostal area narrow, vein M_{3+4} usually not branched. Hind wing veins ScP+R and M do not exit basal cell far apart. Vein A_2 usually widens apically, never reaches wing margin [unknown character]. Median fold reaching wing margin.

After the key to Myconinae tribes of Stroiński et al. (2025), the new fossil keys into the Plectoderini because of the following characters: mesonotum mediolateral carinae present; tegmen RP vein with more than one terminal; CuA never with three terminalia; hind wing median fold exceeding *mp-cua* crossvein; body flattened dorsoventrally; coryphe not extremely elongated; acrometope without lateral compartments; eumetope with full median carina; tibia with one lateral spine; tegmen's cell C1 closed; hind wing veins ScP+R and M leaving basal cell from the same point; tibia with only one lateral spine; tegmen RP with three terminals; tegmen CuA with two terminals; hind wing median fold branched. Stroiński et al. (2025) also indicated that the Plectoderini has a tegmen M with three branches, while it has only one branch in the new fossil. But as in the couplet concerned with this point, the other option is M with six or more terminals in the Myconini, so we can exclude this possibility.

Stroiński et al. (2025) indicated that the Myconini and Plectoderini have a tegmen RP with three terminals, but the exact nature of the first vein reaching the wing margin between RA_1 and RP is rather uncertain in the Plectoderini. For instance, in *Magadhaideus* Long, Chang, Yang and Chen, 2017 the vein is slightly based of RP (Long et al., 2017), the two genera *Clusivius* Distant, 1917 and *Parakosalya* Distant, 1917 have a simple RP, and the genus *Francesca* Kirkaldy, 1906 has a RP with two terminals (Fennah, 1950). Therefore, this character should be interpreted with caution.

The new fossil is assignable to the Plectoderini based on the following combination of characters: ocular distance at least two-thirds the width of pronotum; anterior margin of the pronotum convex or angulate produced medially; tegmina shallowly rounded over dorsum with overlapping membranous areas when folded (as inferred from forewing shape); apical margin strongly convex; venation regular, with ScP+RA bearing a short, sometimes recurved anterior branch; usually six subapical and eight to nine apical areoles; posterior tibia bearing a single spine.

Plectoderini is a large tribe within the Achilidae, currently comprising 99 described genera (Bourgoin, 2024). Following the framework of Fennah (1950), the new fossil would fall in the genus *Catonia* Uhler, 1895, based on the following combination of characters: coryphe width less than twice its median length; presence of latero-apical are-

Fig. 2. *Catonia pouilloni* n. sp. (Fulgoromorpha: Achilidae), holotype, IGR.DOM-002, μ-CT scan morphological renderings. (A) Habitus ventral view. (B) Habitus dorsal view. (C) Habitus lateral view. (D) Head anterior view. (E) Head and thorax dorsal view. (F) Male genitalia ventral view. (G) Anal segment dorsal view. (H) Male genitalia lateral view.

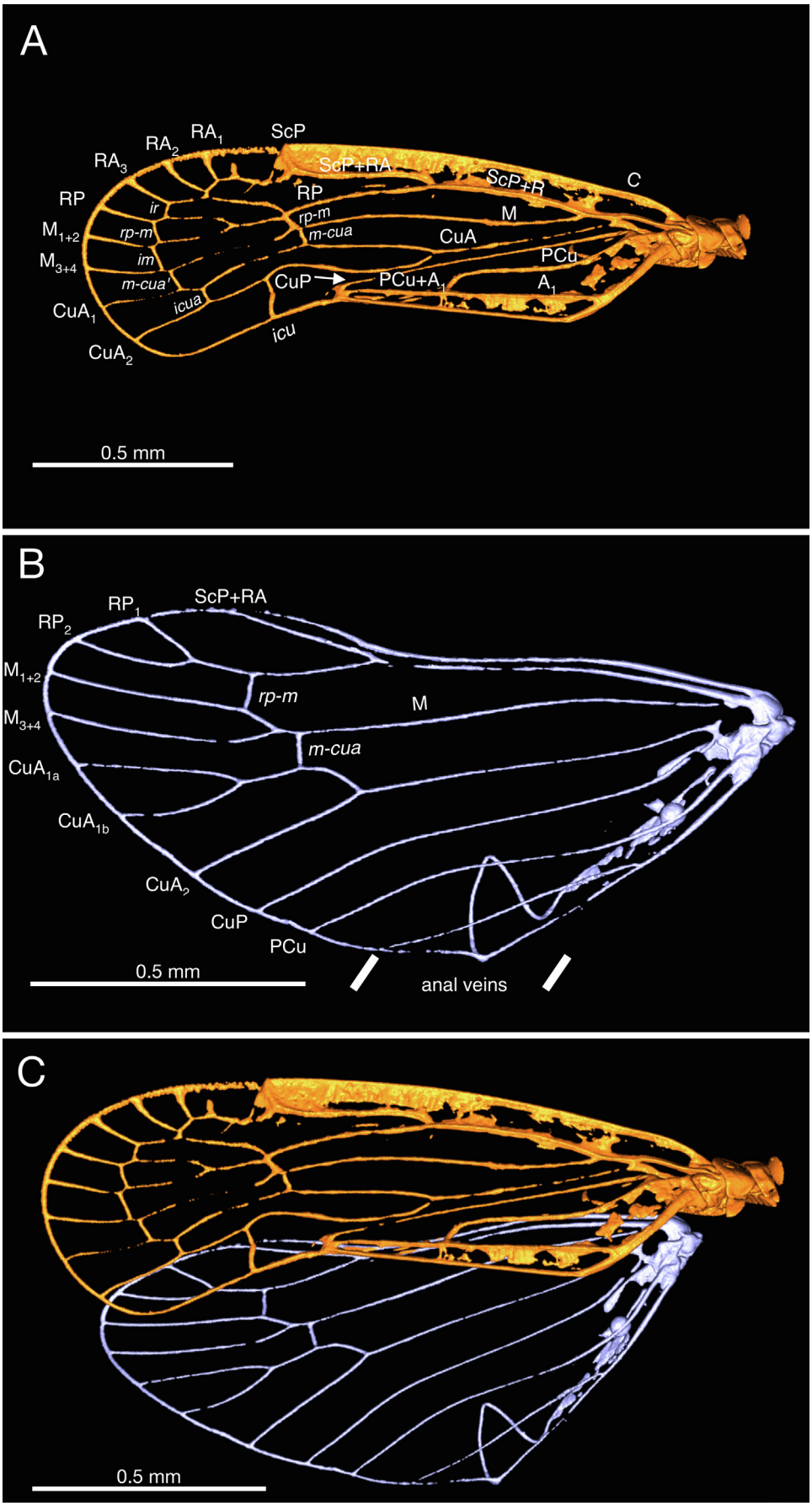


Fig. 3. *Catonia pouilloni* n. sp. (Fulgoromorpha: Achilidae), holotype, IGR.DOM-002. (A) Forewing venation reconstruction. (B) Hind wing venation reconstruction. (C) μ-CT scan morphological rendering of forewing and hind wing isolated from rest of body.

olets; coryphe bearing two transverse carinae at apex, usually enclosing a more or less distinct triangular facet on each side near the base of metope; latero-apical triangular facets of coryphe feebly demarcated on their frontal margin, each traversed horizontally by a short carina arising from lateral margin; coryphe relatively short; latero-apical facets of coryphe not replaced by callus; coryphe strongly so in basal half, when lateral margins are somewhat raised; coryphe acutely angulate at apex, conical in outline; latero-apical facets of coryphe oblique, largely visible in dorsal view; pronotum with areolets laterad of disk, lateral carinae of disk three times as long as median carina; mesonotum without a transverse callus on disk.

Fennah (1965a) noted that some species of *Koloptera* Metcalf, 1938, resemble *Catonia*. The new fossil differs from *Koloptera* by the absence of a sub-horizontal ridge on the side of the head between the eye and the anterior margin.

The attribution in *Catonia* is further supported using O'Brien (1971)'s identification key for Nearctic achilid genera, based on the following combination of characters: hind tibia with one spine in basal half; medioventral lobe of male pygofer present; metope less than 1.5 times as long medially as broad; ScP+R fork of forewing near level of union of claval veins, subcostal cell about half length of forewing; medioventral lobe of male pygofer bifurcate. The apically bifurcate medioventral lobe of the male pygofer is a particularly strong argument for the placement in *Catonia* (O'Brien, 1971), as character is otherwise only found in *Plectoderes* Spinola, 1939. Nevertheless, an attribution to *Plectoderes* is excluded due to the much narrower coryphe and the presence of nine post-pterostigma cells in the fossil *versus* 10 in *Plectoderes* (Fennah, 1950).

Wilson and McPherson (1980) and Bartlett et al. (2011) separated *Catonia* from *Synecdoche* O'Brien, 1971 based on the forewing subcostal cell, between ScP+RA and RP about 1/3 length of forewing, wider before its apex *versus* longer than 1/3 length of forewing, narrow throughout. The new fossil shares a similar character state to most representatives of the genus *Catonia*. However, this character alone seems insufficient to separate these two genera, as *Catonia ornatipennis* (Blanchard in Spinola, 1852) has a subcostal cell narrow throughout and much longer than 1/3 length of the forewing (Fennah, 1965b: fig. 136).

Other non-genitalic characters supporting the assignment include: a long rostrum reaching the apex of the hind coxae; paired lateral marginal carinae running from the base of the tegulae toward the eye; and simplified hind wing venation with RP two-branched, M two-branched, and CuA three-branched (O'Brien, 1971).

In the new fossil, M is simple, while forked in all *Catonia* (Fennah, 1950; Caldwell and Martorell, 1951), a rare character among the Plectoderini (e.g., present in *Paragandecca* Fennah, 1950). However, *Paragandecca* strongly differs from the fossil in the shape of the head (coryphe distinctly wider than longer, without any median carina, no carina between coryphe and metope). *Opsiplanon* Fennah, 1945 also has a simple M, although Fennah (1950: p. 134, fig. 92) interpreted it as having two branches, but if its alleged anterior branch was present, then it would be fused with RP, a situation identical to that of the new fossil. *Opsiplanon* has a short ScP+RA distal of RP base, the coryphe produced before the eyes for about a third of their length, while one fourth in the new fossil. Also, its rostrum is attaining post-trochanters *versus* distinctly longer in the new fossil, and hind wing RP is simple *versus* forked in the new fossil. Nevertheless, in at least one *Catonia* species, the anterior branch of M is rudimentary, viz. in *C. pallida* Fennah, 1945 (Fennah, 1945: fig. 361). This species has a fore- and hind wings venation strongly similar to that of the new fossil. Consequently, we consider that the simple M is not sufficient, alone, to exclude the new fossil from *Catonia* and attribute it to a new genus.

Catonia is widespread in the New World and includes 40 species (Bourgoin, 2024). Fennah (1950: p. 147) distinguished the subgenus *Catonia* from the subgenus *Pyren* Fennah, 1950 based on the following characters: 'coryphe distinctly broader than long; greatest width of metope about 1.5 times width at base' in *Pyren versus* 'coryphe about as long as broad; greatest width of metope fully twice width at base' in *Catonia*. In the new fossil, the coryphe is about as long as broad (supporting an attribution to *Catonia*), but the greatest width of metope about 1.5 times width at base (supporting an attribution to *Pyren*). Therefore, the new fossil questions the separation between these two subgenera. A phylogenetic analysis of all the species of *Catonia* would be necessary to precise this point.

Nevertheless, this combination of traits distinguishes the fossil from all species of *Catonia* studied by Fennah (1950), viz. *C. intricata* Uhler, 1895, *C. sobrina* (Fowler, 1904), *C. albidovariegata* (Fowler, 1904), *C. chiriquensis* (Fowler, 1904), *C. sancti-vincenti* Fennah, 1950, *C. sanctae-luciae* Fennah, 1950, *C. mitrata* Fennah, 1950, *C. antiguana* Fennah, 1950, *C. major* Fennah, 1950, *C. digitalis* Fennah, 1950, *C. dominicana* Fennah, 1950, *C. montserratensis* Fennah, 1950, *C. sancti-geronimi* Fennah, 1950, *C. bugabae* Fennah, 1950, *C. zunilana* Fennah, 1950, *C. championi* Fennah, 1950, *C. muscosa* Fennah, 1950, *C. moraballi* Fennah, 1950, *C.* (*Pyren*) *saltator* Fennah, 1950.

Among the species not studied by Fennah (1950), *Catonia antillicola* Wolcott, 1936 differs from the new fossil by its narrow coryphe, which projects anteriorly to about half its length before the eyes (Caldwell and Martorell, 1951). A similarly produced coryphe is also observed in *C. sobrina* (Fowler, 1904) and *C. pallida* Fennah, 1945 (Fowler, 1904; Fennah, 1945). Other species, including *C. nava* (Say, 1830), *C. cinctifrons* (Fitch, 1856), *C. picta* Van Duzee, 1908, *C. pumila* Van Duzee, 1908, *C. bicinctura* Van Duzee, 1915, *C. carolina* Metcalf, 1923, *C. lunata* Metcalf, 1923, *C. pini* Metcalf, 1923, *C. pallidistigma* Fennah, 1945, *C. texana* O'Brien, 1971, and *C. antillicola* all have a metope with the greatest width roughly twice the width at its base (Wolcott, 1936; Fennah, 1945;

O'Brien, 1971), unlike the condition observed in the new fossil. Additionally, *C. cinerea* Osborn, 1935, and *C. dorsovittata* Caldwell, 1951 possess a coryphe that extends only to about half the length of the compound eye posteriorly, whereas in the new fossil, the coryphe reaches approximately two-thirds the length of the eye (Caldwell and Martorell, 1951).

C. arbutina Ball, 1933 has a metope whose greatest width is about 1.5 times the width at its base, but its body is much larger than that of the new fossil (O'Brien, 1971). *C. arida* Caldwell in Caldwell and Martorell, 1951, also has a very broad metope at its base, yet its coryphe extends only to about half the length of the eye (Caldwell and Martorell, 1951). Similarly, *C. haitiensis* Dozier, 1931 has a very broad metope basally, but it narrows markedly posteriorly (Dozier, 1931). In *C. rufula* Osborn, 1926, the coryphe tapers towards the tip, unlike in the new fossil (Osborn, 1926). Both *C. ornatipennis* and *C. maculata* (Blanchard in Spinola, 1852) have a coryphe that is distinctly shorter than wide (Fennah, 1965b; Campodonico, 2021: fig. 12). Taken together, these morphological differences clearly distinguish the new specimen from all previously described species, justifying the establishment of a new species within the genus *Catonia*.

5. Conclusion

The discovery of *Catonia pouilloni* n. sp. helps to better understand the past diversity of planthoppers, providing the first and only record of Achilidae in the Miocene, as well as providing a calibration point for the Plectoderini tribe, which is highly diverse today. Our study highlights the importance of pursuing the description of the Fulgoromorpha fossils from the Miocene Dominican amber, as the diversity of this group is still significantly underestimated.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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