



A new fossil inchworm moth discovered in Miocene Dominican amber (Lepidoptera: Geometridae)

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ABSTRACT

We report a fossil geometrid moth, a male, virtually complete, preserved in a clear piece of Miocene Dominican amber dating from 19 to 16 Mya. Fore- and hindwings appear partially overlapped, and all body characters are visible externally in dorsal and ventral views, including the outer surface of the valvae of the genitalia. The scale pattern on the wing membrane is preserved, whereas the wing color pattern is not. It belongs to the genus *Dolichoneura* (Geometridae: Desmobiathrinae) and is named *Dolichoneura jorelisa* Sarto i Monteys, Hausmann, Baixeras and Peñalver sp. n., based on wing features. Because of the poor fossil record of lepidopterans, both in amber and compression rocks, the description of the available well-preserved specimens is of considerable interest for phylogenetic studies. Furthermore, it could also serve for calibrating molecular clocks and for paleo-biogeographic inferences.

1. Introduction

So far, the oldest known fossil lepidopteran, *Archaeolepis mane* Whalley (1985), is from the Lower Jurassic (Sinemurian, ca. 190 Mya) of England (Whalley, 1985). Yet, phylogenomic studies by Kawahara et al. (2019) suggest that the most recent common ancestor of crown Lepidoptera appeared perhaps significantly earlier, in the Late Carboniferous, ca. 300 Mya, although this estimation might be biased (this age is very close to the initial appearance of the Holometabola) and should be confirmed by further studies.

Although Lepidoptera is one of the megadiverse orders of insects and one of the most abundant around different terrestrial ecosystems, they are, due to taphonomical processes (Martínez-Delclòs and Martinell, 1993), among the rarest findings amid insect orders in deep time, mostly occurring in ambers. Yet, imagoes of macrolepidopterans are rare as

inclusions in ambers, principally because they live and eat far from the trunk or big branches of resiniferous trees, from where the resin would mostly ooze (Solórzano Kraemer et al., 2018). Actually, macrolepidopteran wings can get caught very easily in resin, so their size is not that important. If they get trapped in resin emissions on a tree trunk or branch, the ants will have easy access and will eat them before the next flow arrives covering the carcasses (MMS-K, XD, EP, personal observation, Madagascar). All this contributes to the scarcity of their inclusions in ambers.

Geometridae, whose age was estimated at about 54 Mya, in the Eocene (credibility interval of 62 to 48 Mya corresponding to Middle Paleocene–Early Eocene) (Yamamoto and Sota, 2007; Wahlberg et al., 2013), stand as the second most species-rich family of Lepidoptera, comprising ca. 24,000 described species (van Nieukerken et al., 2011; Murillo-Ramos et al., 2019). They belong to the superfamily

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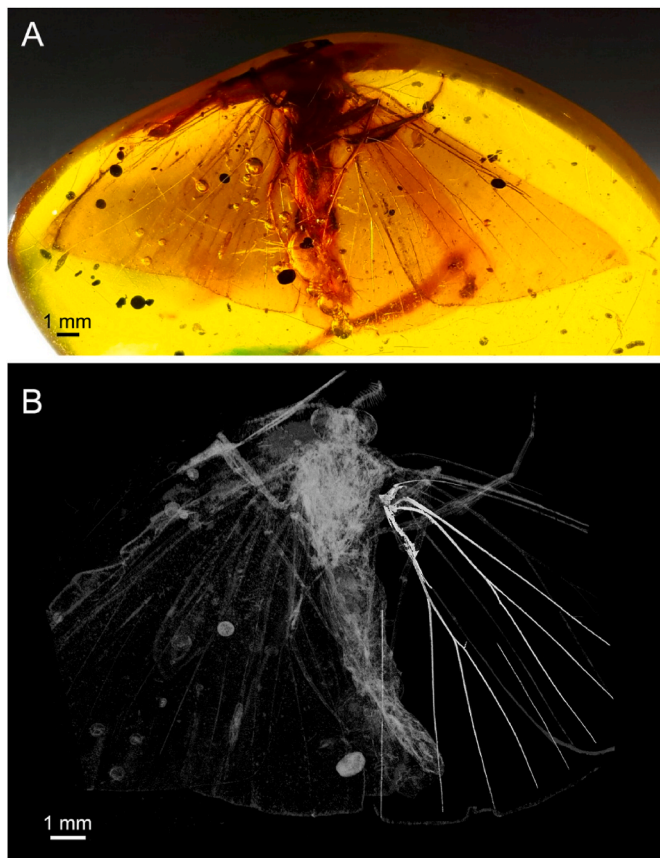


Fig. 1. Habitus of †*Dolichoneura jorelisae* sp. n. (Geometridae: Desmoba-thrinae), holotype. (A) Dominican amber piece with the geometrid specimen, ventral view. (B) Virtual representation (SR μ CT) of the geometrid specimen in ventral view, with the hind wing venation enhanced.

Geometroidea, which traces back to 83 Mya (Wahlberg et al., 2013). Geometrids are characterized by the presence of paired tympanal organs placed at the base of the abdomen; they occur throughout the family, in both sexes, although they are secondarily reduced or lost in a very few flightless females (Cook and Scoble, 1992). The prolegs of their larvae are usually reduced to two pairs causing the larvae to move by ‘looping’ (Minet and Scoble, 1999), that is where the names “inchworm”, “loopers” and “Geometridae”, as for ‘earth-measuring’, come from. A comprehensive molecular study by Murillo-Ramos et al. (2019, 2021) proposed recognizing nine mostly monophyletic geometrid subfamilies: Sterrhinae, Larentiinae, Archiearinae, Desmoba-thrinae, Orthostixinae (validity controversial), Epidesmiinae, Oenochrominae, Geometrinae, and Ennominae.

Despite of being one of the most specious family groups of Lepidoptera, the fossil record of Geometridae is comparatively very scarce, with only 19 findings formally reported worldwide, most of them of difficult systematic assignment. The affiliation of two of them is disputed by Sohn et al. (2012). They were all listed and reviewed by Zhang et al. (2020), who noted that *Eogeometer vadens* Fischer, Michalski and Hausmann, 2020 (Bartonian–Priabonian, Baltic amber), *Geometridites larentiiformis* Jarzembowski, 1980 (Upper Priabonian, Bembridge Marls, of the Isle of Wight), and *Hydriomena protrita* Cockerell, 1922 (Priabonian, Florissant Fossil Beds), all from the Late Eocene, were believed to be the earliest representatives of Geometridae.

To date, 31 fossil specimens within seven superfamilies of ditrysian Lepidoptera had been reported from amber collected in the Dominican Republic (Grimaldi and Engel, 2005; Sohn et al., 2012; Zhang et al., 2020), with an estimated age of ca. 19–16 Mya (Iturralde-Vinent and MacPhee, 2019). Among the known fossil geometrids worldwide, four

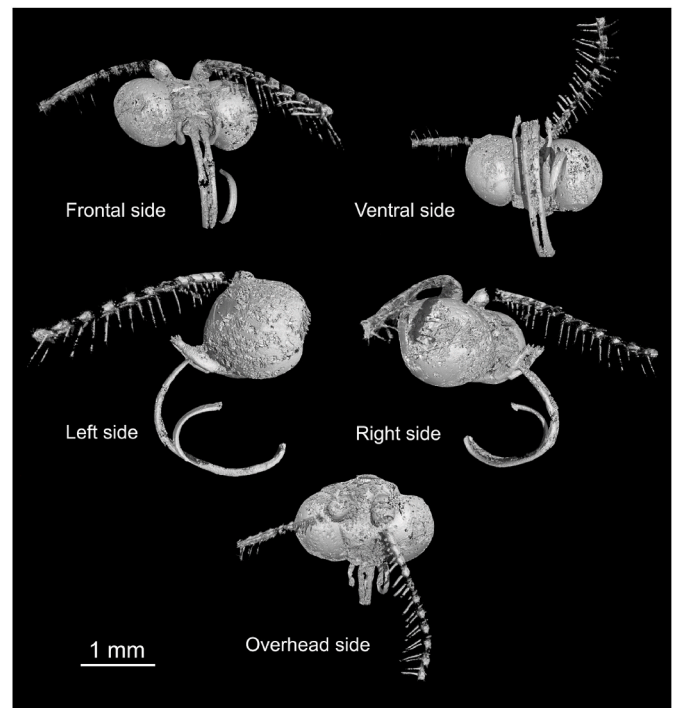


Fig. 2. Virtual representation (SR μ CT) in different views of the head of †*Dolichoneura jorelisae* sp. n. (Geometridae: Desmoba-thrinae), holotype. Both antennae are distally incomplete due to the limits of the scan; in the amber piece one distal end was kept within it (see Fig. 3B).

are from amber collected in this area: (1) an adult assigned to Ennominae, plus (2) a caterpillar and (3) another adult, both unassigned, figured but undescribed (Grimaldi and Engel, 2005), and (4) an adult assigned to Ennominae, described as *Miogeometrida chungjenshihi* Zhang et al., 2020 (Zhang et al., 2020). Here we report a fifth geometrid moth included in Dominican amber.

2. Materials and methods

The type specimen in amber described herein is housed at the Museo Nacional de Historia Natural “Prof. Eugenio de Jesús Marcano”, Santo Domingo, Dominican Republic, with the accession number MNHNSD FOS 16.01. The piece that includes the moth originates from the eastern amber mines of Hato Mayor-El Valle Region, Dominican Republic (Eastern district in Iturralde-Vinent and MacPhee, 2019); it is oval, weighs 3.58 g, with dimensions 31 mm by 20 mm, and a height of 10 mm–2 mm since it is flattening from one side to the other, no internal cracks are visible and no syninclusions are observed. The moth is situated centrally within it, with its head contacting one outer border (Fig. 1). The piece was delivered to us by Mr. Jorge Caridad, from his private collection in the Amber World Museum. Mr. Jorge Caridad is known to most authors, and is an established and trusted source.

2.1. Spectroscopy

The amber piece was kept at constant temperature in plastic clip bags within metal boxes during the study to exclude oxygen and light. To determine its origin and establish a molecular fingerprint, we carried out a Fourier Transform Infrared Spectroscopy (FTIR) (see results below). To ensure the piece containing the moth was amber, and not copal or Defaunation resin (*sensu* Solórzano-Kraemer et al., 2020), its FTIR spectrum was compared to that of two pieces of amber found by us in the field, one in the Northern district (Palo Quemado) and another in the Eastern district (El Valle - Mina Siete Cañadas), the latter belonging to

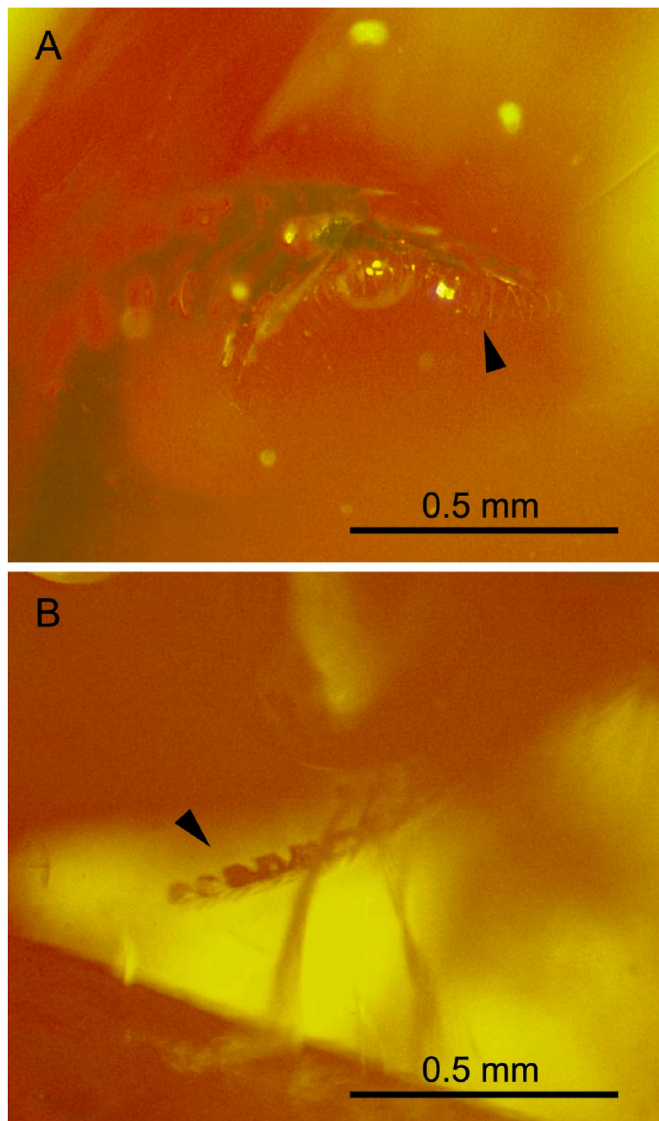


Fig. 3. Cilia on antennal flagellum of †*Dolichoneura jorelisa* sp. n. (Geometridae: Desmobathrinae), holotype. (A) Flagellum densely setose ventrally (arrowhead), seen on the left antenna, sectioned in the amber surface. (B) Cilia shorten progressively as they approach the distal end, where the antennae look serrate (arrowhead). Both images are Z-stacked.

the same location from where the piece including the moth was collected.

A tiny bit was removed from the amber sample for FTIR analysis at one edge. The latter was conducted using an IR PerkinElmer Frontier spectrometer that utilizes a diamond ATR system with a temperature stabilized DTGS detector and a CsI beam splitter at the Molecular Spectrometry Unit of the CCiTUB (Centres Científics i Tecnològics of the Universitat de Barcelona). To avoid breaking the piece of amber containing the moth, the FTIR was performed using a Thermo SCIENTIFIC NICOLET iN10 MX, reflexion, detector MCT, overtone 100 μ , accumulation 64 scans, spectral resolution 4 cm^{-1} , Kramers-Kronic.

2.2. Stereomicroscopy and photography

The specimen was examined and drawn by using an optical microscope Olympus BH-2 equipped with an Olympus camera lucida, and photomicrographs were taken using a digital camera (Leica M80 Camera) attached to a Leica IC90 E stereomicroscope, at the laboratory of the Museu Valencià d'Història Natural (Alginet, València). These devices

used cool white LED illuminators. Images were prepared for illustration using Adobe Photoshop CS2, and some of them were z-stacked. The body length was measured from the frons to the end of the abdomen.

2.3. Synchrotron radiation micro-computed tomography (SR μ -CT)

In order to observe morphological details which could not be properly seen under a stereomicroscope, the inclusion was additionally studied by synchrotron radiation based x-ray micro tomography (SR μ CT). Imaging was performed at the Imaging Beamline – IBL P05 – PETRA III at Deutsches Elektronen Synchrotron (DESY) in Hamburg operated by the Helmholtz-Zentrum Hereon (Greving et al., 2014; Wilde et al., 2016). Due to the size of the specimen imaging was done in an extended field of view (eVoF) mode ($\sim 12 \text{ mm} \times 5 \text{ mm}$). 12,602 projections have been recorded at 6001 angular steps equally spaced between 0 and π . Projections were recorded at a photon energy of 18 keV and a sample to detector distance of 30 mm using a custom build CMOS detector (Lytaev et al., 2014). Tomographic reconstruction was done with a beamline specific stitching and processing workflow (Moosmann et al., 2014; Beckmann pers. comm., June 2019) implemented in Matlab (Math Works) and IDL (Harris Inc) using the filtered back projection algorithm implemented in the Astra Toolbox (van Aarle et al., 2015, 2016; Palenstijn et al., 2011). Raw projections have been binned two times for processing, resulting in an effective pixel size of 1.28 μm in the reconstructed tomographic volume.

2.4. Systematics

Family-level classification follows van Nieuwerkerken et al. (2011). Terminology of veins follows Hausmann (2001).

3. Results

3.1. Systematic paleontology

Order Lepidoptera Linnaeus, 1758
 Suborder Glossata Fabricius, 1775
 Clade Ditrysia Börner, 1925.
 Superfamily Geometroidea Leach, 1815
 Family Geometridae Leach, 1815
 Subfamily Desmobathrinae Meyrick, 1886
 Genus *Dolichoneura* Warren, 1894

†*Dolichoneura jorelisa* Sarto i Monteys, Hausmann, Baixeras and Peñalver, sp. n.

Figs. 1–7.

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3.2. Diagnosis (male)

The species can be distinguished from other species of the genus by the following combination of wing characters: pointed forewing apices, relatively straight forewing termen, a well-developed double areole and absence of anastomosis between $\text{Sc} + \text{R}_1$ and Rs in the forewing, the size of the forewing discal cell relatively longer than in other species of the genus, the point where M_2 arises from the forewing discal cell relatively closer to M_1 than to M_3 in comparison to other species of the genus, an evenly rounded hindwing termen, and a rather weak but tubular M_2 vein in the hindwing.

Holotype: Specimen code MNHNSD FOS 16.01, male (Figs. 1–7).

Repository: Museo Nacional de Historia Natural “Prof. Eugenio de Jesús Marciano”, Santo Domingo, Dominican Republic.

Etymology: The specific name is dedicated to Ms. Jorelis Caridad, daughter of Mr. Jorge Caridad, who entrusted us with this piece. She is well-known for her dedication to preserving and promoting the study of Dominican amber.

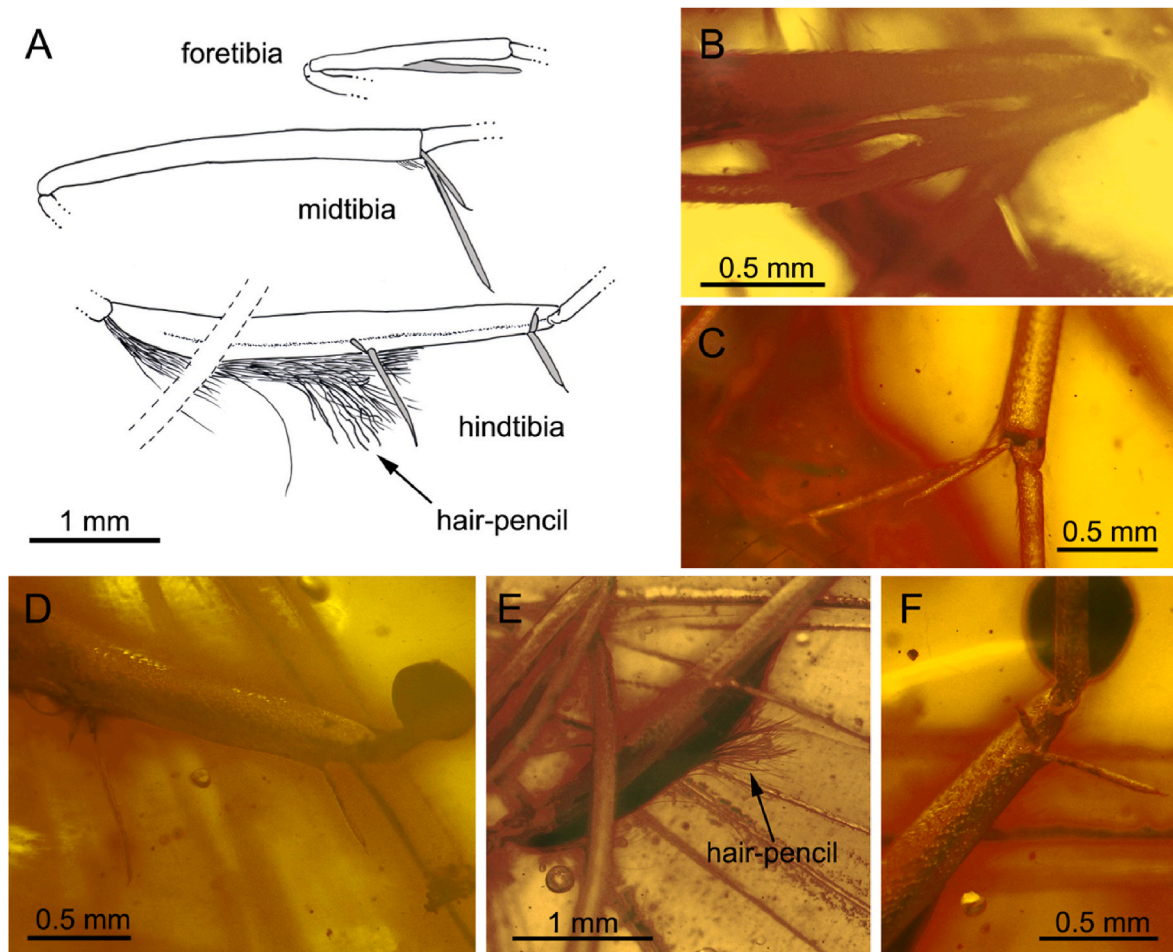


Fig. 4. Tibiae of †*Dolichoneura jorelisae* sp. n. (Geometridae: Desmobathrinae), holotype. (A) Camera lucida drawings of left tibiae; note that mid and hindtibiae show spurs not present in foretibia. (B) Left foretibia. (C) Left midtibial spurs. (D) Left hindtibia. (E) Left hindtibia: detail of hair-pencil; also two unequal spurs projecting from its central part. (F) Left hindtibia: two unequal spurs projecting from its distal part. Images D and F are Z-stacked.

Locus typicus: Amber mine of Hato Mayor-El Valle Region, Dominican Republic.

Stratum typicum: The piece was found in stratigraphic levels of the Yanigua Formation, in the boundary between Early–Middle Miocene, 17–16 Mya (Iturralde-Vinent and MacPhee, 2019).

3.3. Description. Male

Head: Vertex and frons scaled. Eyes well developed. Antennae dentate, scaled dorsally, densely ciliate-setose ventrally, length of cilia at basal part of antennae *ca.* three times the width of flagellum (Fig. 2); cilia shorten progressively as they approach the distal end, where the antennae look serrate (Fig. 3B). Ocelli not visible. Chaetosemata present, paired. Labial palpi upturned, not extending dorsally beyond frons, first and second segments about the same length, the second being slender, third segment small, about one fourth the length of the first two segments. Maxillary palpi not visible. Haustellum well developed, *ca.* 4.5 mm in length, coiled, unscaled, with distal part broken and kept next to the main part (Fig. 2).

Thorax: Scaled. Legs elongate; foretibia without tibial spurs, but showing a conspicuous single process arising from its centre; spur formula 0-2-4, pairs of spurs unequal; hindtibia with well developed hair-pencil, partially retractable in a groove (Fig. 4).

Wings. Forewing length: 15.7 mm, with pointed apexes; no trace of wing color pattern (Fig. 5). Costa slightly convex at base, central portion rather straight, distal part convexly curved from the point where R_2 meets the costa to pointed apex, termen straight, tornus broadly curved;

forewing venation fairly complete with characteristic double areole involving distal part of Sc , basal half of R_1 and base of Rs , R_1 from the areole, R_2 and R_3+R_4 connate in the areole, R_4 to costa, R_5 from areole to termen; discal cell 0.4 the length of the wing, discocellular vein complete, M_1 , M_2 and M_3 approximately equidistant at base; CuA_1 closer at base to M_3 than to CuA_2 ; hindwing venation unmodified, $Sc + R_1$ and Rs unanastomosed, $Sc + R_1$ rather straight to apex, Rs sinuous on discal cell, M_1 , M_2 , M_3 rather equidistant on the discal cell, M_2 tubular although less developed than M_1 and M_3 (Fig. 6), base of CuA_1 closer to M_3 than to CuA_2 .

Abdomen: Long, slender, covered by appressed scales. Male genitalia with valvae closed, well delimited externally but structural details poorly visible, uncus apparently robust, prominent, valva elongate with rounded edges (Fig. 7).

3.4. Infrared absorption spectrum of amber piece studied

The infrared absorption spectrum of the amber piece that includes the moth is shown in Fig. 8 (in red), where the basic skeleton of amber is an aliphatic structure. It is dominated by an asymmetric telescopic vibration of ν (CH₂) located at 2928 cm^{-1} (small C–H stretching band), symmetric telescopic vibration of ν (CH₂) located at 2865 cm^{-1} , transformative vibration of δ (CH₂, CH₃) located at 1465 cm^{-1} (intense C–H band), the symmetric transformative vibration of δ (CH₂, CH₃) located at 1380 cm^{-1} , and telescopic vibration of ν (C=O) located at 1725 cm^{-1} (intense carbonyl band), and telescopic vibration of ν (C–O) located at 1245 cm^{-1} , 1135 cm^{-1} , and 1030 cm^{-1} . Hydroxyl bands near 3500

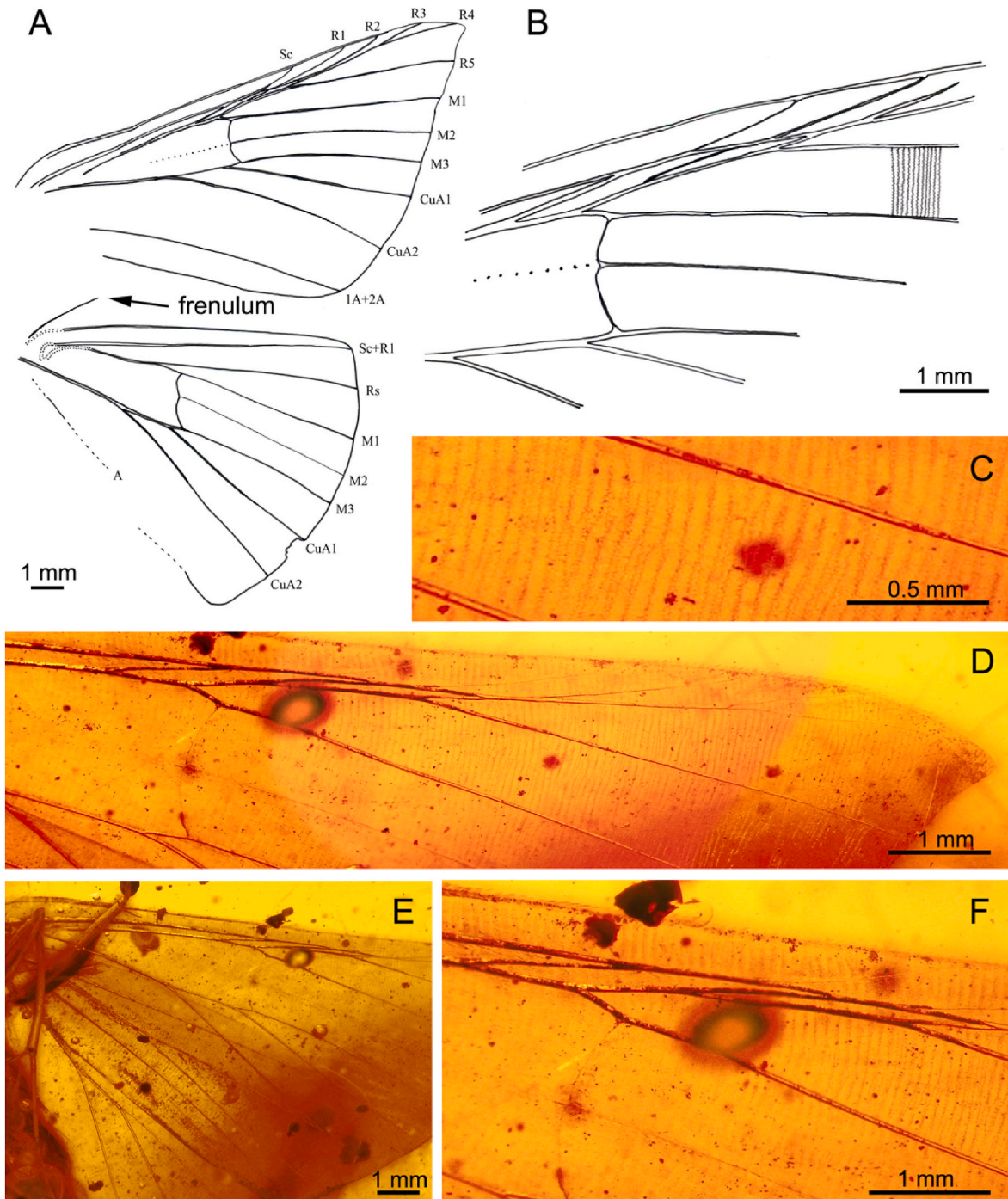


Fig. 5. Wing venation and preserved scale pattern of *Dolichoneura jorelisa* sp. n. (Geometridae: Desmobathrinae), holotype. (A) Camera lucida drawing of fore- and hindwing. Note the absence of anastomosis between Sc + R₁ and Rs on the hindwing. (B) Same, showing detail of anterior venation and scale pattern of forewing. (C) Detail of scale pattern preserved on forewing. (D) Costal part of left forewing (underside). (E) Detail of left fore- and hindwing (underside) partially overlapped. (F) Detail of the well-developed double areole on forewing. Images D and F are Z-stacked.

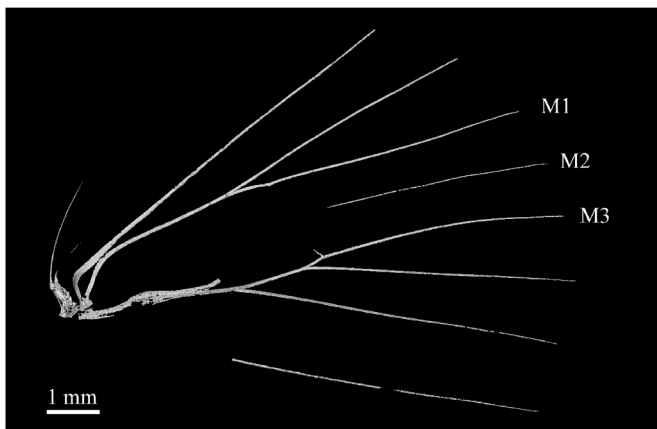


Fig. 6. Virtual representation (SR μ CT) showing hindwing venation of *Dolichoneura jorelisa* sp. n. (Geometridae: Desmobaethrinae), holotype. Note that M₂ is tubular although less developed than M₁ and M₃.

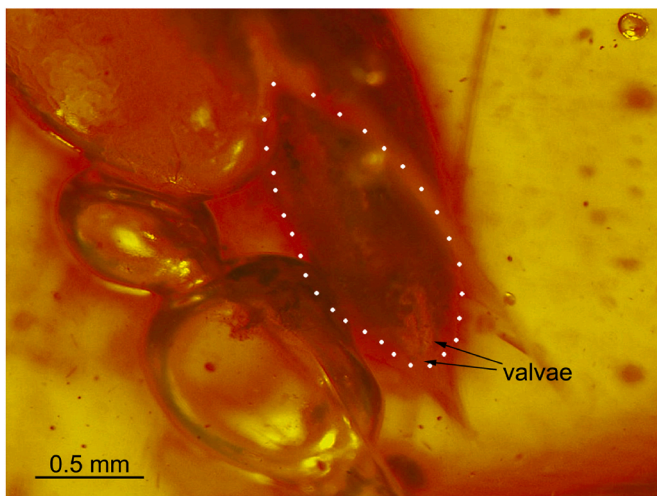


Fig. 7. Micrograph showing the male genitalia, delimited by white dots (ventral view), of *Dolichoneura jorelisa* sp. n. (Geometridae: Desmobaethrinae), holotype. Z-stacked image.

cm^{-1} are also present. The spectrum of the piece that contains the geometrid is very similar to those from two geological Dominican amber localities. These are El Valle-Siete Cañadas (2018 own extraction in the Eastern district of the island, in Iturralde-Vinent and MacPhee, 2019, in blue) and Palo Quemado (2019 own extraction in the Northern district, in green), their main difference being the presence of a small band near 1200 cm^{-1} in the latter.

4. Discussion

As usual in the study of fossil Lepidoptera, characters of the genitalia, which are of most interest for a suitable identification, are not accessible despite 3D preservation in amber and having explored the structure through SR μ -CT.

The wings show pointed forewing apex, relatively straight forewing termen and an evenly rounded hindwing termen, rather unusual wing shape characters that deserve some attention. Except for minor damage

in the posterodistal margin of the left hindwing, the wings are quite well preserved. We may conjecture that the moth became trapped in resin shortly after emerging and was rapidly and entirely covered by subsequent resin flows. Yet, their venation, usually of supraspecific value, is reasonably well marked and allows, in some detail, a taxonomical assignment.

The most striking venation characters of this fossil moth are the presence of a well-developed double areole in the forewing, and the absence of anastomosis between Sc + R₁ and Rs, as well as a rather weak but tubular M₂ vein in the hindwing. A forewing areole is common in some subfamilies of Geometridae, mostly Orthostixinae, Desmobaethrinae, Larentiinae and Sterrhinae (Hausmann, 2001). The areole is formed by a variable degree of anastomosis of R₁ and Rs veins, occasionally involving Sc. In this fossil, the areole is clearly affecting distally Sc as well as basally R₁ and Rs veins. Although Sc and R veins meet the wing edge separately, all of them arise from the areole. In addition, the areole is subdivided by a cross vein between basal Rs and R₁ giving rise to two areoles. The presence of a tubular M₂ in the hindwing is a generalized feature in the above-mentioned subfamilies, but the absence of anastomosis between Sc + R₁ and Rs rules out our fossil moth from being a Larentiinae member. Holloway (1996) included representatives of slender-bodied moths with long and narrow appendages in the subfamily Desmobaethrinae. Pointed forewing apex, among other wing shape traits, as present in our fossil, are common among representatives of this subfamily. Examination of this subfamily representatives, and especially of the genus *Dolichoneura* Warren, 1894 (e.g., *D. oxyptera* (Guenée, 1858)), revealed striking similarities in venation and wing shape with our fossil. Indeed, we compared the wing venation of the type species of the genus *Dolichoneura*, *D. oxyptera*, with that of our fossil. Minor differences are found in fore- and hindwing venations. These are (1) the relative size of the forewing discal cell (being longer and narrower in *D. oxyptera* vs. shorter and broader in *D. jorelisa*), (2) the relative size of the hindwing discal cell (being shorter and broader in *D. oxyptera* vs. longer and somewhat narrower in *D. jorelisa*), and (3) the point (in both, fore- and hindwings) where M₂ arises from the discal cell (relatively closer to M₁ than to M₃ in *D. oxyptera* vs. equidistant in *D. jorelisa*) (Fig. 9). There is also a coincidence between *D. jorelisa* and other *Dolichoneura* spp. concerning the spur number in legs and antennal features (dentate flagellum, densely ciliate-setose in males, Figs. 2 and 3).

Although the monophyly of Desmobaethrinae has been challenged by recent multigene analysis (Murillo-Ramos et al., 2019, 2021), the phylogenetic position of *Dolichoneura* remains unquestionable. The similarity between our fossil and the extant representatives of the genus *Dolichoneura* is so high that the description of a new genus does not seem appropriate. Actually, taking into account the relatively little antiquity of Dominican amber (19–16 Mya), there is no surprise that arthropods preserved in it have been assigned to extant genera several times and sometimes even to living species (e.g., Arillo and Ortuño, 2005; Hoernschemeyer et al., 2010). Based on this evidence, the former paleoenvironment is considered to be not so different from a typical extant lowland Neotropical rainforest (Grimaldi, 1996). Therefore, we conclude that, based on wing shape and venation, our amber geometrid is congeneric with *Dolichoneura*.

According to Iturralde-Vinent and MacPhee (2019) the main amberiferous deposits in the Dominican Republic were formed in a single sedimentary basin in the boundary between Early and Middle Miocene, 19–16 Mya, due to accumulation of abundant resin produced by an extinct legume tree, *Hymenaea protera* Poinar, 1991 (Leguminosae). The genus *Hymenaea* consists today of fourteen extant species, all but one native to the tropics of the Americas, with one additional species

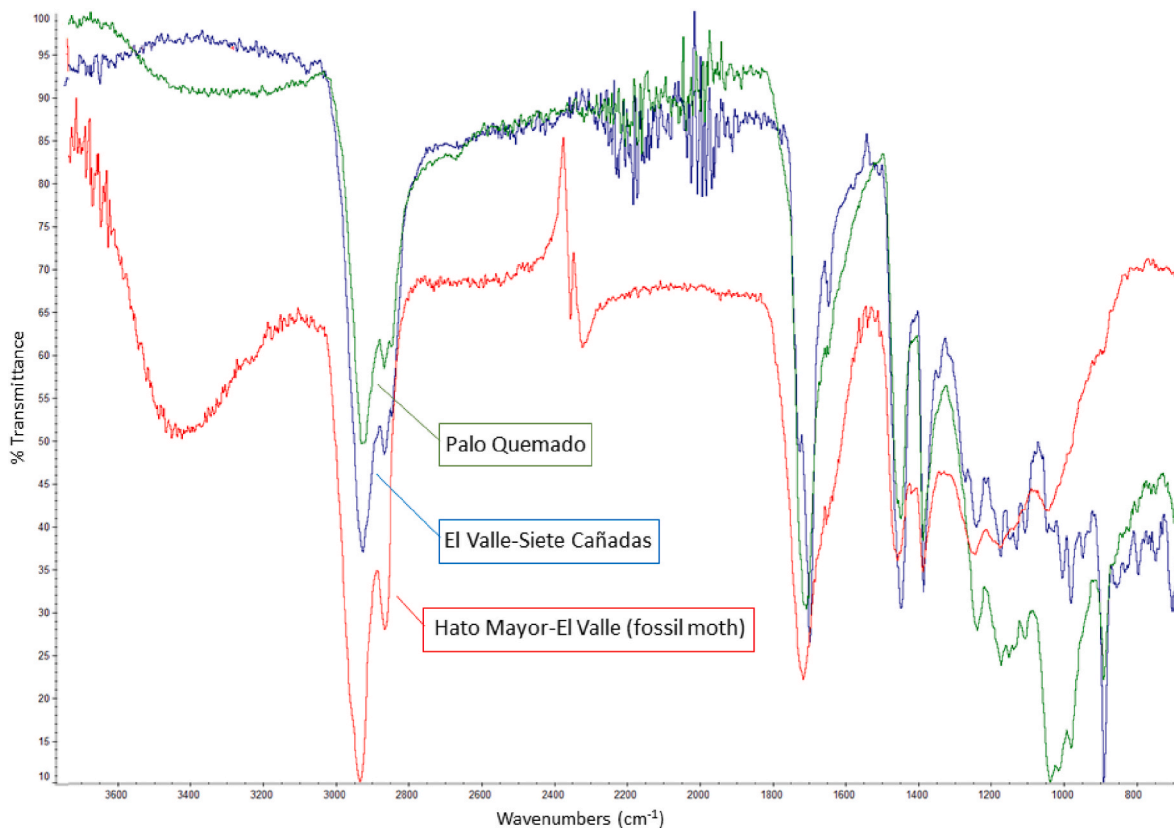


Fig. 8. Infrared absorption spectrum of the amber piece containing the moth (red line) from Hato Mayor-El Valle and spectra of two geological samples from El Valle-Siete Cañadas (blue line) and Palo Quemado (green line), for comparison.

(*Hymenaea verrucosa* Gaertner, 1791) on the east coast of Africa and Madagascar, considered sister to all other Neotropical species (Pinto et al., 2018). Although, so far, fossils of *Dolichoneura* or Desmobaethrinae have not been reported anywhere from the Miocene, our finding of †*Dolichoneura jorelisae* sp. n. evidences that they were already present at this time in Central America.

The genus *Dolichoneura*, in which the fossil herein has been classified, includes eleven extant species distributed from Central to South America (between Costa Rica and Argentina) (Scoble and Hausmann, 2007; GBIF Secretariat, 2021). The sister genus *Pycnoneura* Warren, 1894 includes ten species exclusively distributed in South America (Scoble and Hausmann, 2007). Prout (1932) stated that both genera might have to be merged into one. The biology of *Dolichoneura* is poorly known; all species are nocturnal and have been collected in well sunny slope forest and ridge forest in the lowland rainforest of Costa Rica, where the resiniferous legume trees *Hymenaea courbaril* Linnaeus, 1753 and *H. osanigraseminae* Aguilar Fernández, Poveda Álvarez and Santamaría-Aguilar, 2018 live today, but not in creek forest (Rabl, 2016). Two larvae of an unidentified *Dolichoneura* species were collected by canopy fogging a *Pouteria caimito* (Ruiz & Pav.) Radlk, 1882 (Sapotaceae) tree in Peru; molecular gut content analysis suggested this tree to be the feeding plant.

5. Conclusions

We report a fossil geometrid moth, a male, virtually complete, preserved in a clear piece of Miocene Dominican amber dating from 19 to 16 Mya. Despite of being one of the most specious family groups of

Lepidoptera, the fossil record of Geometridae is comparatively very scarce, with only 19 findings formally reported worldwide, most of them of difficult systematic assignment, so that this fossil is of remarkable interest for phylogenetic studies. It belongs to the genus *Dolichoneura* (Geometridae: Desmobaethrinae) and is named *Dolichoneura jorelisae* Sarto i Monteys, Hausmann, Baixeras and Peñalver sp. n., based on wing features. Furthermore, it could also serve for calibrating molecular clocks and for paleobiogeographic inferences. The head and wings of this specimen were analyzed through SRμCT which provided superb virtual representations.

CRedit authorship contribution statement

Victor Sarto i Monteys: Conceptualization, Investigation, Writing – original draft. **Axel Hausmann:** Conceptualization, Investigation, Writing – review & editing. **Mónica M. Solórzano-Kraemer:** Data curation, Funding acquisition, Investigation, Methodology, Writing – review & editing. **Jörg U. Hammel:** Methodology. **Joaquín Baixeras:** Investigation, Writing – review & editing. **Xavier Delclòs:** Funding acquisition, Investigation, Writing – review & editing. **Enrique Peñalver:** Conceptualization, Investigation, Writing – review & editing.

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.

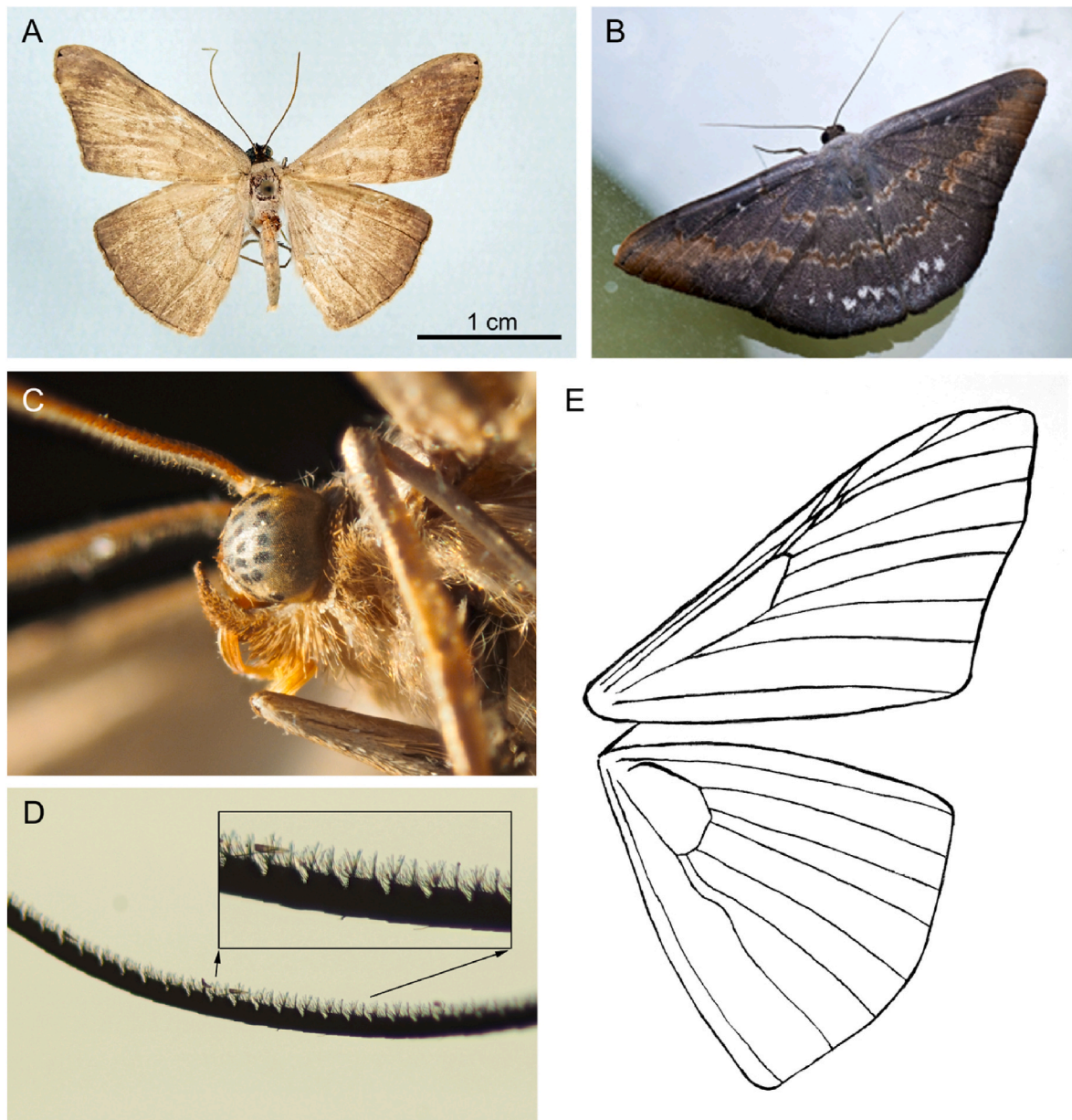


Fig. 9. *Dolichoneura oxypteraria* (Guenée, 1858). (A) male, from French Guyana, Cayenne, Rte. Regina, PK 32.5, Piste de Nancibo, 8.II.1986, ex coll. Herbulot; wingspan 29 mm, forewing length 15 mm. (B) Live specimen of *Dolichoneura* spp. from Canelos, Pastaza, Ecuador, Eerika Schulz, 15.02.2020, Source iNaturalist, <http://www.inaturalist.org/pages/privacy>. (C) Close-up of head, proboscis comparatively short, labial palpi strongly curved, length equal to diameter of eye. (D) Close-up of male antenna, slightly dentate, ciliate-fasciculate. (E) Forewing venation: typical characters are the double areole with R5 arising from second areole; Hindwing venation: typical characters are the lack of anastomosis between Sc + R₁ and R_s and the full number of M-veins (both characters pointing to Desmobaethrinae).

Data availability

Data will be made available on request.

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