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
The second North American fossil horntail wood-wasp (Hymenoptera: Siricidae), from the early Eocene Green River Formation

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Abstract

Eoteredon lacoï **gen. et sp. nov.**, is described from the early Eocene Green River Formation in Wyoming, the second fossil siricid genus and species described from North America. We propose *Eoteredon* as sister to the genus *Teredon*, whose sole species is one of the rarest of extant Siricidae. The majority of siricids today inhabit temperate Northern Hemisphere forests; *Teredon cubensis*, however, is one of its few species that live in megathermal tropical lowlands. The Eocene forest that *Eoteredon* inhabited had a mesothermal to megathermal climate. We place *Eoteredon* in the context of broad Cenozoic climate change.

Key words: Insecta, ‘Symphyta’, *Teredon*, paleobiogeography

Introduction

Horntail wood-wasps (Siricidae) consist of ten extant genera (Schiff *et al.* 2012) that are mainly distributed in Hol-arctic forests, from the northern tree line through mid-latitudes, with few outside of this range. Most Mesozoic taxa ascribed to the family require revision of their higher level systematics (see Archibald & Rasnitsyn 2016), and the few fossils known of its crown group are mainly from the Cenozoic of Eurasia (*e.g.*, Nel 1988, 1991; Wedmann 1998; Rajchel & Uchman 1998; Riou 1999; Wedmann *et al.* 2014). Only two are known from the New World: the Early Cretaceous *Cratosirex sennlaubi* Jouault *et al.* 2020 from Brazil, and the Ypresian (early Eocene) *Ypresiosirex orthosemos* Archibald & Rasnitsyn 2016 from British Columbia, Canada. Here we describe the second North American fossil crown group siricid, from the Ypresian Green River Formation of Wyoming.

Geologic Setting

The Green River Formation is comprised of lacustrine sediments deposited in three basins by intermittently interconnected lakes over a span of eight million years (Smith *et al.* 2008 and others cited therein). Fossil Basin, the smallest of the three, formed behind the leading edge of the Wyoming thrust in what is now southwest Wyoming, USA (Fig. 1). Lacustrine deposits in Fossil Basin are approximately 120 meters thick (Buchheim *et al.* 2011) (Fig. 2). Over a hundred air-fall ashes are documented but only the 51.98 ± 0.35 Ma (Smith *et al.* 2008; Smith *et al.* 2010; Smith & Carroll 2015) K-spar Tuff has been dated. The tuff is six meters above the 18-inch Layer (named for its average thickness) where the wasp was found. Although deposition rates are unknown, this appears to be well within the Early Eocene Climatic Optimum (EECO) in the latter half of the Ypresian (*e.g.*, Inglis *et al.* 2020; Luciani *et al.* 2020).

Material and methods

An imperfect split of the laminated limestone containing the specimen caused portions of it to adhere to the counterpart. The specimen was prepared by Mike Eklund using silicon wafer probes under a Leica MZ16F microscope. During preparation, it was determined that further removal of obscuring matrix would cause irreparable damage to the specimen and so portions of limestone were thinned rather than removed. Thinned matrix then becomes translucent when wetted with ethyl alcohol, revealing hidden morphology. Photography was done by Harold Ikerd at the United States Department of Agriculture's Pollinating Insect-Biology, Management, Systematics Research (Bee Lab) in Logan, Utah, USA using a Keyence VHX-5000 microscope and camera system. The specimen was photographed both dry and wetted. Line drawings are composites done from dry, wet, part and counterpart images.

We follow the morphological terminology and systematics of Schiff *et al.* (2012), except that we follow Rasnitsyn (1968, 1969), Wedmann *et al.* (2014), and Archibald & Rasnitsyn (2016) in recognizing the Siricinae as the sole defined subfamily of Siricidae *sensu stricto*, assuming that revision of Mesozoic taxa will establish others. Contrary character states of compared taxa are provided in brackets. Mean annual temperature (MAT) categories are *sensu* Wolfe (1975): microthermal, $\leq 13^{\circ}\text{C}$; mesothermal, $> 13^{\circ}\text{C}$, $< 20^{\circ}\text{C}$; megathermal, $\geq 20^{\circ}\text{C}$.

Systematic paleontology

Order Hymenoptera Linnaeus 1758

Family Siricidae Billberg 1820

Genus *Eoterodon* gen. nov.

Type species. *Eoterodon laco* sp. nov.

Etymology. The genus name is derived from *Eos*, the Latin name for the Greek goddess of the dawn, and that of the extant genus *Teredon* Norton 1869. Gender, masculine.

Diagnosis. Female characters only. Closest to *Teredon* (see discussion), but easily separated from *Teredon* females by any of the following: broad metathoracic femur, much broader than tibia; forewing character states: cell 1R width about a third length [about a fifth]; cell 3R1 distinctly closed (R1 joins Rs) [open]; 1r-rs distinct [very short or R1, Rs meet at pterostigma]; Rs and M only touch without distinct Rs+M [distinct Rs+M].

Eoterodon laco sp. nov.

(Figs 3, 4)

Material. Holotype FOBU13582 (part and counterpart of a nearly complete female) (Fig. 3). Housed in the collections of Fossil Butte National Monument, Kemmerer, Wyoming.

Etymology. The specific epithet is formed from the surname of Greg Laco, who donated the holotype to Fossil Butte National Monument, recognizing his contribution.

Diagnosis. As for the genus.

Type locality and horizon. The type and only specimen was found in the 18-inch Layer of the Fossil Butte Member of the Green River Formation in Fossil Basin, approximately six meters below the K-spar Tuff dated at 51.98 ± 0.35 Ma. The Smith Hollow type locality is 11 miles west of downtown Kemmerer, Wyoming, USA.

Description. Female, preserved in ventral aspect, except head in frontal aspect. Head poorly preserved, 4.5 mm long, 3.5 mm wide, with compound eyes, mandibles poorly visible; ocelli, antenna, antennal sockets not discernible; thorax 8.7 mm long, 5.5 mm wide; only parts of metathoracic legs preserved, poorly: femur 2.2 mm long and 1.0 mm wide, 3.5 as broad as metatibia; metatibia ca. 3.8 mm long as preserved, 0.3 mm wide; fragments of

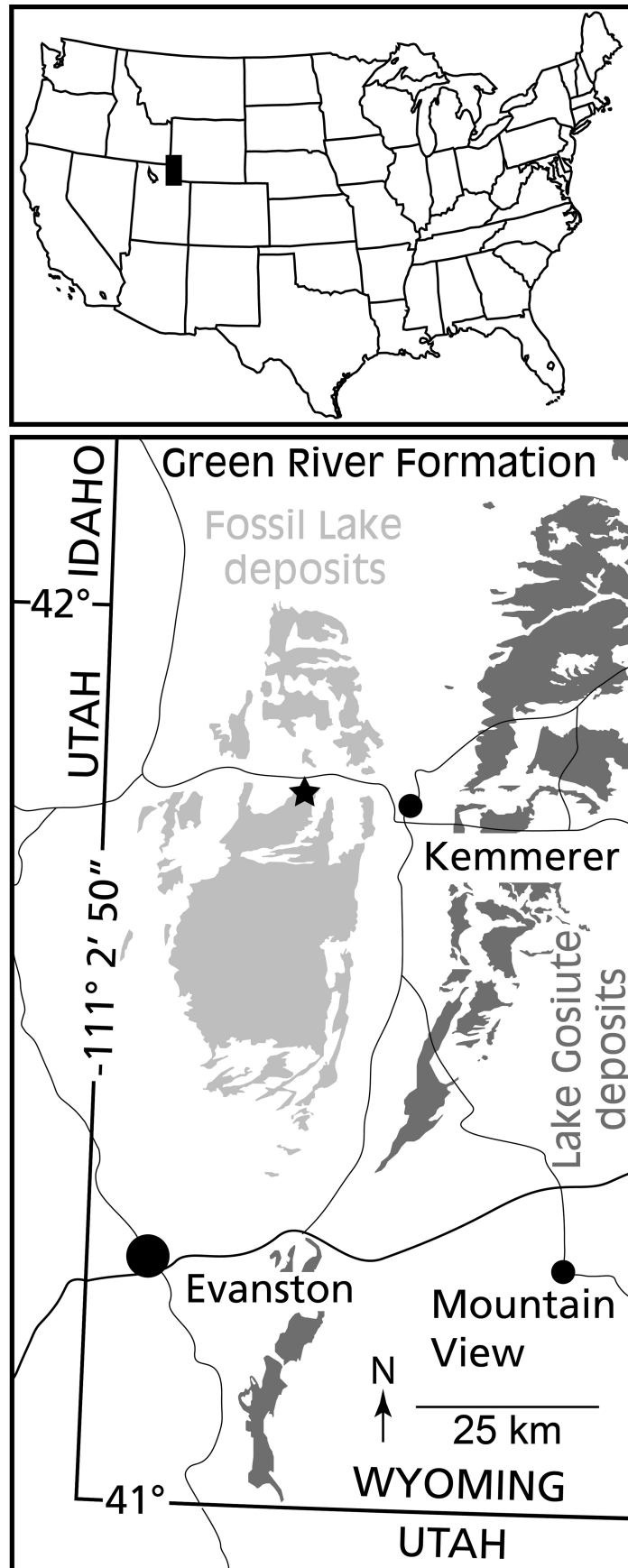


FIGURE 1. Fossil Lake occupied southwest Wyoming, USA, extending westward into Idaho and Utah. After lithification the laminated limestones were eroded exposing the fossil bearing layers. The star marks where the siricid wasp was found about 8.8 km from the eastern shore.

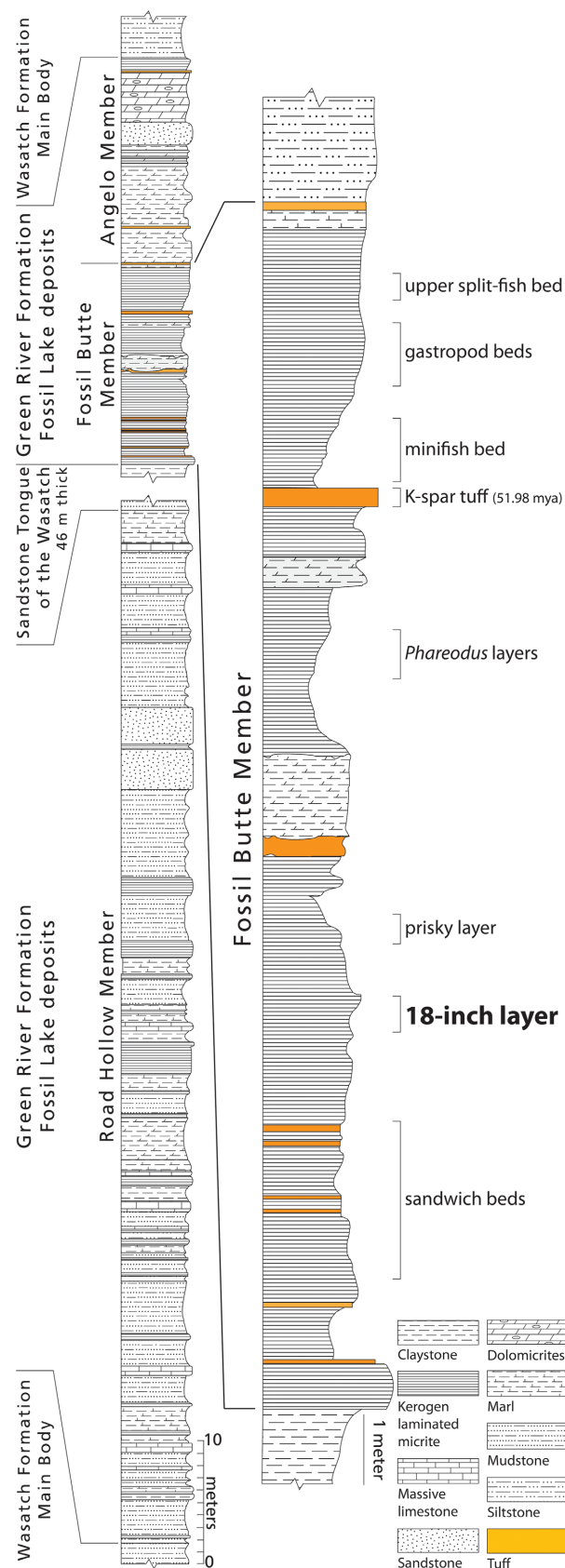


FIGURE 2. Fossil bearing layers are primarily laminated limestones interspersed with volcanic tuffs. The K-spar Tuff is the thickest, making it an easily recognized marker bed. Five layers produce prolific fossils, two below and three above the K-spar Tuff. The siricid wasp was found in the 18-inch Layer about six meters below the K-spar Tuff. Stratigraphic column modified from Buchheim *et al* (2011).

metabasitarsomere possibly present. Forewing 17.5 mm long, 5.0 mm wide, with apex poorly preserved; 2r-m present, joins cell 2M; cell 1Rs2 clearly longer than wide; cell 1R1 rather broad, only 2.8 times as long as broad; cell 2R1 about 0.7 times as long as cell 3R1; 2r-rs joins stigma in its distal half; stigma gradually attenuated evenly distal to junction with 2r-rs; Cu1 absent; 1cu-a joining Cu midway between 1m-cu, M; Sc faint, present in basal third of wing; 2A extending along posterior edge of wing about 0.5 times cell 1A length; 3A possibly distorted (see text). Hind wing ca. 11.3 mm long; anal cell presumed open (see below); hamuli not discernible; 1r-m clearly shorter than M; 1r-m at basal third of cell 1M; M markedly curved; abdomen 16.3 mm long, 7.0 mm wide, tergites not discernible (preserved in ventral aspect); distinct but incomplete ovipositor, preserved portion 8.8 mm long, extending 2.2 mm from abdomen; annuli not discernible.

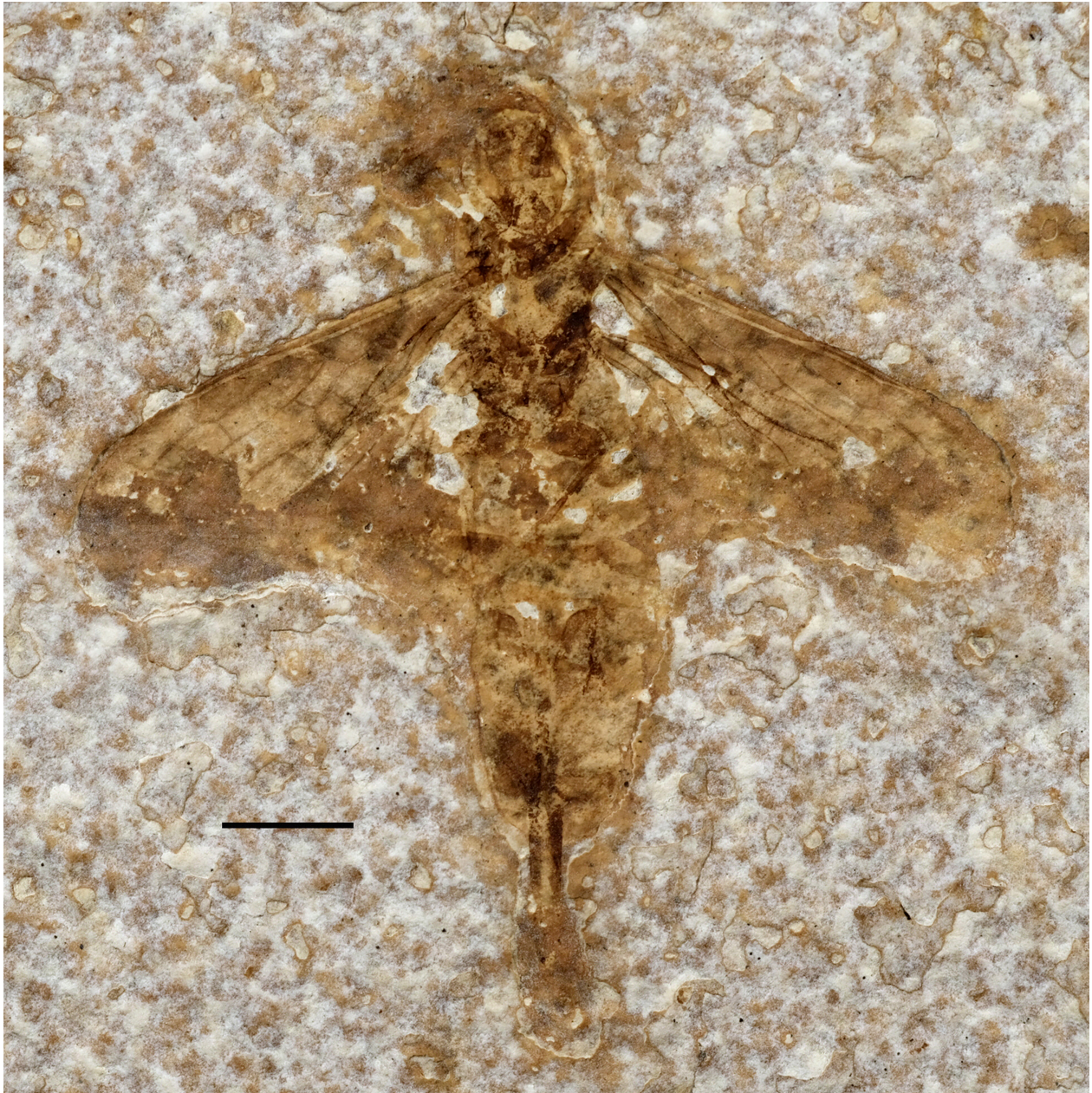


FIGURE 3. *Eoteredon lacoi* gen. et sp. nov., holotype in ventral aspect, photographed dry. Scale bar = 5 mm.

Discussion

Teredon has one rare species, *T. cubensis* (Cresson 1865). Its male and female differ to such a degree that they had originally been considered two species (see Schiff *et al.* 2012). The most distinct character states of *Teredon* of both sexes are their flattened, widened metatarsomere 1 and antennae with fewer than 9 flagellomeres. Neither can be assessed on the sole specimen of *E. lacoi* by preservation.

Although poorly preserved, the compound eye of *Eoterodon* **gen. nov.** seems to be rather narrow compared to its height, as in females of *Teredon cubensis* (Schiff *et al.* 2012: fig. C34.4).

The forewing venation of *Eoterodon* **gen. nov.** is very similar to that of *Teredon*. According to Schiff *et al.* (2012), *Teredon* wings are distinct from those of other Siricidae by a combination of 2r-m present and 1cu-a joining Cu midway between M and 1m-cu in the forewing, and the hind wing with 1r-m shorter than M and M markedly curved. All of these are shared by *Eoterodon* **gen. nov.** Further, in the forewing of both, the apex is acutely and angularly rounded, 2r-m is basal to 2r-rs and joins cells 2R1 and 2M; cell 1Rs2 is clearly wider than long; it is without vein Cu1; and 1cu-a joins Cu about midway between 1m-cu and M.

The forewing of *Eoterodon* **gen. nov.** differs as in the diagnosis (above) and 2r-rs appears to join the stigma more distally than in *Teredon*, but this is indistinct as the region is poorly preserved. Some details of 2A and 3A cited by Schiff *et al.* (2012) appear not clearly discernable by preservation in *Eoterodon* **gen. nov.** What we interpret as portions of 3A in both the left and right forewings (see Fig. 4) appear to be unusually curved parallel to 2A, but this might be due to partial crumpling of the posterior forewing bases; future specimens are needed to confirm this.

We believe that the hind wings are without a closed anal cell because although this region is incompletely preserved in both, the vein closing the hind wing anal cell in other Siricidae is not detected where it should be visible if present (see Schiff *et al.* 2012, fig. A3.29). We cannot judge hamuli morphology by preservation.

Wedmann (1998, fig. 1) proposed the absence of the hind wing anal cell as a synapomorphy of (*Eriotremex* Benson 1943, *Afrotremex* Pasteels 1951, *Tremex* Jurine 1807); it is also absent in the female of *Teredon* (Schiff *et al.* 2012). This relationship is supported by the morphological phylogenetic analysis of Schiff *et al.* (2012, fig. C1.14), who recovered *Eriotremex*, *Afrotremex*, *Tremex* and *Teredon* as a clade.

A remarkable character of *Eoterodon* **gen. nov.** is the greatly broadened hind femora compared to the width of the hind tibia, broader than in any other Siricidae (AN pers. obs.; Konow 1905). In *Teredon* the hind femur is narrower than the maximum width of the hind tibia (Schiff *et al.* 2012, fig. C35.2).

Paleobiogeography and paleoclimate of *Eoterodon* **gen. nov.**

The great majority of modern Siricidae occupy boreal temperate forests from mid-latitudes north to the tree line and are mostly found at higher, cooler elevations in the southern parts of their range. This is a pattern seen in various insect taxa such as Panorpidae (Archibald *et al.* 2013) and Polystoechotidae (Archibald & Makarkin 2006). For example, *Sirotemex flammeus* Smith 1988 is known from near Durango, Mexico at 2500 meters elevation (Schiff *et al.* 2012) and *Sirex hispaniola* Goulet (in Schiff *et al.* 2012) in the Cordillera Central of Hispaniola above 1000 meters.

A few taxa in the southern portion of their distribution do, however, inhabit hot, lowland climates, *e.g.*, *Afrotremex* is only known from equatorial Africa (Uganda, Congo, Democratic Republic of Congo, Cameroon, Ghana: reviewed by Schiff *et al.* 2012), and *Eriotremex* species occur through east and southeast Asia in a variety of climates from Japan south to Vietnam, Indonesia, Malaysia, Papua New Guinea and Borneo (Smith 2010; Schiff *et al.* 2012; Taeger *et al.* 2018).

Teredon is one of these, known from La Habana Province of Cuba, the Dominican Republic, and Belize (Goulet *et al.* 2015), all south of the Tropic of Cancer in lowlands with megathermal mean annual temperatures (MAT). La Habana Province is rarely over 100 meters in elevation; its capital, Havana, has a MAT of 24.9 °C (Climate-Data.Org 2021). The Dominican Republic specimen is from the north coast town of Soúsa, which has an average temperature of 25°C (Climate-Data.Org 2021). The Belize specimen is from northern Belize at Lamanai Research Station, Orange Walk District (17.74995, -88.65477), at about 22 meters elevation. The Orange Walk District has a mean annual temperature of 26.3°C (National Meteorological Service of Belize 2021).

Mesothermal to megathermal MAT values have been estimated for various Green River Formation sites using leaf margin analysis (Wilf 2000; Fricke & Wing 2004; Archibald *et al.* 2011; Kester and Aase current research). However, these estimates may be low by taphonomic biases and their confidence intervals may be underestimated or are lacking (Little *et al.* 2010). The 18-inch Layer where *Eoterodon* **gen. nov.** was recovered was within the Early Eocene Climatic Optimum, an interval of the late Ypresian of increased atmospheric carbon and the highest sustained global MAT values of the Cenozoic (Zachos *et al.* 2008; Inglis *et al.* 2020).

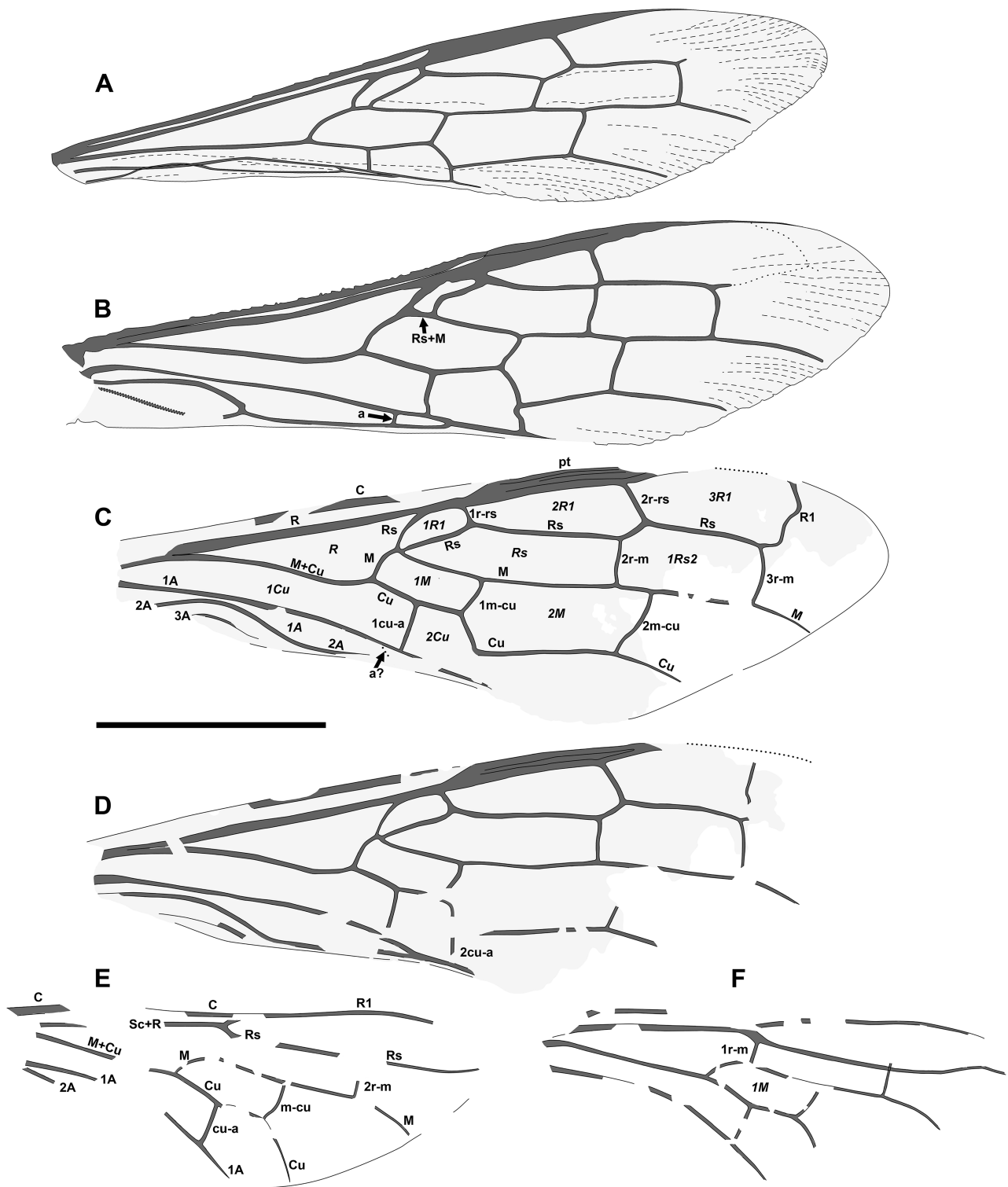


FIGURE 4. Drawings of wings of A, B, *Teredon cubensis* and C–F, *Eoteredon lacoi* **gen. et sp. nov.**, holotype. A, *T. cubensis* male forewing, somewhat crushed in the basal posterior region. B, *T. cubensis* female forewing. C, right forewing of *E. lacoi*. D, left forewing of *E. lacoi*. E, *E. lacoi* female left hind wing. F, *E. lacoi* female right hind wing. Veins labelled in Roman font, cell names in italics. A, B re-drawn from Schiff *et al.* (2012, figs. C1.36, C34.5, no scale bars on originals). Scale bar = 5 mm (C–F).

A siricid close to *Eriotremex* or *Afrotremex* is known from the Oligocene of Enspel, Germany, and a *Tremex* sp. from the Pliocene of Willerhausen, Germany (Wedmann 1998). Dispersal of members of the clade (*Eriotremex*, *Afrotremex*, *Tremex*, *Teredon*, *Eoterredon* **gen. nov.**) between North America and Eurasia could have been in either direction, possibly during the Late Cretaceous through Eocene by Holarctic land connections across the North Atlantic or Beringia (Brikiatis 2014); land connected the Caribbean region after the Middle Eocene (Iturralde-Vinent 2006). Members of the clade requiring higher MAT environments would have had to make a North Atlantic land bridge crossing during brief hyperthermal intervals (Archibald *et al.* 2011). *Eoterredon* **gen. nov.** went extinct sometime after the Ypresian and *Teredon* originated at an unknown time, today restricted to the tropical Caribbean region.

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