


Cloeon tzeltal sp. nov. (Ephemeroptera: Baetidae), a Miocene mayfly from Mexican amber

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Abstract

A new fossil species of mayfly of the genus *Cloeon* Leach, 1815 (Ephemeroptera, Baetidae) is described. The type material comprises female imagines from 24 amber inclusions, from Miocene strata of Chiapas in southern Mexico. The fossil species, *Cloeon tzeltal* sp. nov., closely resembles those in the genus *Cloeon* by the following diagnostic characters: absence of hind wings; two major crossveins between R1 and R2 not in line with the crossveins below them; single marginal intercalaries; and basal crossveins between veins R and Rs situated more basally than the following vein. The new species can be distinguished from extant species of *Cloeon* by the absence of colored costal and subcostal fields in the forewings and the absence of transversal veins in vitta broadly bordered with white. Extant species of the genus *Cloeon* in America have an exclusive distribution in the northern part of the continent; with the exception of one introduced taxon, no valid species have been recorded in the tropics. As such, the fossil record of *Cloeon* in the southernmost part of North America suggests a broader geographic distribution of this genus in the geological past, including the southernmost part of North America.

Key words: amber, *Cloeon*, Ephemeroptera, fossil, mayfly, Mexico, new species

Résumé

Une nouvelle espèce fossile d'éphémère du genre *Cloeon* Leach, 1815 (éphéméroptères, baétidés) est décrite. Le matériau type comprend des imagines de femelles de 24 inclusions dans l'ambre, de strates miocènes du Chiapas (sud du Mexique). L'espèce fossile, *Cloeon tzeltal* sp. nov., ressemble étroitement à celles du genre *Cloeon* en ce qui concerne les caractères diagnostiques suivants : l'absence d'ailes postérieures, deux veines croisées majeures entre R1 et R2 non alignées avec les veines croisées sous elles, des intercalaires marginaux simples et des veines croisées basales entre les veines R et Rs en position plus basale que la veine suivante. La nouvelle espèce se distingue des espèces modernes de *Cloeon* par l'absence de domaines costaux et subcostaux colorés dans les ailes antérieures et l'absence de veines transversales dans des bandes médianes largement bordées de blanc. Les espèces modernes du genre *Cloeon* en Amérique présentent une aire de répartition exclusive à la partie nord du continent; à l'exception d'un taxon introduit, aucune espèce valide n'a été observée dans les Tropiques. Aussi, la présence de *Cloeon* dans le registre fossile à l'extrémité sud de l'Amérique du Nord indiquerait une répartition géographique plus large de ce genre durant le passé géologique, qui englobait l'extrémité sud de l'Amérique du Nord. [Traduit par la Rédaction]

Mots-clés : ambre, *Cloeon*, éphéméroptères, fossile, éphémère, Mexique, nouvelle espèce

1.0 Introduction

Ephemeroptera (Insecta: Pterygota) are considered to be the most basal of winged insects displaying distinctive plesiomorphic characters, such as caudal, median filament, and a subimaginal winged molting stage (Grimaldi and Engel 2005; Ogden et al. 2009). The Paneremorphera stem group probably emerged in the Early Permian (Staniczek et al. 2011; Sinitshenkova et al. 2015), and several modern families were already present in the Late Jurassic (Grimaldi and Engel 2005). Diversity estimates of Ephemeroptera count approximately 3330 extant species in more than 440 genera and

42 families worldwide (Barber-James et al. 2008, tables 1 and 2; Sartori and Brittain 2015, table 34.1). The Mexican territory has close to 138 extant species in 38 genera and 11 families (Randolph and McCafferty 2000). In contrast, the fossil record of Ephemeroptera from Mexico is limited to a few amber inclusions from the Miocene: a species described as *Maccaffertium annae* Macadam and Ross, 2016 from the family Heptageniidae; a morphotype of the genus *Cloeodes* Traver, 1938 within the family Baetidae; and another morphotype of the genus *Leptohiphes* Eaton, 1882 within Leptohiphidae; as well as an undetermined specimen referred to the

family Leptophlebiidae (Solórzano-Kraemer 2007). In this contribution, we report on the first fossil record of the genus *Cloeon* Leach, 1815 from the Miocene of Mexico; specimens of *Cloeon tzeltal* sp. nov. are preserved in amber as inclusions, and we include this new species in a preliminary inventory of Ephemeroptera from Mesozoic and Cenozoic amber deposits worldwide, based on available published literature.

2.0 Materials and methods

The amber inclusion comes from La Pimienta locality, in the town of Simojovel, Chiapas, southern Mexico. The amber-bearing sediments here consist of sandstones, lignite, friable coal, nonconsolidated conglomerates, and clay lenses, all of which are part of the Mazantic shale and Balumtum sandstone strata, which are considered Miocene in age (Riquelme et al. 2015).

Anatomical data and measurements were collected using an Olympus AZ dissecting binocular microscope, with a U-OCM10/100 Eyepiece Micrometer of 0.1 mm intervals and applying multi-image stacking to expand three-dimensional focus following Riquelme et al. (2015). Female imagines' measurements follow Bae and Park (1997). The schematic drawing was done by hand using an electronic pen, photomicrographs, stereomicroscope, and CorelDRAW for graphic editing. Taxonomic nomenclature and anatomical terminology follow Burks (1953), Edmunds et al. (1976), and Elliott and Humpesch (1983).

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2.1 Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; BAC, Ron Buckley private amber collection, Kentucky, USA; Bxl. priv.coll., Brussels private collection of Jules De Walsche, Brussels, Belgium; CCHH, private collection of Christel and Hans Werner Hoffeins, Hamburg, Germany; CNUB, Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China; CPAL-UAEM, Colección Paleontológica maintained at the Universidad Autónoma del Estado de Morelos, Cuernavaca, Mexico; GZG, Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen, Germany; HU, Humboldt University, Berlin, Germany; MAI, Museum of Amber Inclusions, Department of Invertebrate Zoology, University of Gdańsk, Gdańsk, Poland; MNB, W. Simon's amber collection of the Institute of Palaeontology, Humboldt University, Berlin, Germany; MNHK, amber collection of the Natural History Museum of the Institute of Systematics and

Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NASU, National Museum of Natural History at the National Academy of Sciences of Ukraine, Kiev, Ukraine; NHM, Natural History Museum, London, UK; NMR, Swedish Museum of Natural History, Stockholm, Sweden; NMS, National Museums Collections Centre, National Museum Scotland, Edinburgh, UK; PERC, Purdue Entomological Research Collection, West Lafayette, Indiana, USA; PGM, Geological Museum of China, Beijing, China; RAS, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; SGPIH, Collection of the Geological-Palaeontological Museum, University of Hamburg, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SNSB, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; ZMUC, University of Copenhagen Zoological Museum, Copenhagen, Denmark.

3.0 Systematic paleontology

Class Insecta Linnaeus, 1758
Order Ephemeroptera Hyatt and Arms, 1890
Family Baetidae Leach, 1815
Subfamily Cloeoninae Newman, 1853
Genus *Cloeon* Leach, 1815

Cloeon tzeltal sp. nov.

Fig. 1, 2

ZOOBANK NUMBER: urn:lsid:zoobank.org:pub:5ED38E2A-7B83-49F8-B0A3-855727AAF58B

TYPE SPECIES: *Ephemerella diptera* Linnaeus, 1761

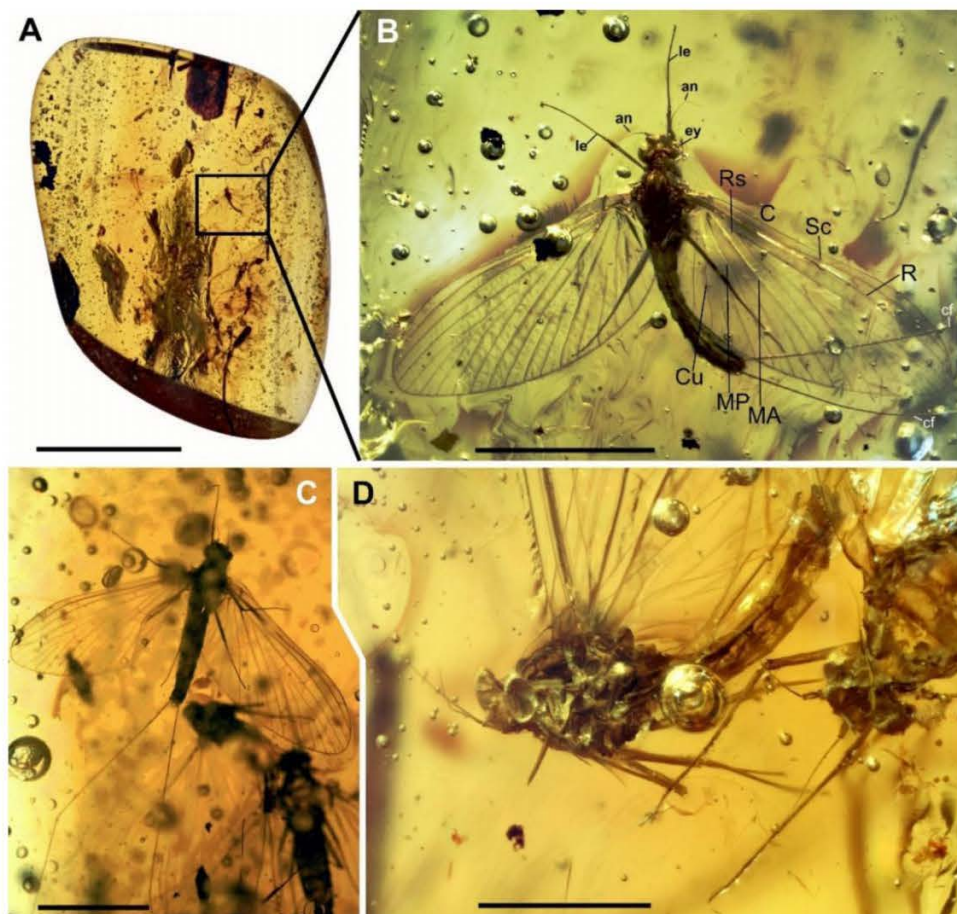
ETYMOLOGY: The specific epithet alludes to one of the original indigenous communities from southern Mexico, including Chiapas, the state from which the amber comes from.

TYPE MATERIAL: Holotype CPAL.417, amber inclusion, female imago (Fig. 1). Paratypes CPAL.402, CPAL.403, CPAL.404, CPAL.405, CPAL.406, CPAL.407, CPAL.408, CPAL.409, CPAL.410, CPAL.411, CPAL.412, CPAL.413, CPAL.414, CPAL.415, CPAL.416, CPAL.418, CPAL.419, CPAL.420, CPAL.421, CPAL.422, CPAL.423, CPAL.424, and CPAL.425, amber inclusions, female imagines (Fig. 1). Holotypes and paratypes are currently housed in the Colección de Paleontología maintained at the Laboratorio de Sistemática Molecular, Universidad Autónoma del Estado de Morelos, Mexico (CPAL-UAEM).

LOCALITY AND HORIZON: La Pimienta site: 17°09'11"N, 92°46'08"W, Simojovel, Chiapas, México. Mazantic shale and Balumtum sandstone strata, Miocene (Riquelme et al. 2015).

TAPHONOMIC NOTES: The hypodigm consists of 24 fossil mayflies, all female imagines embedded in a single amber piece, golden in color, with translucent glossiness (Fig. 1). This amber piece also contains plant debris, litter, flower stamens, and other insects, such as an ant and few dipteran specimens. There are also soil remains and bubble impressions that, for some of the mayfly specimens, make it difficult to visualize morphological features. In extant mayflies, the female imagines are associated with the short terrestrial

Fig. 1. *Cloeon tzeltal* sp. nov. (A) Amber inclusion; scale bar = 2 cm. (B) Dorsal habitus of holotype CPAL.417 showing venation pattern; scale bar = 1 mm. (C) Paratypes CPAL.422 and CPAL.421; scale bar = 1 mm. (D) Lateral view of paratype CPAL.421; scale bar = 1 mm. Abbreviations: an, antenna; C, costa; cf, caudal filaments; Cu, cubitus; ey, compound eye; le, foreleg; MA, medius anterior; MP, medius posterior; R, radius; Rs, subradius; Sc, subcosta. [Colour online.]



phase of their life cycle, adults swarm and mate in the air, and then females need to oviposit in watersheds (Sartori and Brittain 2015); this suggests that females should be close to an aquatic environment where the resin trapped them.

DIAGNOSIS: Adult imago, with the absence of hind wings, two major crossveins between R1 and R2 that are not in line with the crossveins below them, and single marginal intercalaries, veins MA2 and MP2 detached basally, crossveins not pigmented.

DESCRIPTION: Holotype CPAL.417, adult imago, amber inclusion, complete specimen, body length: 0.5–0.7 cm without cerci; cerci 7.5 mm. The additional 23 specimens with similar morphological traits and similar size are distributed throughout the inclusion near the holotype.

Head: Compound eyes widely interspaced and positioned laterally, protruding from the lateral edges of the head in dorsal view; in lateral view, compound eyes protruding from the vertex of the head; antenna three-segmented with first segment about twice the length of the second, antennae length: 3.0–3.7 mm.

Thorax: Prothorax small; in lateral view, pronotum and metathorax protruding from mesothorax, forming two convexities with respect to the mesothorax outline; in dorsal

view, mesothorax oval in shape, and in dorsal view one median and two lateral longitudinal carenas extended along the mesothorax in its entirety.

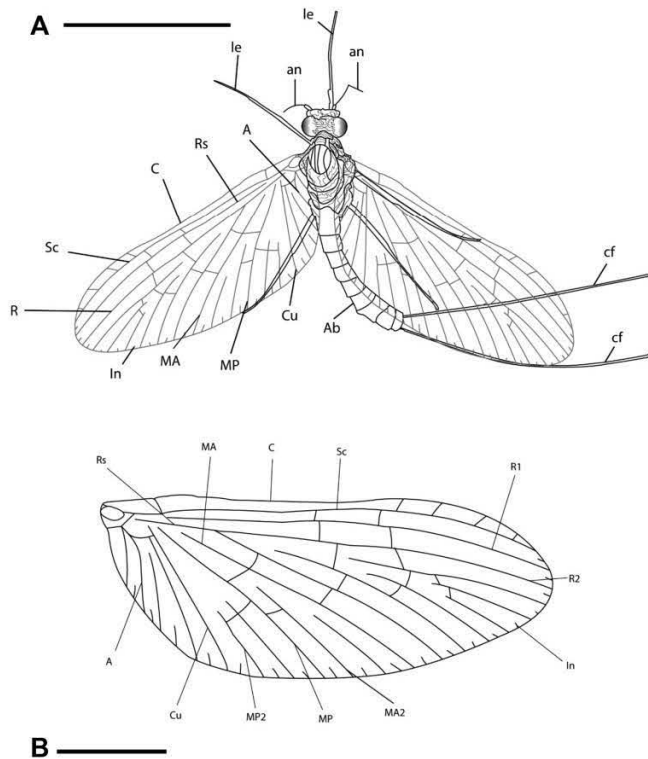
Legs: Leg dimensions: forefemora 0.5–0.6 mm; foretibiae 0.45 mm; foretarsal segments 0.52–0.55 mm; midfemora 0.7–0.72 mm; midtibiae 0.5–0.6 mm; midtarsal segments 0.35–0.40 mm; hindfemora 0.6–0.7 mm; tarsus four segmented, first segment as twice as long as the second.

Wings: Forewing hyaline, lacking crossveins in the S field, except at the pterostigma area (four to seven veins), Sc and R1 fields with two crossveins, Rs fork about one-fifth the distance from base of wing to margin, with veins MA2 and MP2 detached basally, crossveins not pigmented; single marginal intercalaries along the outer wing margin; wing dimension: forewing length 3.9–4.3 mm; forewing width 1.6–2.0 mm (Figs. 2 and 3); hind wing absent.

REMARKS: The holotype CPAL.417 and paratypes closely resemble the Baetidae in having veins MA2 and MP2 detached basally, and two long caudal filaments (Edmunds et al. 1976). The genus *Cloeon* is taxonomically diverse, with approximately 75 described species (Gattolliat and Nieto 2009). The extant species of *Cloeon* generally can be recognized by their color pattern of the body; for example, see the description



Fig. 2. *Cloeon tzeltal* sp. nov. (A) Line drawing of holotype CPAL.417 in dorsal view, amber inclusion, female imago; scale bar = 1 mm. (B) Schematic representation of the wing; scale bar = 0.5 mm. Abbreviations: A, anal; Ab, abdomen; an, antenna; C, costa; cf, caudal filaments; Cu, cubitus; In, intercalaries; le, foreleg; MA, medius anterior; MA2, medius anterior 2; MP, medius posterior; MP2, medius posterior 2; R, radius; Rs, subradius; R1, radius 1; R2, radius 2; Sc, subcosta.



of *Cloeon dipterum* (Linnaeus, 1761) (Traver 1962). Although the quality of color patterns preserved in the current sample is quite variable, the wing venation is nonetheless well preserved and provides important information bearing on taxonomic identity. Specimens from the current sample were referred in the genus *Cloeon* by the combination of the following characters: (1) absence of hind wings (Edmunds et al. 1976); (2) two major crossveins between R1 and R2 that are not in line with the crossveins below them, which differentiates *Cloeon* from *Procloeon* Bengtsson, 1915 (Elliott and Humpesch 1983); (3) single marginal intercalaries (Burks 1953); and (4) crossvein between veins R and Rs situated more basally than the succeeding vein (Bauernfeind and Soldán 2012). An absence of hind wings is also observed in the closely related genera *Procloeon* and *Pseudocentropiloides* Jacob, 1986 (Jacob and Glazaczow 1986) but these genera differ from *Cloeon* in that the distance between the compound eyes in females is about twice as wide as eye width (Bauernfeind and Soldán 2012). *Cloeon tzeltal* sp. nov. differs from species of *Anafroptilum* Kluge, 2011 and *Callibaetis* Eaton, 1881 by the absence of hind wings (Burian 2019), and from *Neocloeon* in lacking present abdominal sternums with dark lateral triangular marks or dark spots, as the females of this

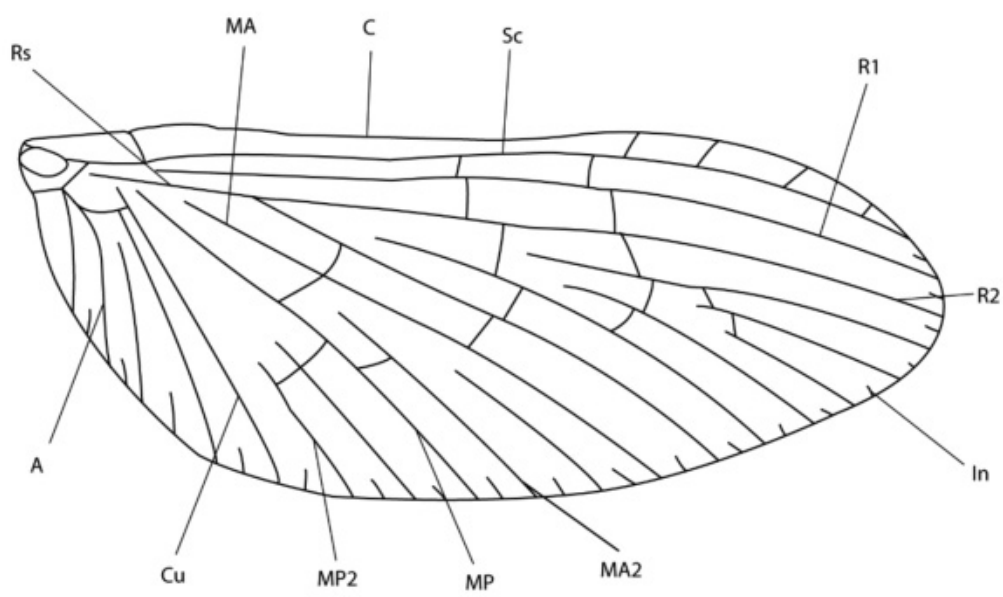
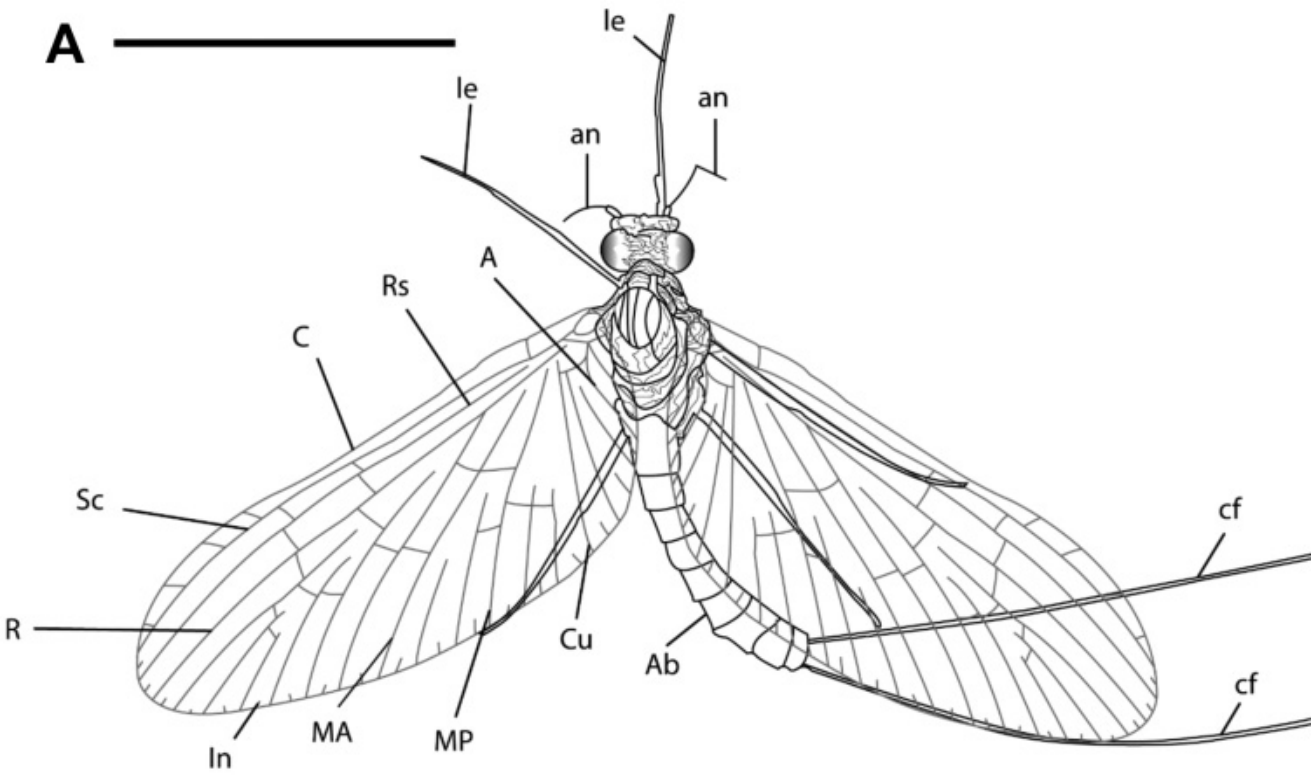
Fig. 3. (A) Ventral habitus of paratype CPAL.410 showing venation pattern; scale bar = 1 mm. (B) Paratype CPAL.420; scale bar = 0.5 mm. (C) Ventral view of holotype CPAL.417; scale bar = 0.5 mm. Abbreviations: A, anal; C, costa; Cu, cubitus; In, intercalaries; MA, medius anterior; MP, medius posterior; R, radius; Rs, subradius; Sc, subcostal. [Colour online.]



taxon present (Burian 2019). Although Bauernfeind and Soldán (2012) claimed that *Cloeon* also shows the basal crossvein between R and the anterior branch of Rs more basally than the following crossveins, extant species of *Cloeon* notably vary in crossvein patterns (e.g., Bae and Park 1997). Extant species of *Cloeon* are distinguished from one another mainly by coloration patterns on the wings, body parts in imagines, and the venation pattern. Based on these features, Sowa (1975) was able to distinguish *C. dipterum* from closely related taxa, with *Cloeon cognatum* Stephens, 1835 and *Cloeon inscriptum* Bengtsson, 1914 for example, being distinguished by the pattern of costal and subcostal fields, as well as the presence of crossveins between the costal and subcostal fields. *Cloeon tzeltal* sp. nov., in not presenting the costal and subcostal coloration patterns as described for *C. cognatum* and *C. inscriptum*, and the multiple crossveins in the costal and subcostal fields as in *C. dipterum* (Sowa 1975; Bauernfeind and Soldán 2012), can be distinguished from these extant species, with the latter (*C. dipterum*) being the only species of the genus currently recorded in the New World.

4.0 Discussion

Extinct mayflies have been identified in many of the world's major amber deposits, and from several different geological



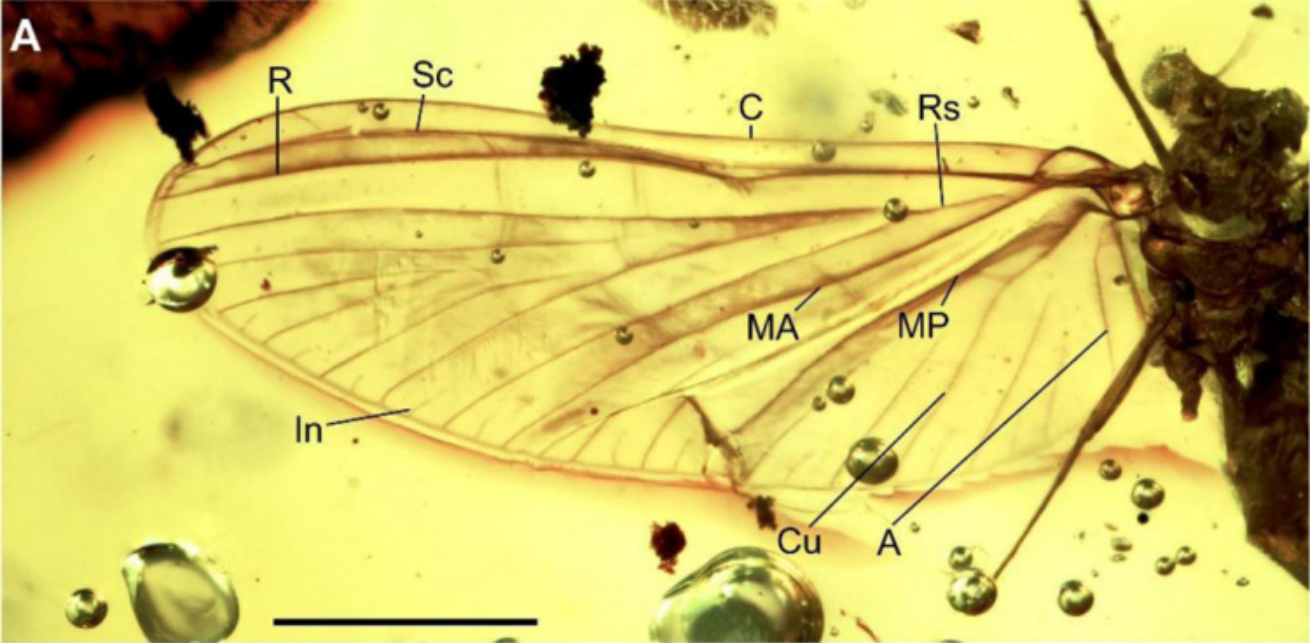


Table 1. Fossil species of the order Ephemeroptera Hyatt and Arms, 1890 from Mesozoic and Cenozoic amber deposits, including *Cloeon tzetlal* sp. nov. (Mexico, Miocene).

Family	Genus	Species	Amber	Age	Repository	Source
1 Acanthametropodidae Edmunds et al. 1963	<i>Analetris</i> Edmunds and Koss, 1972	<i>Analetris secunius</i> Godunko and Klonowska-Olejnik, 2006	Baltic	Eocene	SGPH	Godunko and Klonowska-Olejnik 2006: pp.786–790
2 Ameletidae McCafferty, 1991	<i>Baltameletus</i> Demoulin, 1968	<i>Baltameletus oligoacenicus</i> Demoulin, 1968	Baltic	Eocene	MNB	Godunko et al. 2008: pp.105–114
3	<i>Electroletus</i> Godunko and Neumann, 2006	<i>Electroletus solarii</i> Godunko and Neumann, 2006	Baltic	Eocene	MNB	Godunko and Neumann 2006: pp.178–179
4 Ametropodidae Bengtsson, 1913	<i>Prewittia</i> Demoulin, 1968	<i>Prewittia intricans</i> Demoulin, 1968	Baltic	Eocene	SMNS	Demoulin 1968: p.247
5	<i>Palaeometropus</i> Sinitshenkova, 2000a	<i>Palaeometropus cassis</i> Sinitshenkova, 2000a	New Jersey	Late Cretaceous	AMNH	Sinitshenkova 2000a: p.117
6 Australiphemeridae McCafferty, 1991	<i>Borephemera</i> Sinitshenkova, 2000a	<i>Borephemera goldmani</i> Sinitshenkova, 2000a	New Jersey	Late Cretaceous	AMNH	Sinitshenkova 2000a: pp.115–116
7	<i>Nanopphemera</i> McCafferty and Santiago-Blay, 2008	<i>Nanopphemera myanmarensis</i> McCafferty and Santiago-Blay, 2008	Myanmar	Late Cretaceous	PERC	McCafferty and Santiago-Blay 2008: p.494
8 Babiidae Kluge et al. 2006	<i>Baba</i> Kluge et al. 2006	<i>Baba lapidea</i> Kluge et al. 2006	Baltic	Eocene	MNHK	Kluge et al. 2006: pp.182–185
9 Baetidae Leach 1815	<i>Baetis</i> Leach, 1815	<i>Baetis anomala</i> (Pictet, 1854) (= <i>Baetis longipes</i> Hagen, 1856) (= <i>Cronica anomala</i> (Pictet, 1854))	Baltic	Eocene	HU	Demoulin 1968: pp.241–245
10		<i>Baetis gigantea</i> Hagen, 1856	Baltic	Eocene	Not stated	Hagen 1856: p.19
11		<i>Baetis grossa</i> Hagen, 1856	Baltic	Eocene	Not stated	Hagen 1856: p.19
12	<i>Cloeon</i> Leach, 1815	<i>Cloeon tzetlal</i> sp. nov. Varela-Hernández and Riquelme 2022	Mexico	Miocene	CPAL-UAEM	Varela-Hernández et al. 2022 (present work)
13	<i>Palaeooleon</i> Kluge, 1997	<i>Palaeooleon taimyricum</i> Kluge, 1997	Taymyr	Late Cretaceous	RAS	Kluge 1997: p.532
14	<i>Vetiformosa</i> Poinar, 2011	<i>Vetiformosa buckleyi</i> Poinar, 2011	Myanmar	Late Cretaceous	BAC	Poinar 2011: pp.369–372
15 Baetiscidae Edmunds and Traver, 1954	<i>Balticobaetisca</i> Staniczek and Beachly, 2002	<i>Balticobaetisca stuttgardia</i> Godunko and Krzemiński, 2009	Baltic	Eocene	SMNS	Godunko and Krzemiński 2009: pp.126–131
16		<i>Balticobaetisca velteni</i> Staniczek and Beachly, 2002	Baltic	Eocene	SMNS	Staniczek and Beachly 2002: pp.7–8
17 Ephemerellidae Klapálek, 1909	<i>Ephemerella</i> Walsh, 1862	<i>Ephemerella trigonoptera</i> Staniczek et al. 2017	Baltic	Eocene	MAI	Staniczek et al. 2017: pp.1–17
18	<i>Eurylophella</i> Tiensuu, 1935	<i>Eurylophella visata</i> (Demoulin, 1968) (= <i>Ephemerella visata</i> (Demoulin, 1968)) (= <i>Tiempuoga visata</i> (Demoulin, 1968))	Baltic	Eocene	MNB	Staniczek et al. 2017: pp.1–17
19	<i>Philohimias</i> Hong, 1979	<i>Philohimias sinica</i> Hong, 1979	China	Eocene	PGM	Hong 1979: p.336
20	<i>Xenophlebia</i> Demoulin, 1968	<i>Xenophlebia aenigmatica</i> Demoulin, 1968	Baltic	Eocene	SNSB	Demoulin 1968: p.268
21 Ephemeridae Latreille 1810	<i>Denia</i> McCafferty, 1987	<i>Denia abilioa</i> McCafferty, 1987	Baltic	Eocene	RAS	McCafferty 1987: pp.472–474
22 Heptageniidae Needham, 1901	<i>Amerogenia</i> Sinitshenkova, 2000a	<i>Amerogenia macrops</i> Sinitshenkova, 2000a	New Jersey	Late Cretaceous	AMNH	Sinitshenkova 2000a: pp.116–117
23	<i>Bursihyogena</i> Godunko and Sontag, 2004	<i>Bursihyogena fereci</i> Godunko and Sontag, 2004	Baltic	Eocene	MAI	Godunko and Sontag 2004: p.517
24	<i>Cinygmia</i> Eaton, 1885	<i>Cinygmia baltica</i> Demoulin, 1968	Baltic	Eocene	HU	Demoulin 1968: pp.254–255

Table 1. Continued

Family	Genus	Species	Amber	Age	Repository	Source
25	<i>Ecdyonurus</i> Eaton, 1868	<i>Ecdyonurus groehnorium</i> Godumko, 2007	Baltic	Eocene	SGPIH	Godumko 2007: pp.63–68
26		<i>Ecdyonurus leopoliensis</i> Godumko, 2004	Baltic	Eocene	NASU	Godumko 2004: pp.324–326
27	<i>Electrogenia</i> Demoulin, 1956	<i>Electrogenia dewalschei</i> Demoulin, 1956	Baltic	Eocene	Bxl. priv.coll.	Demoulin, 1956: pp.96–99
28	<i>Heptagenia</i> Walsh, 1863	<i>Heptagenia atypica</i> Demoulin, 1968	Baltic	Eocene	HU	Demoulin, 1968: pp.258–259
29		<i>Heptagenia bachofeni</i> Demoulin, 1968	Baltic	Eocene	SNSB	Demoulin 1968: pp.256–258
30		<i>Heptagenia fuscogrisea</i> (Retzius, 1783) (= <i>Kageronia fuscogrisea</i> (Retzius, 1783)) (= <i>Ephemera fuscogrisea</i> (Retzius, 1783))	Baltic	Eocene	NMR	Kluge 1986: pp.106–107
31		<i>Heptagenia gleissi</i> Demoulin, 1968	Baltic	Eocene	HU	Demoulin 1968: pp.259–260
32		<i>Heptagenia ligata</i> Demoulin, 1968	Baltic	Eocene	SMNS	Demoulin 1968: pp.260–261
33		<i>Heptagenia senex</i> Demoulin, 1968	Baltic	Eocene	HU	Demoulin 1968: pp. 255–256
34	<i>Maccaffertium</i> Bednarik, 1979	<i>Maccaffertium amae</i>	Mexico	Miocene	NMS	Macadam and Ross 2016: pp.2–5
35	<i>Rhithrogena</i> Eaton, 1882	<i>Rhithrogena spulita</i> Demoulin, 1968	Baltic	Eocene	HU	Demoulin 1968: p.261
36	<i>Succinogenia</i> Demoulin, 1965	<i>Succinogenia larssoni</i> Demoulin, 1965	Baltic	Eocene	ZMUC	Demoulin 1965: pp.151–152
37	Hexagenitidae Lameere, 1917	<i>Hexameropsis</i> Tshernova and Sinitschenkova, 1974	Myanmar	Late Cretaceous	AMNH	Lin et al., 2018a: pp.8–11
38	Isonychiidae Ulmer, 1914	<i>Cronica</i> Eaton, 1871	Baltic	Eocene	HU	Demoulin 1968: p.245
39	Leptophlebiidae Banks, 1900	<i>Aureophlebia</i> Peters and Peters, 2000	New Jersey	Late Cretaceous	AMNH	Peters and Peters 2000: p.128
40		<i>Elasturophlebia</i> Demoulin, 1968	Baltic	Eocene	SNSB	Demoulin 1968: p.270
41		<i>Borinquena</i> Traver, 1938	Dominican R.	Miocene	SMNS	Staniczek 2003: pp.13–15
42		<i>Borinquena maculata</i> Staniczek, 2003	Dominican R.	Miocene	SMNS	Staniczek 2003: pp.6–9
43		<i>Borinquena parva</i> Staniczek, 2003	Dominican R.	Miocene	AMNH	Godumko and Krzeminski, 2009: pp.131–136
44		<i>Borinquena schawallfussi</i> Staniczek et al., 2017	Dominican R.	Miocene	MNHK	Staniczek et al. 2017: pp.114–117
45		<i>Conowirtus</i> McCafferty, 1997	Lebanese	Early Cretaceous	AUB	McCafferty 1997: pp.78–81
46		<i>Cretometa</i> Tshernova, 1971	Taymyr	Late Cretaceous	RAS	Kluge 1993: pp.38–39
47		<i>Cretometa zherichini</i> Tshernova, 1971	Baltic	Late Cretaceous	RAS	Kluge 1993: pp.38–39
48		<i>Hagenulites</i> Staniczek, 2003	Dominican R.	Miocene	SMNS	Staniczek 2003: pp.2–6
49		<i>Leptophlebia</i> Westwood, 1840	Baltic	Eocene	RAS	Kluge 1993: pp.47–48
50		<i>Paraleptophlebia</i> Lestage, 1917	Baltic	Eocene	SNSB; HU	Demoulin 1968: pp.263–264

Table 1. Continued

	Family	Genus	Species	Amber	Age	Repository	Source
51	Metretopodidae Traver, 1935	<i>Metretopus</i> Eaton, 1901	<i>Metretopus divivius</i> Staniczek and Godunko, 2014	Baltic	Eocene	SMNS	Staniczek and Godunko 2014; pp.1-5
52			<i>Metretopus hemmingseni</i> Staniczek and Godunko, 2012	Baltic	Eocene	ZMUC	Staniczek and Godunko 2012; pp.81-82
53			<i>Metretopus triternis</i> Demoulin, 1968	Baltic	Eocene	GZG	Staniczek and Godunko 2012; pp.82-84
54		<i>Siphoplecton</i> Clemens, 1915	<i>Siphoplecton barabani</i> Staniczek and Godunko, 2012	Baltic	Eocene	MNB; MNHN	Staniczek and Godunko 2012; pp.65-71
55			<i>Siphoplecton demoulini</i> Staniczek and Godunko, 2012	Baltic	Eocene	MNHN	Staniczek and Godunko 2012; pp.75-78
56			<i>Siphoplecton gattoiliani</i> Staniczek and Godunko, 2016	Baltic	Eocene	CCHH	Staniczek and Godunko 2016; pp.20-23
57			<i>Siphoplecton hageni</i> Staniczek and Godunko, 2012	Baltic	Eocene	MNB	Staniczek and Godunko 2012; pp.71-72
58			<i>Siphoplecton jaegeri</i> Demoulin, 1968	Baltic	Eocene	MNB	Godunko, Neumann and Staniczek, 2019; pp.3-10
59			<i>Siphoplecton landolti</i> Godunko, Neumann and Staniczek, 2019	Baltic	Eocene	SMNS	Godunko et al. 2019; pp.10-14
60			<i>Siphoplecton macrops</i> (Pictet-Baraban and Hagen, 1856) (= <i>Pailgenia macrops</i> (Hagen, 1856))	Baltic	Eocene	MNB	Staniczek and Godunko 2016; pp.2-4
61			<i>Siphoplecton picteti</i> Staniczek and Godunko, 2012	Baltic	Eocene	MNB	Staniczek and Godunko 2012; pp.63-65
62			<i>Siphoplecton sartorii</i> Staniczek and Godunko, 2016	Baltic	Eocene	CCHH	Staniczek and Godunko 2016; pp.17-20
63			<i>Siphoplecton staedemanna</i> Godunko, Neumann and Staniczek, 2019	Baltic	Eocene	SMNS; MNHK	Godunko, Neumann and Staniczek 2019; pp.14-19
64	Palaeoanthidae Kluge, 1993		<i>Palaeoanthus minutus</i> Kluge, 1993	Taymyr	Late Cretaceous	RAS	Kluge 1993; p.45
65			<i>Palaeoanthus orthostylus</i> Kluge, 1993	Taymyr	Late Cretaceous	RAS	Kluge 1993; pp.44-45
66	Polymitarcyidae Banks, 1900		<i>Cretomitarcyus luzzi</i> Sinitshenkova, 2000a	New Jersey	Late Cretaceous	AMNH	Sinitshenkova 2000a; pp.114-115
67	Prosopistomatidae Lameere, 1917	<i>Myanmarrella</i> Sinitshenkova, 2000b	<i>Myanmarrella rossi</i> Sinitshenkova, 2000b	Myanmar	Late Cretaceous	NHM	Sinitshenkova 2000b; pp.25-27
68		<i>Proximicornus</i> Lin et al., 2018a	<i>Proximicornus redivivus</i> Lin et al., 2018a	Myanmar	Late Cretaceous	CNUB	Lin et al. 2018a; pp.402-404
69	Siphonuridae Ulmer, 1920		<i>Balticophlebia hemitig</i> Demoulin, 1968	Baltic	Eocene	SMNS	Demoulin 1968; pp.237-238
70			<i>Siphonurus aethosus</i> Demoulin, 1968	Baltic	Eocene	HU	Demoulin 1968; pp.240-241
71	Vietnamellidae Allen, 1984	<i>Burmella</i> Godunko, Martynov and Staniczek, 2021	<i>Burmella clypeata</i> Godunko, Martynov and Staniczek, 2021	Myanmar	Late Cretaceous	SMNS	Godunko et al. 2021; pp.110-118
72			<i>Burmella pauavenosa</i> Godunko, Martynov and Staniczek, 2021	Myanmar	Late Cretaceous	SMNS	Godunko et al. 2021; pp.101-110

ages and stratigraphic levels. An inventory of fossil species of the order Ephemeroptera Hyatt and Arms, 1890, including *C. tzeltal* sp. nov., from Mesozoic and Cenozoic amber deposits, is summarized in Table 1. Baetidae Leach, 1815 is a monophyletic family of Ephemeroptera with 97 genera and about 833 species, distributed throughout the world, with a probable Pangean origin (Barber-James et al. 2008). The oldest baetid specimen from an amber inclusion is a morphotype, an adult female from Lebanese amber, which dates back to the Barremian (Early Cretaceous) (McCafferty 1997). *Cloeon tzeltal* sp. nov. represents the first record of the genus from the Miocene of the Americas. It has been suggested previously that the current geographic distribution of the genus *Cloeon* in the Americas is limited to the northern part of the continent (McCafferty and Waltz 1990). In Pliocene sediments of Australia, a mayfly is referred provisionally to the genus *Cloeon* within Baetidae by Riek (1954) from fossil material based exclusively on nymphal instar specimens; this Pliocene material was described as *Cloeon emnavillensis* Riek, 1954 (Riek 1954; Jell 2004).

The genus *Cloeon* has a near-cosmopolitan distribution, but is conspicuously absent from the Neotropics (Gattolliat and Nieto 2009). Initially, Burks (1953) recognized eight species of *Cloeon* exclusively distributed in the Nearctic. McCafferty and Waltz (1990) later transferred all of these species to the genus *Procloeon*, except for *C. dipterum*, which remains the sole representative of the genus *Cloeon* in the New World. More recently, *Cloeon* has been identified at several localities in the Neotropics, but these appear to be introduced rather than endemic (Vera et al. 2015; Salles et al. 2016; Banegas et al. 2020). In this context, the occurrence of *C. tzeltal* sp. nov., which is the first record of *Cloeon* in the Miocene tropics of southern Mexico, extends the distribution of this genus to the southernmost part of North America; consequently, *C. tzeltal* sp. nov. is probably more closely related to those species that are currently distributed in the Nearctic and Western Palearctic.

The wide geographic distribution of extant *Cloeon* makes it difficult to establish a center of origin for the genus. According to Gattolliat and Nieto (2009), the Afrotropical realm encompasses a large percentage of endemism at the genus and species level of Baetidae. Monaghan et al. (2005) concluded that the genetic difference between several species of mayflies and their wide geographic distribution is more congruent with dispersal, rather than vicariance. According to these authors, extant species of *Cloeon* possess traits that allow them to increase colonization by dispersal over long distances. Furthermore, Degrange (1960), in discussing the longevity of adult females of *C. dipterum*, stated that "...not inseminated females have increased their lifespan" (Degrange 1960, p. 28). Yanai et al. (2020) support the idea of dispersal colonization by the extant species *Cloeon perkinsi* Barnard, 1932, while asserting an Afrotropical origin with dispersal to the north and east. Rutschmann et al. (2014) have studied endemism of the species of *Baetis* and *Cloeon* in the Canary Islands and have hypothesized colonization events followed by subsequent diversification. These studies, in total, suggest that a high dispersal potential has been observed in extant representatives of *Cloeon*, with a probable Afrotropical origin. With this background, the most plausible hypothesis for the

occurrence of a fossil representative of *Cloeon* in the Miocene tropics of Mexico posits an extended geographic distribution of the genus in the southernmost part of North America in the geological past, with a subsequent extinction of *C. tzeltal* sp. nov.

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Competing interests

The authors have declared that no competing interests exist.

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