

Earliest occurrence of Embiidae: A new genus
from earliest Eocene Oise amber
(Insecta: Embiodea)

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Earliest occurrence of Embiidae: A new genus from earliest Eocene Oise amber (Insecta: Embiodea)

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KEY WORDS

Insecta,
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new species,
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MOTS CLÉS

Insecta,
Embiodea,
Embiidae,
espèce nouvelle,
genre nouveau,
plus ancien fossile.

ABSTRACT

A new genus and species of webspinner, *Galloembia raholai* n. gen. et n. sp., is described from the earliest Eocene Oise amber of France. The species is currently the oldest record of the family, a taxon previously known from only as far back as the middle Eocene Baltic amber and an exceptionally dubious Eocene-Oligocene impression fossil of the central United States. The genus is diagnosed and compared with other genera of Embiidae.

RÉSUMÉ

Le plus ancien Embiidae : un nouveau genre de l'ambre éocène basal de l'Oise (Insecta: Embiodea).
Un nouveau genre et espèce d'embié, *Galloembia raholai* n. gen. et n. sp., sont décrits de l'ambre éocène basal de l'Oise, France. Il s'agit du plus ancien représentant des Embiidae, un taxon connu de l'ambre de l'Eocène moyen de la Baltique et par un fossile en compression éocène-oligocène douteux du centre des États-Unis. Le genre est diagnostiqué et comparé aux autres genres d'Embiidae.

INTRODUCTION

Webspinners (order Embiodea Lameere, 1900) comprise some of the smallest polyneopterous insects, with presently less than 500 described species. Species are gregarious and live in silken galleries which are spun from characteristic glands in the swollen probasitarsi. Females are apterous and spend much of their lives within these galleries tending to the developing brood, while males are usually fully winged. Although individuals are comparatively soft-bodied and therefore unlikely to preserve in many kinds of sediments, there are remains of Embiodea, albeit few in number, from as far back as the Jurassic. Aside from a single impression from the Eocene-Oligocene boundary of Florissant, Colorado, United States (Cockerell 1908), the fossil record for the order is confined to inclusions in amber and its higher fidelity of preservation. There are well-documented Embiodea in mid-Cretaceous amber from Myanmar (Cockerell 1919; Davis 1939a; Engel & Grimaldi 2006; Engel *et al.* 2016), early Eocene amber of the Cambay Basin (Engel *et al.* 2011), middle Eocene amber of the Baltic region (Ross 1956), and middle Miocene amber of the Dominican Republic (Szumik 1994, 1998; Ross 2003). These fossil occurrences span a number of different families ranging from the putatively primitive Clothodidae to the more derived Scelembiidae Ross, 2001 and Anisembiidae Davis, 1940. The family Embiidae Burmeister, 1839 is a diverse taxon of doubtful monophyly (e.g. Szumik 1996; Miller *et al.* 2012; Szumik *et al.* 2019). Its fossil record is scarce, with a single genus and species in middle Eocene Baltic amber and the aforementioned Eocene-Oligocene fossil of dubious familial attribution. Herein we report the discovery of an early Eocene embiid preserved in Oise amber, which is also the currently oldest representative of the family and the first record of the order for this deposit.

MATERIAL AND METHODS

The fossil is embedded in a small, clear piece of amber. It was prepared using a diamond disk and examined using a Nikon binocular microscope SMZ 1500. Photographs were taken with an Amscope camera MU900, and the images processed using Adobe Photoshop CS6. The fossil is incomplete, head partial and fragmentary and lacking dorsal anterior part of the body lost at the amber surface. The ventral portion of the body is well visible. The wings are along the outer part of the fossil, with the venation clearly visible. The classification followed herein is that proposed by Miller *et al.* (2012), while the morphological terminology is adapted from that of Ross (2000).

ABBREVIATIONS

HP	hypandrium process;
LCB	left cercus basipodite;
LC ₁	basal left cercomere;
LPPT	left paraproct;
LPPT-P	hook of left paraproct;
MA	median vein;
RC ₁	right basal cercomere;

10LP	process of left hemitergite;
10RP	process of right hemitergite.

Institutional abbreviation

MNHN Muséum national d'Histoire naturelle, Paris.

SYSTEMATIC PALAEOLOGY

Class Insecta Linnaeus, 1758
 Order Embiodea Lameere, 1900
 Family Embiidae Burmeister, 1839
 Subfamily *Incertae sedis*

Genus *Galloembia* n. gen.

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TYPE SPECIES. — *Galloembia raholai* n. sp.

DIAGNOSIS. — Male: moderate body size (as preserved), at least 7.6 mm. Metabasitarsus with two ventral bladders (or euplantulae) (medial and apical). Fully winged; MA forked well distad forewing midlength. Tenth tergite cleft to base (i.e., hemitergites completely separated with basal membranous connection); right and left hemitergites with short processes; 10LP short, narrow, and arched with acutely rounded apex (10LP analogous to that of *Embia ramburi* Rimsky-Korsakov, 1905); 10RP exceptionally short, broad, and bluntly rounded; medial flap apparently absent (or scarcely developed); LPPT enlarged, with a short, subapical LPPT-P; HP poorly developed, apically blunt; LC₁ with large, prominent inner lobe subapical in position, lobe slightly echinulate on dorsal surface, otherwise remainder of LC₁ not echinulate; left and right cercomeres with abundant, elongate, erect, simple setae.

ETYMOLOGY. — The new generic name is a combination of the Greek words *Γαλλία* (*Gallia*, meaning, “France”, also of Latin derivation), and *ἐμβίος* (*embios*, meaning, “lively” or “vivacious”; itself the root of the type genus of the family). The gender of the name is feminine.

Galloembia raholai n. sp.
 (Figs 1-3)

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TYPE MATERIAL. — Holotype, MNHN.FA71313 (PA 17338), head only partly preserved, antennae and mouthparts missing, fore legs incomplete, thorax, abdomen, complete wings, mid and hind legs well preserved), deposited in the MNHN, Paris, France.

TYPE LOCALITY AND HORIZON. — France, Oise department, region of Creil, Chevrete, Le Quesnoy. Earliest Eocene, - 53 Ma, “Sparnacian”, level MP7 of the mammal fauna of Dormaal.

ETYMOLOGY. — The specific epithet honors Pompeu Rahola, entomologist who first showed Embiodea to the senior author.

DIAGNOSIS. — As for the genus (*vide supra*).

DESCRIPTION

Male, fully winged; body slender, light brown, 7.6 mm long (as preserved); pronotum longer than wide, 1.18 mm

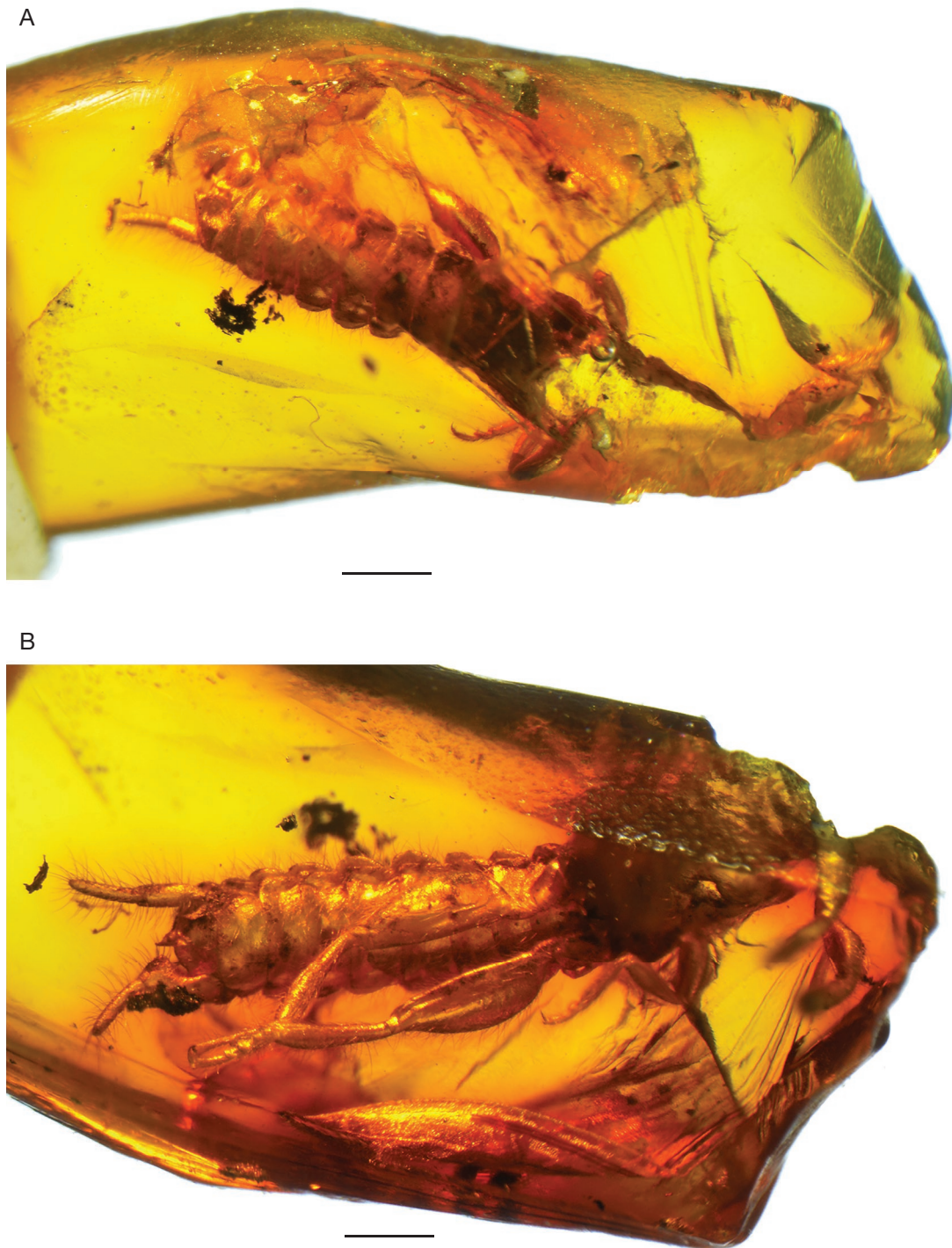


FIG. 1. — *Galloembia raholai* n. gen. et n. sp., holotype MNHN.F.A71313, habitus: **A**, dorsal view; **B**, ventral view. Scale bars: 1 mm.

long, 0.87 mm wide; mesonotum narrower and longer than pronotum, triangular; without visible longitudinal median sulcus; metanotum quadrate; fore legs only partly preserved; mesobasitarsus 0.16 mm long, mesotarsomere III 0.08 mm long; metabasitarsus 0.24 mm long, metatarsomere III 0.16 mm long; metabasitarsus with two ventral

bladders; forewing 5.0 mm long; venation similar to that of *Embia* spp., in particular vein MA bifurcate; abdomen elongate cylindrical, 2.8 mm long, 0.84 wide; terminalia asymmetrical; tergite X completely divided medially, with inner base of left hemitergite well separated from right hemitergite by a membranous area and no median sclerite

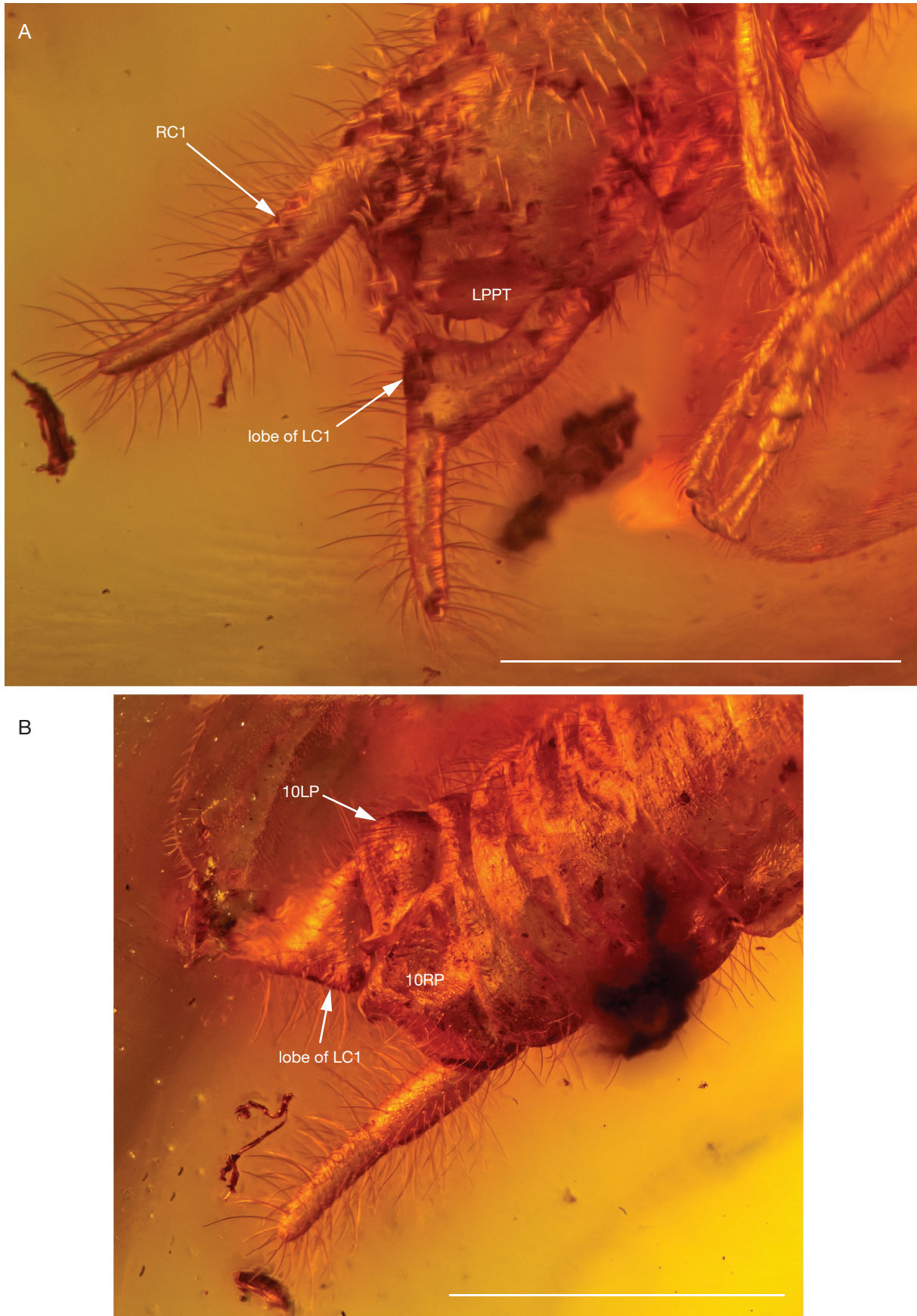


FIG. 2. — *Galloembia raholai* n. gen. et n. sp., holotype MNHN.F.A71313, male terminalia: **A**, ventral view; **B**, dorsal view. Scale bars: 1 mm.

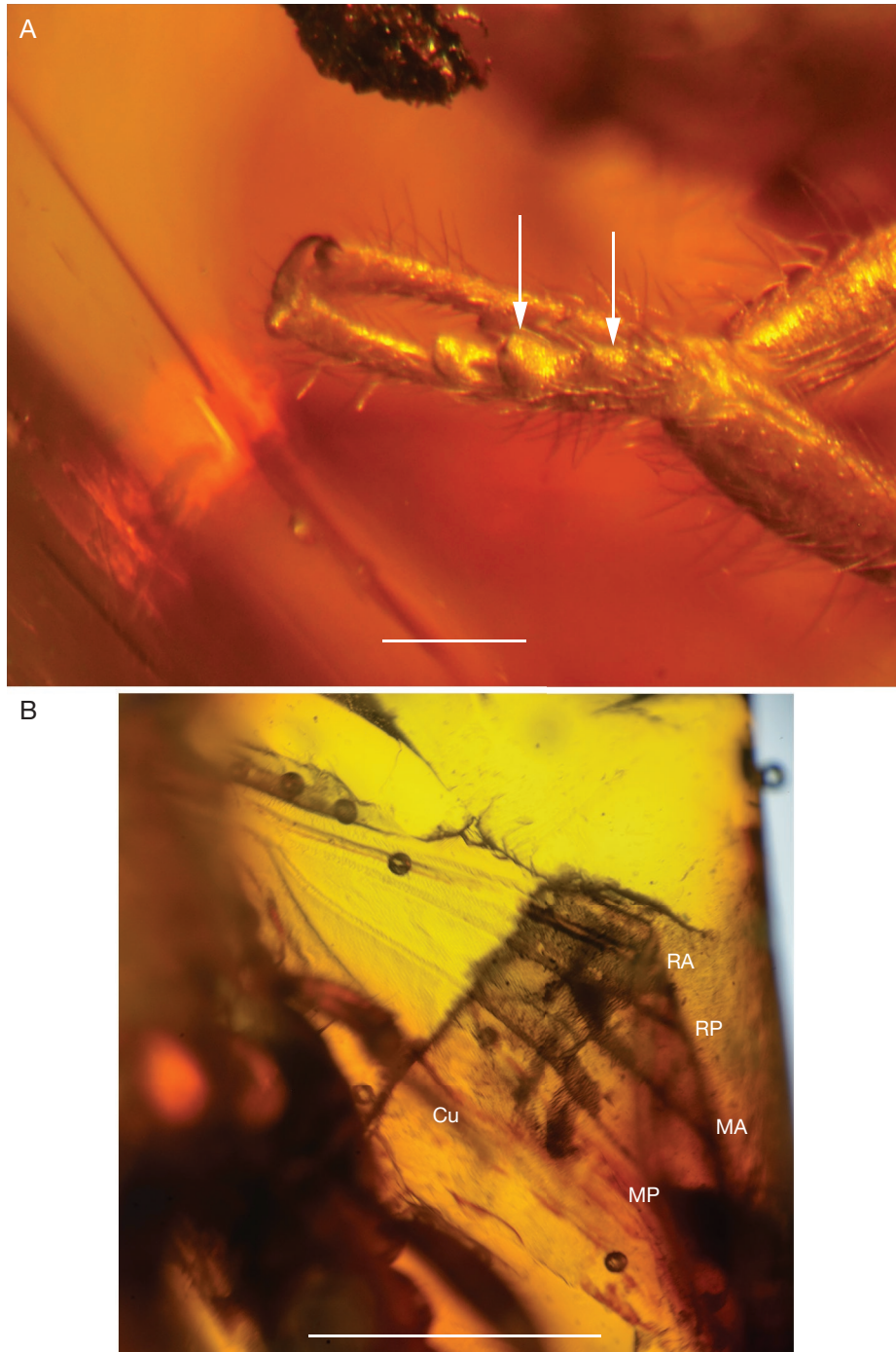


FIG. 3. — *Galloembia raholai* n. gen. et n. sp., holotype MNHN.F.A71313: **A**, metabasitarsus in ventral view, **arrows** indicate position of bladders; **B**, forewing. Scale bars: A, 0.2 mm; B, 2 mm.

between; apical process of left hemitergite (10LP) short, narrow, arched, and acutely rounded apically; process of right hemitergite (10RP) broadly and bluntly rounded, short, and smooth, without apical hook; left paraproct (LPPT) enlarged, with short, subapical hook (LPPT-P); left cercomeres not fused; basal left cercomere (LC_1) with a prominent, inner, subapical lobe, dorsal surface of lobe weakly echinulate, remainder of LC_1 not echinulate; right basal cercomere (RC_1) elongate and slender.

DISCUSSION

Although Embiidae are likely not a monophyletic group (e.g. Szumik 1996; Szumik *et al.* 2008; Miller *et al.* 2012), the present fossil would generally fall among this assemblage of genera based on the characters outlined by Ross (2007) and Miller *et al.* (2012). Specifically, *Galloembia* n. gen. would be classified within Embiidae as currently circumscribed owing to the following attributes: male fully winged; metabasitarsus

with two ventral bladders (medial and apical); forewing vein MA forked; terminalia strongly asymmetrical; tenth tergum completely divided medially, with distinct membranous area between hemitergites; inner base of left hemitergite well separated from right one by a membranous area, no median sclerite between the two halves; right basal cercomere elongate and slender; left cercomeres not fused; basal left cercomere with distinct inner, subapical lobe, with dorsal surface of lobe weakly echinulate.

Given its diversity and lack of homogeneity, there has been no modern attempt to provide a comprehensive revision of Embiidae. Accordingly, we provide comparisons between *Galloembia* n. gen. and the various extant and fossil genera currently placed therein.

Galloembia n. gen. differs from the embiid genera as follows:

– from *Acrosembia* Ross, 2006: simple, short, narrowly arched 10LP (elongate with inner talon in *Acrosembia*); short, bluntly rounded 10RP (projecting and hooked in *Acrosembia*) (Ross 2006);

– *Aptereambia* Ross, 1957: 10R shortened (10R with a sharp apex); LPPT as wide as long (LPPT wider than long) (Krauss 1911: pl. 3, fig. 15; Esben-Petersen 1920; Davis 1939c: figs 1-10);

– *Arabembia* Ross, 1981: no basal lobe on LC₁ (presence of such a lobe); absence of small echinulations proximally on LC₁ (small echinulations on proximal part of LC₁); a broader LPPT, as wide as long (LPPT longer than wide) (Ross 1981: fig. 2);

– *Berlandembia* Davis, 1940: absence of small echinulations proximally on LC₁ (echinulations present in basal part of LC₁); longer LPPT, as long as wide (LPPT wider than long) (Davis 1939c: figs 3-5);

– *Chirembia* Davis, 1940: shorter 10LP (10LP with long processes); longer LPPT, as long as wide (LPPT wider than long) (Davis, 1940: figs 14, 17; Ross 2006);

– *Cleomia* Stefani, 1953: only one median lobe of basal left cercomere (two such lobes); longer LPPT, as long as wide (LPPT wider than long) (Stefani 1953: fig. 4e, f; Ross 1966);

– *Dihyboercus* Enderlein, 1912: short apical process of left hemitergite (long apical process); only one median lobe of basal left cercomere (two such lobes); larger LPPT, as long as wide (wider than long) (Davis 1939b: figs 6, 9);

– *Dinembia* Davis, 1939: absence of indentation on basal right cercomere (present in *Dinembia*); broad LPPT, as wide as long (longer than wide) (Davis 1939c: figs 6, 7);

– *Donaconethis* Enderlein, 1909: absence of a basal lobe and small echinulations at base of left cercomere (structures present); left paraproct longer than wide (rounded); larger LPPT (LPPT small) (Ross 1951: fig. 2);

– *Embia* Latreille, 1829: presence of two ventral bladders on metabasitarsus (medial bladder absent in *Embia*) (Ross 1966, 2006);

– *Electroembia* Ross, 1956 (middle Eocene Baltic amber): more pronounced median lobe of basal left cercomere (basal inner margin straight); curved and shorter apical process of left hemitergite (sharp and straight process) (Ross 1956: fig. 2; 1966: fig. 1);

– *Enveja* Navás, 1916: median lobe of basal left cercomere rounded (quadrangular); shape of left paraproct; large LPPT (LPPT very small) (Davis 1939b: 491, figs 5, 6);

– *Leptembia* Krauss, 1911: crenulation only on median lobe of basal left cercomere (crenulation in basal inner part); median lobe of basal left cercomere larger than in *Leptembia* (Krauss 1911: pl. 5, fig. 23; Ross 2006);

– *Lithembia* Ross, 1984, *nomen nudum* (Eocene-Oligocene Nearctic, based on an impression fossil without any detail of body structures, terminalia, or most venational elements (Ross 1984). It is impossible to attribute this species, “*Embia*” *florissantensis* Cockerell, 1908, to the Embiidae, nor can it be meaningfully assigned to a genus. In fact, Ross (1984) was unable to give any characters to circumscribe the taxon, leaving the generic name as a *nomen nudum*;

– *Machadoembia* Ross, 1952: presence of two well developed ventral bladders on metabasitarsus (medial bladder absent in *Machadoembia*); vein MA forked well distal of middle of forewing (forked more basally); LPPT separated from LCB (fused) (Ross 1952: 43-44);

– *Metembia* Davis, 1939: only one lobe one LC₁ (two lobes); large left paraproct (reduced); large LPPT (reduced) (Davis 1939b: figs 2, 3; Ross 1950: fig. 3);

– *Macreambia* Davis, 1940: LC₁ without a basal indentation (a basal indentation); large left paraproct (reduced); LPPT as long as wide (wide than long) (Davis 1940: figs 39-41);

– *Odontembia* Davis, 1939: only one median lobe one LC₁ (two lobes); large LPPT (reduced) (Davis 1939b: figs 23, 25);

– *Oedembia* Ross, 2007: median lobe of LC₁ close to its apex (in a more basal position); right hemitergite not rounded (rounded) (Ross 2007: fig. 1);

– *Parachirembia* Davis, 1940: exceptionally short apical process of right hemitergite (very long process); a larger left paraproct (narrow); large LPPT (very small) (Davis 1940: figs 30, 34);

– *Parembia* Davis, 1939: smaller median lobe of LC₁; apical process of left hemitergite shorter and less sharp; left paraproct with a more pronounced lobe; large LLPT (small) (Davis 1939b: figs 23-27; Ross 1981: fig. 1);

– *Parthenembia* Ross, 1960 (female material, male unknown): hardly comparable to our male fossil; nevertheless, in *Parthenembia*, the second bladder of metabasitarsus is medial, instead of being subapical as in *Galloembia* n. gen. (Ross 1960);

– *Pseudembia* Davis, 1939: absence of a basal lobe and presence of a larger median lobe on LC₁ (basal lobe present and median lobe reduced) (Davis 1939b: figs 9-19).

CONCLUDING REMARK

The Embiodea live in the litter, generally under rather warm conditions, but some species are known under Mediterranean climates. Flying males can disperse. Our fossil was probably trapped in resin on the trunk of the producing tree. The order appears extremely rare in the Oise amber (one specimen for *c.* 20 000 insects), which is probably due to their cryptic way of life.

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REFERENCES

- COCKERELL T. D. A. 1908. — Descriptions of Tertiary insecta. *American Journal of Science* (4) 25: 51-52, 227-232, 309-312.
- COCKERELL T. D. A. 1919. — Two interesting insects in Burmese amber. *The Entomologist* 52: 193-195.
- DAVIS C. 1939a. — Taxonomic notes of the order Embioptera. 3. The genus *Burmitembia* Cockerell. *Proceedings of the Linnean Society of New South Wales* 64: 369-372.
- DAVIS C. 1939b. — Taxonomic notes of the order Embioptera. 6-10. *Proceedings of the Linnean Society of New South Wales* 64: 474-495.
- DAVIS C. 1939c. — Taxonomic notes of the order Embioptera. 11-14. *Proceedings of the Linnean Society of New South Wales* 64: 559-575.
- DAVIS C. 1940. — Taxonomic notes on the order Embioptera. 15. The genus *Rhagadochir* Enderlein and genera convergent to it. *Proceedings of the Linnean Society of New South Wales* 65: 171-191.
- ENGEL M. S. & GRIMALDI D. A. 2006. — The earliest web-spinners (Insecta: Embiidea). *American Museum Novitates* 3514: 1-15.
- ENGEL M. S., GRIMALDI D. A., SINGH H. & NASCIBENE P. C. 2011. — Web-spinners in Early Eocene amber from western India (Insecta, Embiidea). *ZooKeys* 148: 197-208. <https://doi.org/10.3897/zookeys.148.1712>
- ENGEL M. S., HUANG D.-Y., BREITKREUZ L. C. V., CAI C.-Y. & ALVARADO M. 2016. — Two new species of mid-Cretaceous web-spinners in amber from northern Myanmar (Embiidea: Clothodidae, Oligotomidae). *Cretaceous Research* 58: 118-124. <https://doi.org/10.1016/j.cretres.2015.10.007>
- ESBEN-PETERSEN T. 1920. — New species of neuropterous insects from South Africa (Ephemerida, Megaloptera, Embiida). *Annals of the South African Museum* 17: 499-506.
- KRAUSS H. A. 1911. — Monographie der Embien. *Zoologica* 60: 1-78.
- MILLER K. B., HAYASHI C., WHITING M. F., SVENSON G. J. & EDGERLY J. S. 2012. — The phylogeny and classification of Embioptera (Insecta). *Systematic Entomology* 37: 550-570. <https://doi.org/10.1111/j.1365-3113.2012.00628.x>
- NAVÁS L. 1916. — Neurópteros nuevos o poco conocidos (Séptima serie). *Memorias de la Real Academia de Ciencias y Artes de Barcelona* (3) 12: 219-243.
- ROSS E. S. 1950. — The Embiidae of India (Embioptera). *The Wasmann Journal of Biology* 8: 133-153.
- ROSS E. S. 1951. — Three new African Embiidae. *Annals and Magazine of Natural History* (12) 4: 381-389.
- ROSS E. S. 1952. — The Embioptera of Angola. *Publicacoes Culturais Companhia de Diamantes de Angola* 14: 41-54.
- ROSS E. S. 1956. — A new genus of Embioptera from Baltic amber. *Mitteilungen aus dem Geologischen Staatinstitut in Hamburg* 25: 76-81.
- ROSS E. S. 1960. — Parthenogenetic African Embioptera. *The Wasmann Journal of Biology* 18: 297-304.
- ROSS E. S. 1966. — The Embioptera of Europe and the Mediterranean region. *Bulletin of the British Museum, (Natural History), Entomology* 17: 273-326. <https://www.biodiversitylibrary.org/page/2236507>
- ROSS E. S. 1981. — Insects of Saudi Arabia. Embiidina. *Fauna of Saudi Arabia* 3: 201-212.
- ROSS E. S. 1984. — A synopsis of the Embiidina of the United States. *Proceedings of the Entomological Society of Washington* 86: 82-93. <https://www.biodiversitylibrary.org/page/16360535>
- ROSS E. S. 2000. — EMBIA. Contributions to the biosystematics of the insect order Embiidina. Part 1. Origin, relationships and integumental anatomy of the insect order Embiidina. *Occasional Papers of the California Academy of Sciences* 149: 1-53. <https://www.biodiversitylibrary.org/page/40719172>
- ROSS E. S. 2003. — EMBIA. Contributions to the biosystematics of the insect order Embiidina. Part 5. A review of the family Anisembiidae with descriptions of new taxa. *Occasional Papers of the California Academy of Sciences* 154: 1-123. <https://www.biodiversitylibrary.org/page/40720176>
- ROSS E. S. 2006. — The insect order Embiidina of northeastern Africa and the Red Sea region. *Fauna of Arabia* 22: 287-343.
- ROSS E. S. 2007. — The Embiidina of eastern Asia, part I. *Proceedings of the California Academy of Sciences* 58: 23-30.
- STEFANI R. 1953. — Nuovi Embiotteri della Sardegna. *Bollettino della Società Entomologica Italiana* 83: 84-98.
- SZUMIK C. A. 1994. — *Oligoembia vetusta*, a new fossil teratembiid (Embioptera) from Dominican amber. *Journal of the New York Entomological Society* 102: 67-73.
- SZUMIK C. A. 1996. — The higher classification of the order Embioptera: a cladistic analysis. *Cladistics* 12: 41-64.
- SZUMIK C. A. 1998. — Una nueva especie de Anisembiidae en ambar dominicana. *Revista Brasileira de Entomologia* 42 (1-2): 7-8.
- SZUMIK C., EDGERLY J. S. & HAYASHI C. Y. 2008. — Phylogeny of embiopterans (Insecta). *Cladistics* 24: 993-1005. <https://doi.org/10.1111/j.1096-0031.2008.00228.x>
- SZUMIK C., JUÁREZ M. L., RAMÍREZ M. J., GOLOBOFF P. & PEREYRA V. V. 2019. — Implications of the tympanal hearing organ and ultrastructure of chaetotaxy for the higher classification of Embioptera. *American Museum Novitates* 3933: 1-31. <https://doi.org/10.1206/3933.1>

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