A new peculiar species of the genus *Helius* Lepeletier & Serville, 1828 (Diptera, Limoniidae) from Cretaceous Álava amber (Spain)

Iwona Kania^{1*}, Wiesław Krzemiński² and Antonio Arillo³

¹ Department of Environmental Biology; University of Rzeszów; Zelwerowicza 4; 35-601 Rzeszów; Poland. E-mail: ikania@univ.rzeszow.pl

² Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17; 31 – 016 Kraków, Poland.

³ Departamento de Zoología y Antropología Física, Facultad de Biología, Universidad Complutense, Madrid 28040, Spain.

*Corresponding author

ABSTRACT: *Helius spiralensis* sp. nov., is a very peculiar species of the genus *Helius* (Diptera: Limoniidae), with a characteristic morphology of hypopygium not found in other representatives of this genus. This is the second *Helius* species described from Early Cretaceous Álava amber (Spain), and one of the oldest representatives of the genus.

KEY WORDS: fossil insects, *Helius spiralensis* sp. nov., inclusions, morphology, new species, taxonomy.



The Cretaceous is one of the most important periods in Earth's history. Major changes of entomofauna started at the beginning of this period with the rapid radiation of various groups of insects, co-evolving with Angiospermae (Grimaldi 2010). In the Early Cretaceous (early Barremian (Granier *et al.* 2016; Maksoud *et al.* 2016) and Aptian (Menor-Salván *et al.* 2016)), species with a very elongated rostrum, such as *Helius ewa* Krzemiński, Kania & Azar, 2014, started appearing, which is probably connected with the early appearance of angiosperms (Krzemiński *et al.* 2014).

The Recent fauna of Limoniidae is diverse, with over 11,000 species (Oosterbroek 2015), and these are associated mainly with moist, temperate environments, such as wooded areas, both in temperate and tropical regions, but also with open habitats, such as meadows, deserts and oases (Starý & Freidberg 2007). The imago of the Recent representatives of the genus *Helius*

occur in sunny meadows near streams, or in moist coppice habitats. It could be assumed that their ancestors probably lived in similar ecological niches. A number of Cretaceous amberiferous localities with insect inclusions are known, but only a few of them have yielded representatives of the genus *Helius*. Only five species are known from this period (Table 1) (Rayner & Waters 1990; Ribeiro 2002; Kania *et al.* 2013; Krzemiński *et al.* 2014), with only one from Álava, Spain (Kania *et al.* 2016). Many more species are known from younger periods, such as the Eocene (Loew 1850; Meunier 1906; Alexander 1931; Krzemiński 1985, 1993; Podenas 2002; Kania 2014), the Oligocene (Statz 1934, 1944; Krzemiński 1991) and the Miocene (Krzemiński 2002).

Helius spiralensis sp. nov, described below, is one of the smallest fossil representatives of the genus. It has an elongated rostrum, with a peculiar morphology of the hypopygium and

Table 1	List of fossils	belonging to the	genus Helius,	known fron	n the Cretaceous	. Localities r	marked with	asterisk (*) are	e amber o	utcrops (part
after Kar	nia <i>et al.</i> 2013);	, stage marked by	/ double asteris	sk (**) – info	ormation about s	tage accordii	ng to latest d	ata (Maksoud	et al. 2016).

Species	Age	Stage	Locality
Helius botswanensis Rayner & Waters 1990	Late Cretaceous	Turonian	Orapa Diamond Mine (Botswana)
Helius krzeminskii Ribeiro 2002	Late Cretaceous	lower Cenomanian	Tanai village (Myanmar (Burma))*
Helius alavensis Kania, Krzemiński & Arillo 2016	Early Cretaceous	upper Albian	Peñacerrada I, Basque-Cantabrian Basin (Alava, Spain)
Helius spiralensis sp. nov.	Early Cretaceous	upper Albian	Peñacerrada I, Basque-Cantabrian Basin (Alava, Spain)
Helius lebanensis Kania, Krzemiński & Azar 2013	Early Cretaceous	lower Barremian**	Tannourine (North Lebanon)* & Hammana– Mdeyrij (Central Lebanon)*
Helius ewa Krzemiński, Kania & Azar 2014	Early Cretaceous	lower Barremian	Caza (District) Baabda Mouhafazet Jabal Loubnan (Governorate Mount Lebanon), Hammana–Mdeyrij (Central Lebanon)*

https://doi.org/10.1017/S1755691017000299 Published online by Cambridge University Press



Figure 1 *Helius spiralensis* sp. nov., holotype, specimen MCNA 15078 (male): (A) drawing of the head (reconstructed), latero-dorsal view; (B) schematic representation of the relation between the length of the antenna (a), rostrum (r), palpus (p) and head (h); (C) drawing of the wing venation; (D) drawing of the last tergites, sternites and gonocoxite, gonostyles. Abbreviations: a = antennae; aed = aedeagus; exl = extra lobe; gx = gonocoxite; ing = inner gonostylus; oug = outer gonostylus; p = palpus; ped = pedicel; r = rostrum; scp = scape; st IX = sternite IX; tg IX = tergite IX.



Figure 2 *Helius spiralensis* sp. nov., holotype, specimen MCNA 15078 (male): (A) photograph of the antenna, dorsal view; (B) photograph of the head, latero-dorsal view; (C) photograph of the head, lateral view; (D) photograph of the palpus, dorsal view.

with an extremely elongated aedeagus. These features clearly differentiate it from other species of the genus *Helius*.

This is the second representative of the genus from Cretaceous Álava amber and the third limoniid described from this locality (Krzemiński & Arillo 2007).

1. Material and methods

The study herein is based on specimen No. MCNA 15078 from the Upper Albian amber of Álava (Barrón et al. 2015),

Peñacerrada I outcrop (northern Spain), located on the northern slope of Sierra de Cantabria, within the Basque–Cantabrian Basin (Peñalver & Delclos 2010) (Figs 1, 2). The material is deposited in the collection of the Museo de Ciencias Naturales de Álava, Vitoria, Spain (MCNA).

The specimen was studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera; the measurements were taken with NIS-Elements D 3.0 software. The length of discal cells was measured from the hind edge of the discal cells to the connection of cross-vein m–m with vein M_3 .



Figure 3 *Helius spiralensis* sp. nov., holotype, specimen MCNA 15078 (male): (A) photograph of the wing; (B) photograph of the wing venation, apical part of the wing; (C) photograph of the wing venation, with end of subcostal vein (Sc) and cross-vein sc-r marked.

The drawings for the analysis were based on the specimen and photographs.

2. Systematic palaeontology

Order Diptera Linnaeus, 1758 Family Limoniidae Speiser, 1909 Subfamily Limoniinae Speiser, 1909 Genus *Helius* Lepeletier & Serville, 1828 Subgenus *Helius* Lepeletier & Serville, 1828

Type species. Helius longirostris (Meigen, 1818).

Helius spiralensis sp. nov. (Figs 1-4)

Diagnosis. Palpus approximately 0.25 times longer than rostrum, approximately nine times as long as wide, slightly longer than antenna; rostrum almost twice the length of head; antenna approximately 0.2 times longer than rostrum; hypo-

pygium with gonocoxite comparatively narrow and elongated, almost 2.5 times longer than outer gonostylus, gonocoxite with extra lobe at the apex on dorsal surface, the extra lobe with elongated, strong setae at apex, the extra lobe comparatively wide and elongated, of comparable size to outer and inner gonostylus, only slightly shorter than outer and inner gonostylus; inner gonostylus not very wide, outer gonostylus elongated, narrow; aedeagus very elongated and convolute (spiral).

Etymology: "spira" (Latin) = spiral.

Material examined: Holotype specimen No. MCNA 15078 (male); Peñacerrada I (Moraza) outcrop, Spain, collection, housed in the Museo de Ciencias Naturales de Álava, Vitoria, Spain.

Description. Small species, body brown. *Head* (Figs 1A, 2B, C): small, 0.26 mm long, with huge eyes; rostrum elongated, narrow, 0.47 mm long, slightly widened at apical part, almost twice the length of head, distinctly shorter than palpus; palpus approximately 0.24 times longer than rostrum, slightly longer than antenna; antenna 0.67 mm long, approximately 0.2 times longer than rostrum (Figs 1A, B; 2A–C), 14-segmented; scape



Figure 4 *Helius spiralensis* sp. nov., holotype, specimen. MCNA 15078 (male): photographs of the hypopygium in (A) lateral, (B) latero-dorsal and (C) latero-ventral views.

cylindrical, pedicel barrel-like, but narrow, flagellomeres elongated and cylindrical, first flagellomere narrowed at base and widened at apex, flagellomeres 2–14 slightly widened at the base, last flagellomere shorter than penultimate one; all segments of antenna covered by wispy, tiny setae and with elongated setae, on segments 4–10 two elongated setae only slightly longer than segments bearing them, on segments 11–14 three very elongated setae over twice as long as segments bearing them; palpus (Figs 1A; 2B, C) typical for the genus, 4-segmented, 0.58 mm long, very elongated and tiny, segments 1–3 cylindrical, tiny, first palpal segment 0.09 mm long, the second one 0.12 mm, third segment 0.12 mm long, last palpal segment tiny and very elongated, 0.28 mm, but as long as the preceding all taken together; labrum elongated and massive, approximately 0.3 times the length of the rostrum.

Thorax. Wing (Figs 1C; 3A–C) 3.21 mm long, 0.84 mm wide; pterostigma not visible; vein Sc elongated, ending far behind half the length of Rs, opposite approximately 0.25 times length of Rs; cross-vein sc–r ending opposite the end of Sc (Figs 3B, C); R_1 ending opposite half of R_{2+3+4} length; R_{2+3+4} almost straight, not very elongated, ending opposite approximately 1/2 of vein R_5 ; r-r (R_2) atrophied; cross-vein r–m elongated, well expressed equal half the length of cross-vein m–cu; situated approximately once its length from the bifurcation of vein R_5 ; d-cell closed; M_3 1.5 times longer than d-cell, M_3 slightly longer than half the length of R_5 ; cross-vein m–cu just behind half the length of d-cell base, A_1 almost straight, elongated, A_2 slightly waved, not very elongated.

Abdomen. Hypopygium (Figs 1D; 4A–C) 0.57 mm long, with gonocoxite comparatively narrow and elongated, almost

2.5 times longer than outer gonostylus; at the apex of gonocoxite extra lobe on dorsal surface with elongated, strong setae at apex; extra lobe 0.11 mm long, comparable size to gonostyles, slightly shorter than these structures; outer and inner gonostylus of comparable size; outer gonostylus elongated, 0.14 mm long, narrow, directed down along gonocoxite; inner gonostylus 0.13 mm long, not very wide; aedeagus very elongated and convolute.

3. Discussion

The earliest representatives of the genus Helius appear in the fossil record in Early Cretaceous Lebanese amber. The cladistic analysis by Ribeiro (2008) and a new phylogenetic classification by Petersen et al. (2010), based on combined morphological characters (adult, larvae and pupae) and nuclear gene sequence data, confirm the theories of Alexander (1948a, b) and Savchenko (1983) about the close relationship between the genera Elephantomyia and Helius. Both groups are characterised by possessing a very elongated rostrum (proboscis), which is usually longer than the head. This structure, in the genus Elephantomyia, is longer than half the body length, whilst in Helius, it is shorter (Savchenko 1983). There are observed morphological similarities of the adults' thorax and wing venation in the two genera. The wings in both of groups are characterised by their two-branched radial sector (Rs) and atrophy of cross-vein r-r (\mathbf{R}_2) . In respect of the male terminalia features of these genera, the outer gonostylus is more sclerotised than the inner gonostylus in all known Elephantomyia species, and in most species



Figure 5 Hypopygium of representatives of the genus *Helius*, species from different periods: (A) *Helius lebanensis* Kania, Krzemiński & Azar, 2013, holotype, specimen T-7A (after Kania *et al.* 2013); (B) *Helius spiralensis* sp. nov., holotype, specimen MCNA 15078; (C) *Helius hoffeinsorum* Kania, 2014 (after Kania 2014); (D) *Elephantomyia wetwoodi* Osten Sacken, 1869 (after Ribeiro 2008). Abbreviation: aed = aedeagus. Not to scale.

of *Helius* (Ribeiro 2008; Petersen *et al.* 2010). The genus *Elephantomyia* appears in the fossil record much later than the genus *Helius*, in the Eocene (Loew 1851).

The newly described species, *H. spiralensis* sp. nov., has a very elongated and convolute aedeagus. This feature is also clearly visible in *Elephantomyia*; e.g., in the Recent *Elephantomyia* westwoodi Osten Sacken, 1869. Cretaceous and Eocene *Helius* species, such as *Helius hoffeinsorum* Kania, 2014, are characterised by having a rather short and thick aedeagus (Fig. 5). However, other characters, such as the very elongated and narrow gonocoxite, the elongated rostrum shorter than half the body length and the extremely elongated last segment of the palpus, allow the placement of the newly described species in the genus *Helius*.

H. spiralensis differs from other species known from this period mainly by the relationships of the rostrum, palpus, antenna and head, and also by the wing venation and morphology of the hypopygium. In contrast to *Helius alavensis* Kania, Krzemiński & Arillo, 2016, the rostrum of *H. spiralensis* is much longer than the head (twice as long) and is approximately nine times as long as wide, whilst in *H. alavensis* it is only slightly longer than the head, approximately five times as long as wide. In *H. spiralensis*, the palpus is very narrow, about 0.25 times longer than the rostrum, whilst the antenna is 0.2 times longer than the rostrum and only slightly longer than the palpus (Figs 1A, 2B, C). The antenna in *H. alavensis* is approximately 1.3 times as long as the rostrum and about 1.3 times as long as the palpus. The palpus in *H. spiralensis* is very narrow, but not so narrow as in *H. alavensis*.

The newly described species distinctly differs from the Barremian and Aptian representatives of the *Helius*. This small species is characterised by having a closed discal cell (d-cell), in contrast to *H. lebanensis* Kania, Krzemiński & Azar, 2013, where the discal cell is open. Moreover, the new species differs from both *H. lebanensis* and *H. ewa* Krzemiński, Kania & Azar, 2014 by the relationship of the rostrum, palpus, antenna and head, as well as by the morphology of the hypopygium. In both species, the aedeagus is not so elongated and there are no additional lobes on the gonocoxite.

This finding of a peculiar new species with a characteristic morphology of the hypopygium, whose aedeagus is similar to that of *Elephantomyia*, additionally confirms the relationship of these two genera. The first representatives of *Elephantomyia* are known from the Eocene; we have no data on the occurrence of this genus in older periods. The oldest representatives of *Helius* are known from the Early Cretaceous fossil record (Rayner & Waters 1990; Ribeiro 2002; Kania *et al.* 2013, 2016; Krzemiński *et al.* 2014). Species such as *Helius ewa*, *H. lebanensis* or *H. alavensis*, with their elongated rostrum, existed just after the time when the Angiospermae appeared. The elongated rostrum, such as in *H. spiralensis*, was probably an adaptation of these insects to a new food source, such as nectar or pollen. We have no data about the occurrence of *Helius* in the Jurassic; it is still unknown from which evolutionary line of Jurassic Limoniidae the genus *Helius* derives. The existence of the representatives of *Helius* with an elongated rostrum in the Early Cretaceous suggests that the elongated rostrum was probably an adaptation to a new food source and the radiation of these crane-flies was probably rapid (Kania *et al.* 2013; Krzemiński *et al.* 2014).

4. Acknowledgements

This study is a contribution the project CGL2014-52163 "Iberian amber: An exceptional record of Cretaceous forests at the rise of modern terrestrial ecosystems" of the Spanish Ministry of Economy and Competitiveness.

We would like to acknowledge the reviewers, Professor Dany Azar and Dr. Guilherme Ribeiro, for their corrections and very valuable comments.

5. References

- Alexander, C. P. 1931. Crane-flies of the Baltic amber (Diptera). Berstein-Forschungen 2, 1–135.
- Alexander, C. P. 1948a. Notes on the tropical American species of Tipulidae (Diptera). IV. The primitive Hexatomini: *Paradelphomyia*, *Austrolimnophila*, *Epiphragma*, *Lecteria*, *Polymera*, and allies. *Revista de Entomología* 19, 149–90.
- Alexander, C. P. 1948b. Notes on the tropical American species of Tipulidae (Diptera). V. The Specialized Hexatomini: *Limnophila*, *Shannonomyia*, *Gynoplistia*, *Hexatoma*, *Atarba*, *Elephantomyia*, and allies. *Revista de Entomología* 19, 509–56.
- Barrón, E., Peyrot, D., Rodriguez-López, J.P., Meléndez, N., López del Valle, R., Najarro, M., Rosales, I. & Comas-Rengifo, M. J. 2015. Palynology of Aptian and Upper Albian (Lower Cretaceous) amber – bearing outcrops of the southern margin of the Basque-Cantabrian basin (northern Spain). *Cretaceous Research* 52, 292– 312.
- Granier B., Toland C., Gèze R., Azar D. & Maksoud S. 2016. Some steps toward a new story for the Jurassic–Cretaceous transition in Mount Lebanon. *Carnets de Geologie* 16(8), 247–69.
- Grimaldi D. 2010. The Co-Radiations of Pollinating Insects and Angiosperms in the Cretaceous. Annals of the Missouri Botanical Garden 86(2), 373–406.

- Kania, I. 2014. Subfamily Limoniinae Speiser, 1909 (Diptera, Limoniidae) from Baltic amber (Eocene): the genus *Helius* Lepeletier & Serville, 1828. *Zootaxa* 3814(3), 333–52.
- Kania, I., Krzemiński, W. & Azar, D. 2013. The oldest representative of *Helius* Lepeletier & Serville 1828 (Limoniidae, Diptera) from Lebanese amber (Early Cretaceous). *Insect Systematics & Evolution* 44, 1–8.
- Kania I., Krzemiński W. & Arillo A. 2016. First representative of the genus *Helius* Lepeletier and Serville, 1828 (Diptera, Limoniidae) from the Lower Cretaceous Álava amber (Spain). *Cretaceous Research* 63, 33–38.
- Krzemiński, W. 1985. Limoniidae (Diptera Nematocera) from Baltic amber (in the collection of the Museum of the Earth in Warsaw). Part I. Subfamily Limoniinae. *Prace Muzeum Ziemi* 37, 113–17.
- Krzemiński, W. 1991. A first fossil *Helius* (Diptera, Limoniidae) from North America. Acta Zoologica Cracoviensia 34, 311–13.
- Krzemiński, W. 1993. Fossil Tipulomorpha (Diptera, Nematocera) from Baltic amber (Upper Eocene) – Revision of the genus *Helius* Lepeletier et Serville (Limoniidae). *Acta Zoologica Cracoviensia* 35, 597–601.
- Krzemiński, W. 2002. Three new species of the genus *Helius* Lepeletier & Serville (Diptera, Limoniidae) from the Middle Miocene of Stavropol (northern Caucasus, Russia). *Acta Zoologica Craco*viensia 45(4), 317–20.
- Krzemiński, W., Kania, I. & Azar, D. 2014. The Early Cretaceous evidence of rapid evolution of the genus *Helius* Lepeletier & Serville, 1828 (Limoniidae, Diptera). *Cretaceous Research* 48, 96– 101.
- Krzemiński, W. & Arillo, A. 2007. Alavia neli, n. gen. and n. sp. the first Limoniidae (Diptera) from the Lower Cretaceous amber of Álava (Spain). Alavesia 1, 11–13.
- Lepeletier, A. L. M. & Serville, J. G. A. 1828. Entomologie, ou histoire naturelle des crustacés, des arachnides et des insectes. *Encyclopedie Méthodique, Histoire Naturelle* 10, 345–833.
- Linnaeus, C. 1758. Systema nature per regna tria naturae, secundum classes, ordines, genera, species, cum caracteribus, differentiis, synonymi, locis. Tomus I. Editio decima, reformata. Holmiae [=Stockholm]: L. Salvii. 824 pp.
- Loew, H. 1850. Über den Bernstein Und die Bernsteinfauna. Program der Keiserischen Realschule Meseritz, 1–44.
- Loew, H. 1851. Beschreibung einiger neuen *Tipularia terricola*. *Linnaea Entomologica* 5, 385–418.
- Maksoud, S., Azar, D., Granier, B. & Gèze, R. 2016. New data on the age of the Lower Cretaceous amber outcrops of Lebanon. *Palaeoworld* 26(2), 331–38.
- Meigen, J. W. 1818. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insecten. Erster Theil. Aachen: F. W. Forstmann. xxxvi + 332 + [1] pp.

- Menor-Salván C., Simoneit B. R. T., Ruiz-Bermejo M. & Alonso J. 2016. The molecular composition of Cretaceous ambers: Identification and chemosystematic relevance of 1,6-dimethyl-5-alkyltetralins and related bisnorlabdane biomarkers. Organic Geochemistry 93, 7–21.
- Meunier, F. 1906. Monographie des Tipulidae et des Dixidae de l'ambre de la Baltique. Annales des Science Naturelle Zoologie 4, 349– 401.
- Oosterbroek, P. 2015. Catalogue of the Crane-flies of the World. (Diptera, Tipuloidea: Pediciidae, Limoniidae, Cylindrotomidae, Tipulidae). http://nlbif.eti.uva.nl/ccw/index.php. Last updated 03 January 2015.
- Osten Sacken, C. R. 1869. Monographs of the Diptera of North America. Part IV. *Smithsonian Miscellaneous Collections* 8(219). x+345 pp.
- Peñalver, E. & Delclòs, X. 2010. Spanish Amber. In Penney, D. (ed.) Biodiversity of fossils in amber from the major world deposits, 236– 70. Manchester: Sri Scientific Press. 303 pp.
- Petersen, M. J., Bertone, M. A., Wiegmann, B. M. & G. W. Courtney. 2010. Phylogenetic synthesis of morphological and molecular data reveals new insights into the higher-level classification of Tipuloidea (Diptera). Systematic Entomology 35(3), 526–45.
- Podenas, S. 2002. New species of *Helius* crane flies (Diptera: Limoniidae) from Baltic amber (Eocene). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 86, 229–38.
- Rayner, R. J. & Waters, S. B. 1990. A Cretaceous crane-fly (Diptera: Tipulidae): 93 million years of stasis. *Zoological Journal of the Linnean Society* 99, 309–18.
- Ribeiro, G. C. 2002. A new fossil *Helius* (Diptera, Limoniidae) from Burmese amber. *Studia Dipterologica* **9**(2), 403–08.
- Ribeiro, G. C. 2008. Phylogeny of the Limnophilinae (Limoniidae) and early evolution of the Tipulomorpha (Diptera). *Invertebrate Systematics* 22, 627–94.
- Savchenko, E. N. 1983. [Limoniidae of south Primorye.] Akademia Nauk ukrainskoj SSR. Kiev: Naukova Dumka. 156 pp. [In Russian.]
- Speiser, P. 1909. 4 Orthoptera. Orthoptera Nematocera. Wissenschaftliche Ergebnisse der Schwedischen Zoologische Expededition nach Kilimandjaro Meru 10(Diptera), 31–65.
- Starý, J. & Freidberg, A. 2007. The Limoniidae of Israel (Diptera). Israel Journal of Entomology 37, 301–57.
- Statz, G. 1934. Neue Tipulidenfunde aus den Braunkohlen-Schiefern von Rott am Siebengebirge. Wissenschaftliche Mitteilungen der Verein fur Natur und Heimatkunde 1(3), 90–106.
- Statz, G. 1944. New Dipteren (Nematocera) aus dem Oberoligocän von Rott. III. Familie Limnobiidae (Stelzmücken). IV. Familie: Tipulidae (Schnaken). V. Familie: Culicidae (Stechmücken). *Palaeontographica* (A) **95**, 93–120.

MS received 29 May 2016. Accepted for publication 17 October 2016.