

A new genus and the limits of the family Radiophronidae (Hymenoptera: Ceraphronoidea)

Новый род и пределы семейства Radiophronidae (Hymenoptera: Ceraphronoidea)

A.P. Rasnitsyn^{*,**}, D.S. Kopylov^{*}
А.П. Расницын^{*,**}, Д.С. Копылов^{*}

^{*} Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya Str. 123, Moscow 117647 Russia. E-mail: aeschna@yandex.ru

^{*} Палеонтологический институт Российской академии наук, Профсоюзная ул., 123, Москва 117647 Россия.

^{**} Natural History Museum, London SW7 5BD UK.

^{**} Музей естественной истории, SW7 5BD Лондон Великобритания.

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Ключевые слова: ископаемые, насекомые, перепончатокрылые, Ceospilidae, Stigmaphronidae, Хасурты, Россия, мел, таксономия, новый вид.

Abstract. A new genus and species of Radiophronidae, *Lelejaphron arkadii* Rasnitsyn et Kopylov, **gen. et sp.n.**, is described from the Lower Cretaceous Khasurty locality in Buryatia, Russia. The new fossil expands the known diversity of this rare family and provides additional evidence for its systematic placement. Based on forewing venation and other morphological characters, Stigmaphronidae and Radiophronidae are returned to Ceraphronoidea, and Ceospilidae is placed in synonymy with Radiophronidae (**syn.n.**). Although Radiophronidae remain extremely scarce in the fossil record, currently comprising only four monotypic genera, they show a broad Early Cretaceous distribution, with records from Spain, East Siberia, and Lebanon. This combination of narrow stratigraphic and wide geographic range suggests that the family may have potential biostratigraphic significance.

Резюме. Из нижнемелового местонахождения Хасурты в Бурятии (Россия) описаны новый род и вид семейства Radiophronidae, *Lelejaphron arkadii* Rasnitsyn et Kopylov, **gen. et sp.n.** Новая ископаемая находка расширяет известное разнообразие этого редкого семейства и предоставляет дополнительные данные о его систематическом положении. На основании жилкования переднего крыла и других морфологических признаков семейства Stigmaphronidae и Radiophronidae возвращены в состав Ceraphronoidea, а семейство Ceospilidae сведено в синонимию с Radiophronidae (**syn.n.**). Хотя Radiophronidae остаются крайне редкими в ископаемой летописи и в настоящее время представлены лишь четырьмя монотипическими родами, они имеют широкое распространение в раннем мелу и известны из Испании, Восточной Сибири и Ливана. Такое сочетание узкого стратиграфического и широкого географического распространения позволяет предположить, что это семейство может иметь потенциальное биостратиграфическое значение.

Introduction

Radiophronidae is a small family of Cretaceous hymenopterans whose taxonomic position remains controversial. Until now, the family has been known from only two specimens preserved in Early Cretaceous Spanish amber [Ortega-Blanco et al., 2010]. Additionally, *Ceospilus phoenicius* Engel, 2025, described from the Early Cretaceous Lebanese amber [Engel, 2025], most likely also belongs to this family.

Radiophronidae was originally described as a member of Ceraphronoidea [Ortega-Blanco et al., 2010], but its placement was subsequently questioned by Miko et al. [2018]. These authors argued that the family does not conform to the diagnostic characters of Ceraphronoidea. However, they did not propose a robust alternative placement, instead treating it as Hymenoptera incertae sedis while suggesting possible affinities with Chrysidoidea.

During our revision of the insect collections from the Early Cretaceous Khasurty locality (Lower Cretaceous of Buryatia, Russia; [Kopylov et al., 2020]), we discovered a single additional representative of Radiophronidae. Here, we describe this new species and re-evaluate the systematic position of the family in light of the new material.

The present paper describes a new and possibly the oldest fossil that satisfies the diagnosis of Radiophronidae. Radiophronidae are similar to Ceraphronidae, Megaspilidae and Stigmaphronidae (in their ground plan) in having forewing with incrassate C, R, pterostigma, 2r-rs and Rs distally it, whilst the remainder veins are at most nebulous (except possibly for dark M+Cu and small fragments of some other veins). At the same time,

Radiophronidae differ from Ceraphronidae, Megaspilidae and Stigmaphronidae in having C and R distant at least distally (vs. tightly align or fused throughout, with no costal space in-between).

Material and methods

The specimen studied here, preserved as part and counterpart in mudstone shale, was recovered in 2004 during a field expedition of the Paleontological Institute (PIN), Russian Academy of Sciences, headed by D.E. Shcherbakov. The fossil originates from the Khasurty locality in the Zakamensk District of the Republic of Buryatia, approximately 10 km south of Tsakir Village (50°21' N, 103°38' E; [Kopylov et al., 2020]). Because the Khasurty section lacks datable volcanic horizons and occurs within a geologically complex setting, its age has been inferred primarily from the associated insect fauna rather than by radiometric or stratigraphic constraints. The deposits are regarded as earliest Early Cretaceous in age and are assigned to the Lowermost (Pre-Ephemeropsis) Jehol Biota sensu Rasnitsyn [2020].

The specimen was collected using standard palaeontological excavation techniques. Laboratory preparation was carried out with preparation needles. The specimen was mounted on a base of thermoplastic adhesive (EVA).

The specimen was examined using Micromed MC-2-Zoom and Nikon SMZ-25 stereomicroscopes under reflected light, oblique illumination, and with the fossil surface covered by a thin layer of ethanol to enhance contrast. Photographs were acquired with a Nikon SMZ-25 imaging system. Each final image was generated from a focus stack of 11 photographs combined in Helicon Focus 7.6.1. Line drawings were prepared from the resulting images using Inkscape 1.4.3.

Wing venation terminology follows Rasnitsyn [1969], with the addition of abscissa numbering for longitudinal veins (Fig. 7).

A complete set of photographs of the new species is provided as an online supplement on Zenodo (<https://doi.org/10.5281/zenodo.21241324>).

The type material described in this study is housed in the Paleontological Institute (PIN) of the Russian Academy of Sciences, Moscow.

This work and all nomenclatural acts contained therein are registered in ZooBank: urn:lsid:zoobank.org:pub:1BFF91AB-7484-4E96-BD1A-F155F796BA48

Results

Hymenoptera Linnaeus, 1758
Ceraphronoidea Haliday, 1833
**Radiophronidae Ortega-Blanco,
Rasnitsyn et Delclos, 2010**

Radiophronidae Ortega-Blanco, Rasnitsyn et Delclos, 2010: 267.

Ceospilidae: Engel, 2025, p. 2 (**syn.n.**).

Type genus. *Radiophron* Ortega-Blanco, Rasnitsyn et Delclos, 2010

Diagnosis. Antenna geniculate, 11-segmented, not clavate, with scape more or less elongate. Forewing with C, R,

pterostigma, 2r-rs and Rs distally it incrassate (C and R often discolored basally), C and R distant at least distally, otherwise venation nebulous, spectral or lost, except sometimes M+Cu and fragments of Rs just basal of 2r-rs and extreme base of 3-Cu. Hind wing with venation lost except R, with few hamuli. Hind coxa large but not shield-like wide as in Stigmaphronidae, tibial spurs 2-2-2 when visible, hind tibial spurs not hypertrophied. Metasomal segmentation ordinary except that first segment short but not forming narrow petiole, ovipositor internal except apically, male genitalia with gonostili and gonocoxae fused, enlarged flap-like, penis and volsellae not visible externally, cerci not visible.

Genera included. *Radiophron* Ortega-Blanco, Rasnitsyn et Delclos, 2010, *Microcostaphron* Ortega-Blanco, Rasnitsyn et Delclos, 2010; *Ceospilus* Engel, 2025; *Lelejaphron* gen.n.

Comparison. Radiophronidae differ from Ceraphronidae, Megaspilidae and Stigmaphronidae in having C and R spaced at least distally and first metasomal segment not narrowed in small petiole, from Ceraphronidae and Megaspilidae also in male genitalia transformed (gonocoxa and gonostylus fused and enlarged, penis reduced in a way), from Stigmaphronidae also in less enlarged hind coxae and, except *Elasmophron* Engel et Grimaldi, 2009, in hind tibial spurs not hypertrophied.

Remarks. Radiophronidae are attributed to the superfamily Ceraphronoidea s.str. (composed otherwise of Ceraphronidae, Megaspilidae and Stigmaphronidae) based on their two protibial spurs and a unique combination of the incrassate forewing C and R (along with 2r-rs and Rs distal to it) with reduced (nebulous to lost) remainder venation (sometimes except M+Cu and fragments of some other veins). Ceospilidae are synonymized under Radiophronidae because in our opinion the differences of *Ceospilus* from other genera are minor comparing the standard interfamilial differences in Ceraphronoidea and related groups (cf. the key to genera below).

KEY TO GENERA AND SPECIES OF RADIOFRONIDAE

1. Stature slim; head much wider than mesosoma wide or high, narrowed behind just from eye (no temple); pedicel twice as long as ordinary flagellomeres (other than most basal or apical ones), flagellum thickest behind middle ..
..... *Ceospilus phoenicius* Engel, 2025
(Lebanese amber, Barremian)
- Stature more robust; head not much wider than mesosoma wide or high, not narrowed just behind eye (temples distinct); pedicel about as long as ordinary flagellomeres, flagellum of uniform width except narrower basally and apically 2
2. 2r-rs & Rs form smoothly bent vein
Radiophron ibericus Ortega-Blanco, Rasnitsyn et Delclos, 2010 (Spanish amber, Albian)
- 2r-rs and Rs meet at angle 3
3. Stature medium; scape and flagellomeres of subequal width; 2r-rs very short; M+Cu and Cu lost; remnant of Rs basal to 2r-rs absent; femora about as long as, or longer than, metasoma wide
..... *Microcostaphron parvus* Ortega-Blanco, Rasnitsyn et Delclos, 2010 (Spanish amber, Albian)
- Stature extra robust; scape about 1.5× as wide as flagellomeres; 2r-rs about half as long as pterostigma wide; M+Cu and terminal section of Cu dark; short remnant of Rs basal to 2r-rs present; hind femur half as long as metasoma high
..... *Lelejaphron arkadii* gen. et sp.n. (Russian Transbaikalia, Khasurty; earlier Early Cretaceous)

***Lelejaphron* Rasnitsyn et Kopylov, gen.n.**

LSID: urn:lsid:zoobank.org:act:509B7E5A-7A63-4F28-A8B8-A1AD33DA54B8

Type species. *Lelejaphron arkadii* sp.n.

Etymology. The genus is named in honor of the eminent Russian hymenopterist, Professor Arkady Lelej. The genus name combines his name with a partial name of genus *Ceraphron*, the type of the superfamily Ceraphronoidea.

Diagnosis. Stature robust; head small, with temples distinct, eye rather small, occupying about half of head side; scape long and thick, pedicel narrower than and about as long as 1st flagellomere; flagellum of uniform width except slightly narrower basally and apically; forewing with distinct bend between 2r-rs and Rs and tubular remnant of Rs before 2r-rs, with dark M+Cu and traces of 1-M, 1m-cu, and with Cu almost complete even though partially pale; legs very short and thick, hind femur and tibia much shorter than mesosoma high; metasoma thick, thickest subbasally.

Species included. Type species only.

Comparison. The new genus differs from others in particularly robust stature, smaller eyes, particularly short legs and less reduced venation (Cu almost completely colored), from *Radiophron* also in distinct boundary between 2r-rs and Rs, from *Ceospilus* also in distinct temples and short pedicel, from *Microcostaphron* also in 2r-rs not very short (0.7× as long as pterostigma wide).

Remarks. In the holotype of *Lelejaphron arkadii*, M+Cu and the terminal section of Cu are distinctly marked by dark pigmentation. At the same time, these veins show no evidence of a tubular structure. Although the preservation of the compression fossil does not permit a detailed examination of vein microanatomy, these veins differ from both typical tubular veins, which are sharply defined on the impression and usually expressed as relief structures, and nebulous veins, which are generally visible only as faintly pigmented traces. We therefore designate this type of veins as 'dark'.

***Lelejaphron arkadii* Rasnitsyn et Kopylov, sp.n.**

Figs 1–7.

LSID: urn:lsid:zoobank.org:act:9C97DAA9-5FF5-4ECE-9BCB-EA183BDB62A3

Material. Holotype PIN 5026/734; part and counterpart of perfectly preserved and almost complete insect with hind wings not preserved and metasomal tip damaged, hence sex is unknown. Hind legs perfectly preserved; fore and mid legs distinct poorly. Khasurty; Buryatia, Russia; earlier Early Cretaceous.

Etymology. The species name is in honor of Arkady Lelej.

Diagnosis. As for genus.

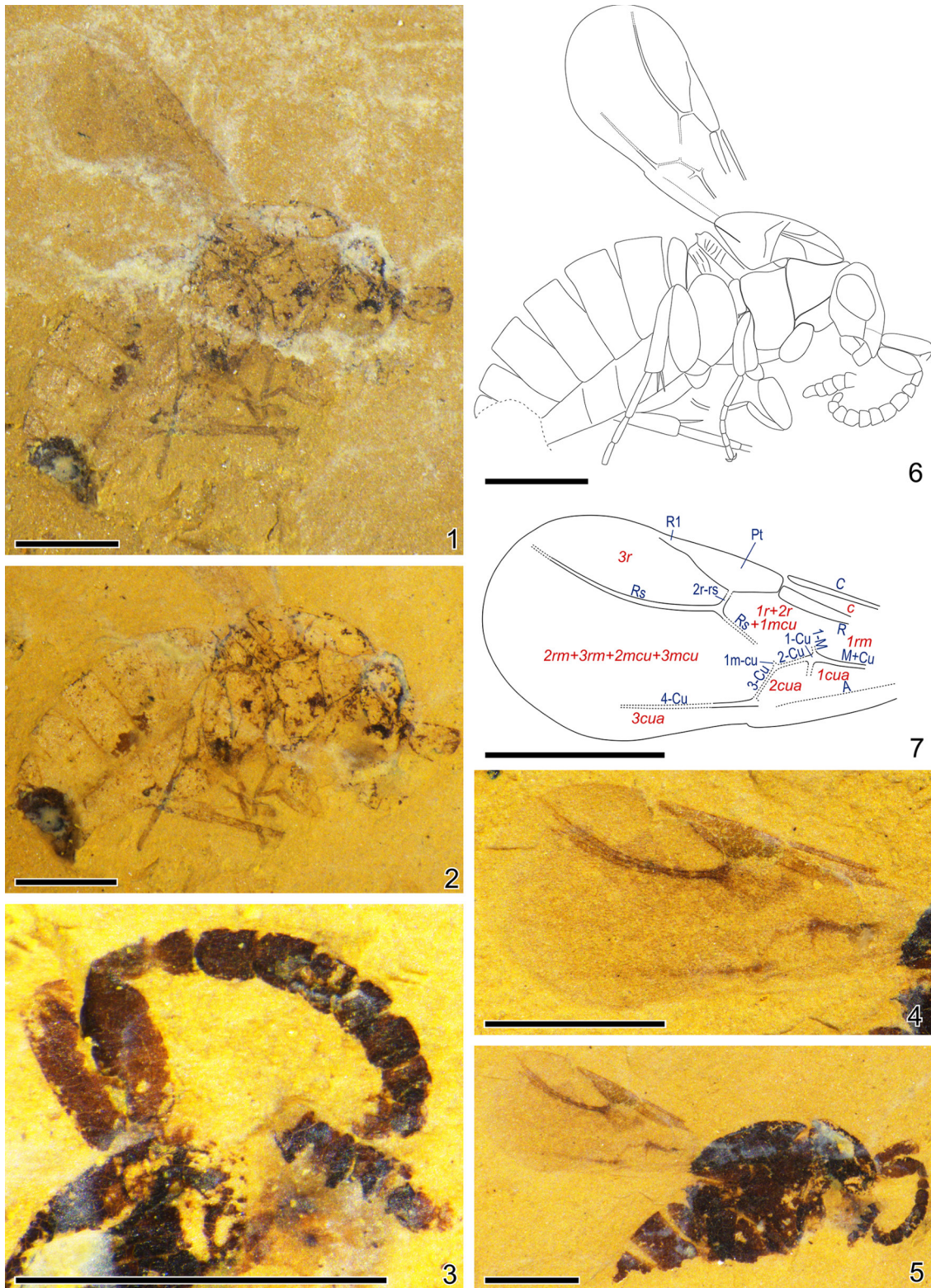
Description. Sex unknown. Color pattern little known (because organic matter is left on the incompletely preserved part of the fossil), body and antennae dark as preserved, forewing slightly infuscated except basally, more dark under distal R and basal pterostigma. Surface microsculpture not apparent. Head short, rather small, with eyes taking some 0.5 head height at and above its midheight, with temples distinct even though narrow above. Antenna attached below lower eye margin, with scape long and wide (almost half as long as head high, 2.3× as long as wide), possibly flat, pedicel subcylindrical, small (shorter than scape wide, about as long as and 0.7× as wide as ordinary flagellomere). Flagellum slightly fusiform, apparently with 9 flagellomeres (detached apex with two small or possibly one larger segment), first flagellomere shorter than others; most flagellomeres apparently subquadrate (visible form varying dependent on position of individual segment). Pronotum subtriangular in side view, scarcely visible from

above. Fore spiracle not distinct. Mesonotum with notauli and longitudinal suture present (poorly preserved on the holotype, the precise structure indiscernible). Scutellum very large, as long as scutum, with V-shaped furrow anteriorly. Metanotum belt-like, almost vertical to mesonotal surface, with longitudinal sculpture. Forewing 0.75× as long as body, 2.4× as long as wide, densely setose. R twice as wide as C; costal space slightly wider than R. Pterostigma 3× as long as wide, apically gradually merging into short R leaving much of marginal cell (3r) open anteriorly; terminal section of R very broad and short; 2r-rs 0.7× as long as pterostigmal width, nebulous in upper part. Rs nebulous basal to 2r-rs, extending to mid-distance toward Cu; terminal section of Rs reaching wing margin, tubular along most of its length, becoming nebulous in apical 0.2; M+Cu before bifurcation heavily sclerotized and distinct, but lacking a well-defined tubular structure. 1-M short, nebulous. Short nebulous cu-a arising opposite the point of bifurcation (interstitial); 2-Cu and 3-Cu nebulous. Short nebulous 1m-cu directed toward Rs. 4-Cu heavily sclerotized in basal third, nebulous distally, not reaching wing margin; A nebulous, barely discernible. Propodeum very short, with transverse sculpture. Hind coxa 0.6× as high as mesosoma, about twice as high as wide (almost as large as mesopleuron), about as high as hind femur and hind tibia long, hind tarsus longer than these. Longer hind tibial spur about as long as tibia wide apically and almost one third as long as hind basitarsus. Metasoma with seven terga, fusiform, widest at 3-rd segment. First metasomal tergum about half as long as following terga, yet dorsally it as high as these (not diminished). Terga 2-5 of subequal length, following two distinctly shorter (apical segment not preserved). Metasomal sterna 0.7× (second) to 0.4× (sixth) as high as respect terga in side view.

Measurements. Body length 2.0 mm; head height 0.48 mm; mesosoma length 0.79 mm, height 0.75 mm; mesosoma length 1.25 mm, height 0.75 mm. Antenna length 0.85 mm. Forewing length 1.5 mm (reconstructed full length, preserved part is 1.2 mm), width 0.6 mm.

Discussion

The family Radiophronidae has been established by Ortega et al. [2010] for two extinct monotypical genera *Radiophron* Ortega-Blanco, Rasnitsyn et Delclos, 2010 and *Microcostaphron* Ortega-Blanco, Rasnitsyn et Delclos, 2010 from the Albian (later Early Cretaceous) amber in N. Spain as a basal sister-group to all other ceraphronoids (Ceraphronidae, Megaspilidae, and Stigmaphronidae). This hypothesis was criticized by Miko et al. [2018] who considered Radiophronidae and Stigmaphronidae as taxa incertae sedis as lacking evidence of the critical synapomorphies of Ceraphronidae and Megaspilidae. However, these lacks mean only that Radiophronidae and Stigmaphronidae cannot represent inner branches of the clade Ceraphronidae + Megaspilidae. Instead, there are putative synapomorphies characteristic of all four families in question that imply the position of Radiophronidae and Stigmaphronidae as basal branches of the clade subtending Ceraphronidae + Megaspilidae. These are two protibial spurs and a unique combination of the incrassate both forewing C and R (along with 2r-rs and Rs distal to it) with reduced (nebulous to lost) remainder venation. Unlike this case, the vein reduction in other Hymenoptera usually accompanies incrassation



Figs 1–7. *Lelejaphron arkadii* sp.n., holotype PIN 5026/734. 1, 2 — part: 1 — general view, dry, 2 — body, wet. 3–5 — counterpart, mirrored, wet: 3 — antennae, 4 — wings, 5 — general view. 6, 7 — reconstruction drawing: 6 — general view, 7 — fore wing with vein (blue) and cell (red) indications. All scale bars: 0.5 mm.

Рис. 1–7. *Lelejaphron arkadii* sp.n., голотип ПИН 5026/734. 1, 2 — отпечаток: 1 — общий вид, сухой; 2 — тело, влажный. 3–5 — противо-отпечаток, зеркально отражённый, влажный: 3 — антенны; 4 — крылья; 5 — общий вид. 6, 7 — рисунок: 6 — общий вид; 7 — переднее крыло с обозначениями жилок (синим) и ячеек (красным). Все масштабные линейки: 0,5 мм.

of only R (particularly characteristic of various Proctotrupomorpha), or only C and R (not 2r-rs + distal Rs) in some tiny Evanidae. Alternatively, the venation is generally reduced except C, R, pterostigma, 2r-rs and distal Rs in various Chrysidoidea, yet many of remaining veins are left tubular. Incrassation and close alignment of C and R is also characteristic of Ichneumonoidea. However, in contrast to the above four ceraphronoid families, these demonstrate only a limited extent of the vein reduction in the posterior part of the forewing (many of them remain tubular). These observations justify the inference that Ceraphronidae, Megaspilidae, Stigmaphronidae and Radiophronidae are synapomorphic in the above characters and hence they form a clade, a monophyletic taxon Ceraphronoidea s.str.

Recently Engel [2025] described in Ceraphronoidea a new monotypic family Ceospilidae from the Early Cretaceous Lebanese amber, which diagnosis agrees completely with that of Radiophronidae. The latter name is not mentioned there, nor is the paper by Ortega-Blanco et al. [2010]. *Ceospilus phoenicius* Engel, 2025 differs from *Radiophron* Ortega-Blanco, Rasnitsyn et Delclos, 2010 and *Microcostaphron* Ortega-Blanco, Rasnitsyn et Delclos, 2010 in having slim stature with head much wider than mesosoma and lacking temples, and in having antenna with pedicel twice as long as middle flagellomeres and with flagellum distinctly widening distal (vs. more robust, with head less wide comparing mesosoma and with distinct temples, with pedicel distinctly shorter and flagellum of subequal width). Based on these observations, we place Ceospilidae in synonymy with Radiophronidae (**syn.n.**).

As a result, Radiophronidae currently comprise a small group of four monotypic genera, most of which are known from a single fossil specimen (the only exception being *Radiophron ibericus*, represented by eight specimens). Although restricted so far to the Early Cretaceous, the family appears to have been geographically widespread, with records from Spain, Lebanon, and East Siberia. This distribution suggests that Radiophronidae may have potential biostratigraphic significance.

Acknowledgements

We warmly congratulate our colleague, Arkady Lelej, on his anniversary and wish him many more years of good health, happiness, and fruitful work for the advancement of entomology!

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Appendix A

ZIP archive (487 MB) containing supplementary photographs, and a source SVG vector drawing of the holotype of *Lelejaphron arkadii* **sp.n.** Available online: <https://doi.org/10.5281/zenodo.21241324>.

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