Another earliest representative of the family Encyrtidae, *Sakhalinencyrtus leleji* Simutnik gen. et sp. nov., is described and illustrated based on a male specimen from the middle Eocene Sakhalinian amber. Similarly to other Encyrtidae from Sakhalinian amber, the new fossil fundamentally differs from encyrtids from late Eocene European ambers as well as from modern ones. Moreover, it probably belongs to a stem group of the family. The new genus is characterized by extremely apical position of cerci, long veins of the forewing with expanded parastigma, stigmal vein with long uncus, and absence of filum spinosum. The forewing venation of the new genus is very similar to that of *Sugonjaevia* Simutnik, 2015, but these genera differ by the structure of Mt8, hypopygium, genitalia, and clava.

**Keywords**
Eocene, cerci, filum spinosum, fossils, Mymaridae, syninclusion
The first described species of fossil Encyrtidae – *Encyrtus clavicornis* Statz, 1938 – is known from an imprint in the late Oligocene shale from the Rott locality in Germany (Statz 1938). The earliest known Encyrtidae, *Archencyrtus rasnitsyni* Simutnik, 2014, *Sugonjaevia sakhalinica* Simutnik, 2015, *Kotenkia platycera* Simutnik, 2015 and *Encyrtoides pronotatus* Simutnik, 2020 were described from the middle Eocene Sakhalinian amber (Simutnik 2014, 2015a, 2020). *Eocencyrtus zerovae* Simutnik, 2001, *Eocencnemus sugonjaevi* Simutnik, 2002, *E. vichrenkoi* Simutnik, 2006, *E. gedanicus* Simutnik, 2014, *Glaesus gibsoni* Simutnik, 2014, *Rovnosoma gracile* Simutnik, 2015, *Sulia glaesaria* Simutnik, 2015, *Protocopidosoma kononovae* Simutnik, 2017, *Dencyrtus vilhelmseni* Simutnik, 2018, *Archaeocercus schuwachinae* Simutnik, 2018, *Trjapitzion cylindracerus* Simutnik, 2018, *Ektopicercus punctatus* Simutnik, 2020, and *Efesus trufanovi* Simutnik, 2020 are known from the late Eocene European ambers (Simutnik 2001, 2002, 2015b; Simutnik and Perkovsky 2006, 2015, 2017, 2018a, b, c, 2020; Simutnik et al. 2014, 2020). One more species, *Copidosoma archeodominica* Zuparko & Trjapitzin, 2014, has been described from Miocene Dominican amber (Zuparko and Trjapitzin 2014).

The age of Sakhalinian amber, the history of its study and the nature of its biota have been discussed in detail in a number of recent works (Baranov et al. 2015; Radchenko and Perkovsky 2016; Marusik et al. 2018; Dietrich and Perkovsky 2019; Simutnik 2020; Davidian et al. in press; Perkovsky et al. 2021; Tikhonenko et al. 2021). At the end of the last century, Kordrul (1999), based on geological and paleobotanical data, convincingly dated the Naibuchi Formation, in which Sakhalinian amber was found in situ, as middle Eocene. Simutnik (2020 and references therein) provided extensive information about the fossil Encyrtidae from European and Sakhalinian ambers. A new genus and species of this family from the Sakhalinian amber with extremely apical position of cerci (Fig. 4A, B) is described below. This character state is absent from any other late Eocene fossil encyrtid or extant one.

**Material and methods**

Terminology and abbreviations follow Trjapitzin (1989), Gibson (1997), Noyes et al. (1997), and Heraty et al. (2013). Material is deposited in the collection of the Borsiskia Palaeontological Institute of the Russian Academy of Sciences (PIN), Moscow.

All measurements are given in millimeters. The images were taken using a Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera and processed with LAS V3.8 software. To improve imaging, we applied sucrose syrup of approximately the same refractive index as the amber itself and then placed a glass cover slip on top; after that, syrup was removed by warm water. Some images were then enhanced using Adobe Photoshop (brightness and contrast only).
The following abbreviations are used in the text and plates of illustrations: Mt1, Mt2, etc. = metasomal terga, numbering starts from petiole (Mt1); OOL = minimum distance between an eye margin and the adjacent posterior ocellus; POL = minimum distance between the posterior ocelli.

**Results**

Systematic palaeontology

**Hymenoptera Linnaeus, 1758**
**Apocrita Gerstäcker, 1867**
**Chalcidoidea Latreille, 1817**
**Encyrtidae Walker, 1837**

**Genus Sakhalinencyrtus Simutnik, gen. nov.**
http://zoobank.org/7C5AD7F2-9E5F-4759-BB0A-4135D744E815

**Type species.** *Sakhalinencyrtus leleji*, sp. nov.

**Species composition.** Type species.

**Etymology.** From “Sakhalin” and “Encyrtus”. Gender masculine.

**Diagnosis.** Habitus not ‘encyrtiform’, body not compact, without metallic shine; vertex above upper level of eyes (frontal view); interantennal prominence not high, without carina; eyes relatively small, convex, almost circular, height of eye as long as malar space; pedicel shorter than first two funicular segments combined; clava with an oblique truncation extending along entire ventral surface and without sutures; pronotum short; all coxae large; parastigma distinctly widened, but not triangular; mesotibial spur slightly longer than basitarsus, cerci located at almost non-dilated apex of gaster; Mt8 small, U-shaped; hypopygium short, almost reaching apex of metasoma, genitalia weakly sclerotized, transparent, with a long phallobase and short aedeagus (excluding apodemes), without visible digiti.

**Remarks.** Placement of the new genus and species into the family Encyrtidae is supported by: presence of the linea calva with long covering setae at distal margin; mesotibial spur thick and long; axillae large, triangular, transverse, medially touching each other; scutellum large, as long as mesonotum; mesopleuron enlarged, convex, mesocoxa inserted at its middle; Mt8 U-like; cercal setae long.

However, cerci of the new genus are located extremely close to the apex of gaster. As in other known males in Sakhalinian amber, such a position of the cerci is not found among the extant Encyrtidae or among the late Eocene ones.

The new genus somewhat resembles the extant genus *Eucoccidophagus* Hoffer, 1963 by widened parastigma, relatively small and almost circular eyes, and cerci situated close to the apex of gaster. However, *Sakhalinencyrtus* well differs by the extremely...
apical position of cerci which are close to each other, long marginal vein, linea calva with a well-developed row of long covering setae on its basal margin (Fig. 3B, cs); long mesotibial spur (longer than mesobasitarsus) and absence of digiti on phallobase. All species of *Eucoccidophagus* have a short, almost absent marginal vein (Fig. 4D and figs I, II6, IV4 in Guerrieri 1994), mesotibial spur always shorter than mesobasitarsus, cerci substantially advanced toward gastral base and located far from each other (fig. 12e in Simutnik 2020 and figs I, II8 in Guerrieri 1994). It should be noted that all known late Eocene encyrtids from European ambers also retain long veins of forewings including the marginal vein. Reduction to complete absence of the marginal (as, for example, in the species of *Eucoccidophagus*) and postmarginal veins, the subsessile stigmal vein is common in many extant encyrtids, but has not been found among fossil encyrtids from either the middle or late Eocene. More detailed comparison of the fossil encyrtids with the extant genera having an apical or near apical position of the cerci is provided by Simutnik (2020) and Simutnik and Perkovsky (2006, 2018).

A close relationship of some examined but undescribed fossil Encyrtidae from the Baltic amber to the extant genera *Eucoccidophagus*, *Quadrencyrtus* Hoffer, 1953, *Oriencyrtus* Sugonjaev & Trjapitzin, 1974, and *Aphycoïdes* Mercet, 1921 with apical or near apical position of the cerci was also earlier reported by Noyes and Hayat (1994). The taxonomic position of these genera is uncertain. The presence or absence of filum spinosum (**fs**) is one of the main characters used to subdivide the Encyrtidae into two subfamilies (Trjapitzin 1968). These short and thickened setae on apical margin of linea calva are an exclusive characteristic of the wasps of the subfamily Encyrtinae as a part of the wing coupling mechanism at the moment of jumping. Another important diagnostic feature of the encyrtid subfamilies is the presence or absence of the special paratergites in the gastral structures of females. Genera *Eucoccidophagus*, *Quadrencyrtus*, and *Oriencyrtus* are characterized by the absence of **fs** and presence of the paratergites, but the latter structures are not homologous to those found in other Tetracneminae (Noyes 2004). According to Noyes (2004), these three extant genera are most closely related to *Aphycoïdes*, species of which have **fs** and should be included into the subfamily Encyrtinae. Therefore, without studying the paratergites of females, it is difficult to determine relationships of the taxa described based on males from Sakhalinian amber. The taxonomic position of the new genus is also considered unplaced within the Encyrtidae.

The forewing venation of the new genus is very similar to that of *Sugonjaevia* Simutnik, 2015, which was also described from Sakhalinian amber. However, *Sugonjaevia* is characterized by large and elliptical (not circular) eyes; interantennal prominence in the form of carina; clava without an oblique truncation and with suture; Mt8 M-shaped between and around cerci, with long and narrow part between cerci; very long hypopygium; genitalia distinctly sclerotized, with digiti and margins of aedeagus dark; aedeagus longer than phallobase (figs 4a–e, 13e, f in Simutnik 2020). The new genus also differs from *Encyrtoides* Simutnik, 2020 by a short pronotum (fig. 7d in Simutnik 2020), and from *Kotenkia* Simutnik, 2015 by size and structure of antennae (figs 5b, c, e in Simutnik 2020).
Sakhalinencyrtus leleji Simutnik gen. et sp. n. of earliest Encyrtidae

Material. **Holotype**, PIN 3387/128, 1♂, Sakhalin Island, village Starodubskoe; Sakhalinian amber, middle Eocene. The inclusion is located close to the surface in a polished piece of amber in a shape of a parallelepiped (ca. 4 × 2.5 × 2 mm (Fig. 2A)). All body parts are preserved.
Syninclusions. An undescribed female of Mymaridae (Fig. 2A–C).

Etymology. The species is named after Prof. Arkady Stepanovich Lelej, a world-class expert on Hymenoptera.

Description of male. Body length, 0.9 mm. Habitus as in Figs 1A, B, 4C. Color. Head, mesosoma and metasoma brownish black; antennae, tegula, legs and veins of forewings brown; apices of femora lighter; wings hyaline. Mesoscutum and scutellum
with reticulate sculpture (Fig. 3A). **Head** hypognathous, slightly wider than thorax; vertex above upper level of eyes (Fig. 2D–F); eyes small, almost circular, height of eye slightly less than length of malar space; form of scrobal depression unclear because face
in holotype deformed (Fig. 2E); toruli located midway between level of lower margin of eyes and mouth margin; face without a high interantennal prominence. Funicle 6-segmented; scape slightly extended and flattened, approximately 4 times as long as broad; pedicel conic, width of its apex slightly less than length, 1.5 times shorter than first two funicular segments; flagellum slightly flattened, not widen towards apex; all segments of funicle almost square and equal to each other; clava not segmented, not wider than

Figure 4. A–C S. leleji gen. et sp. nov., holotype female A apex of metasoma with cercus arrowed, dorso-lateral B apex of metasoma with cercus arrowed and genitalia, dorsal C habitus, lateral D Eucoccidophagus sp., venation of fore and hind wings.
last funicular segment, with oblique truncation extending along entire ventral surface and without sutures, equal in length to three previous funicular segments; flagellum with short and rare setae, lengths of which equal to half width of funicular segments (Fig. 2D); longitudinal multiporous plate sensilla not visible on segments of funicle and clava; mandibles not visible. **Mesosoma** longer than metasoma, not flattened; pronotum short; mesoscutum flat, as long as slightly convex scutellum (Fig. 4C); longer setae at apex of scutellum not visible; notauli not visible; axillae medially touching each other (Fig. 3A); forewing hyaline; lineal calva clearly defined, without filum spinosum, but with a well-developed row of long setae on its basal margin; parastigma widened, hyaline break (unpigmented area) of parastigma present (Fig. 3B, C); venation of fore and hind wings in Fig. 3B, C; stigmal vein with long narrow uncus, and with uncal sensilla; setae of marginal fringe short; procoxa large (Fig. 2D); tarsi 5-segmented; protibia with long, curved spur (Fig. 2D); spur of mesotibia thick, and slightly longer than mesobasitarsus (Fig. 1A, B). **Metasoma.** Mt2-7 transverse; location of cerci in Fig. 4A, B; Mt8 U-like, Mt9 V-like (Fig. 4A); apical sternum (hypopygium) almost reaches apex of metasoma; genitalia (Fig. 4B) hyaline, with a long phallobase and short aedeagus (excluding apodemes), without visible digiti.

**Measurements** are very inaccurate due to optical effects in amber: **Head** height 0.252, width 0.35; length 0.112; eye height 0.126, length 0.112; minimum distance between eyes 0.168; POL 0.07, OOL 0.028, distance between toruli 0.056, between torulus and eye 0.042; pedicel 0.056 × 0.035; flagellum 0.406; clava 0.126 × 0.042. **Mesosoma.** Length 0.426; forewing 0.7 × 0.42, marginal vein 0.07, postmarginal 0.126, stigmal vein with uncus 0.112; procoxal length 0.084; mesobasitarsus 0.07; mesotibial spur 0.077. **Metasoma** length 0.28, width 0.28; phallobase 0.126, aedeagus (excluding apodemes) 0.056.

**Female** unknown.

**Conclusions.** The Encyrtidae from Sakhalinian amber are characterized by a unique position of cerci and forewing venation and represent the basal group of Encyrtidae. But, since so far they are represented by only one poorly preserved female and four males, the determination of their suprageneric relationships without studying female paratergites, seems to be premature.

Comparative morphological analysis of the representatives of middle and late Eocene fossil faunas (Simutnik 2020 and the present publication) confirms that the Sakhalinian amber is much older than the Baltic, Rovno and Danish European ambers are.

**Acknowledgements**

We are sincerely grateful to Alexandr P. Rasnitsyn, Vladimir E. Gokhman, and Emilio Guerrieri for discussion, valuable comments, improving English, and the material provided. The study was supported by the National Research Foundation of Ukraine grant “Leading and Young Scientists Research Support” (registration number 2020.02 / 0369) for the first author.
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