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Darwin wasp *Furpherhombus* gen.n. (Hymenoptera: Ichneumonidae: Pherhombinae) indicates faunal connections between the earliest Eocene Fur formation and late Eocene Baltic amber. Notes on the taphonomy and biology of Darwin wasps in amber

Наездники-ихневмониды рода *Furpherhombus* gen.n. (Hymenoptera: Ichneumonidae: Pherhombinae) указывает на фаунистические связи раннеэоценовой формации Фур и позднеэоценового балтийского янтаря. Заметки по тафономии и биологии ихневмонид в янтаре

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KEY WORDS: Ichneumonidae, Pherhombinae, fossils, new species, Eocene.
КЛЮЧЕВЫЕ СЛОВА: Ichneumonidae, Pherhombinae, ископаемые, новый вид, эоцен.

ABSTRACT. The Darwin wasp *Furpherhombus leleji* **gen. et sp.n.** is being described from the late Eocene Baltic amber (~38.0–33.9 Ma). The new genus also includes the species *F. parvulus* Meier, Walker et Klopfstein, 2022 (**comb.n.**), previously described from the Danish earliest Eocene Fur Formation (~54 Ma). A hypothesis of a mechanism of ichneumonids getting trapped in the amber that takes into account different qualities of the initial resin, which may act in accordance with the laws of either a Newtonian or a non-Newtonian (Bingham) fluid, is proposed. For the extinct subfamily Pherhombinae, parasitization in cocoons of ants (Hymenoptera, Formicidae) is assumed.

РЕЗЮМЕ. Из позднеэоценового балтийского янтаря описан новый вид *Furpherhombus leleji* **sp. et gen.n**. В состав рода также входит описанный из датской раннеэоценовой формации Fur (~54 млн. лет) *F. parvulus* (Meier, Wacker et Klopfstein, 2022) (**comb.n.**). Приведена схема попадания ихневмонид в янтарь учитывающая разные качества исходной смолы, действующей в одних случаях по законам ньютоновских, в других — неньютоновских (бингамовским) жидкостей. Для вымершего подсемейства Pherhombinae предполагается паразитирование в коконах муравьев (Hymenoptera, Formicidae).

Introduction

An extinct subfamily Pherhombinae (Hymenoptera, Ichneumonidae) is one of the notable groups of Darwin wasps in Baltic amber. They stand out both for their peculiar appearance and relatively high frequency of occurrence in Baltic amber. They were first mentioned in the 19th century [Brischke, 1886] as *Mesochorus* sp. (Hymenoptera, Ichneumonidae, Mesochorinae). Later, C. Bruce [Brues, 1923], based on examination of two males found in that material, described the species *Astiphromma brischkei* (Brues, 1923). S. Larsson [1978:16] included a photograph of an ichneumonid that now can be easily identified as *Pherhombus* sp. The position of this group of ichneumonids became more clear after the publication of D. Kasparyan's thesis, where the independent status of the taxon in the rank of the subfamily Pherhombinae was proposed [Kasparyan. 1988], and the species *Pherhombus antennalis* Kasparyan, 1988 and *Ph. brischkei* (Brues, 1923) were included in the subfamily. A third species, *Ph. dolini* Tolkanitz et Narolsky,

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2005, was described from Rovno amber [Tolkanitz *et al.*, 2005]. *Ph. kasparyani* Manukyan, 2019, *Ph. kraxtepellensis* Manukyan, 2019, and *Ph. sorgenauensis* Manukyan, 2019 were described based on materials from the Kaliningrad Amber Museum [Manukyan, 2019]. It has been believed for a long time that the family Pherhombinae was endemic to Baltic amber. However, in 2022 a representative of the subfamily was discovered in the Danish earliest Eocene Fur Formation (~54 Ma), and the species *Ph. parvulus* (Meier, Wacker et Klopfstein, 2022) was described [Meier *et al.*, 2022]. This finding made us reconsider our views on the paleontological history of the subfamily, as it became obvious that the subfamily Pherhombinae had a longer evolution than previously considered. This article provides information about a new finding of Pherhombinae that is unusual for Baltic amber, which became a basis for the revision of the subfamily system.

Material and methods

The amber piece containing the holotype of *Furpherhombus leleji* **sp.n.** (Figs 1, 2) is deposited in the Collection of the Kaliningrad Amber Museum (Russian National Foundation for Paleontology of Baltic Amber; KAM-F). The amber was extracted in the Primorsky quarry, village of Yantarny, Kaliningrad region, the estimated extraction time is 2023. The piece was polished according to the H. Hoffeins [2001] method. The age of the amber is Priabonian (Late Eocene, ~38.0–33.9 Ma) [Alexandrova, Zaporozhets, 2008a, b; Iakovleva *et al.*, 2021; PaleoBioDB, 2024]. Comparative materials of the Paleontological Institute of the Russian Academy of Sciences (PIN), were studied: the holotype of *Pherhombus antennalis*, PIN, 1 ♂, N. 363/57; paratypes, 3 ♂♂, NN. 364/467, 964/231, 964/232. New additions to the collection of the Kaliningrad Amber Museum (KAM-F) after the publication of the article Manukyan, 2019, were studied: 1 ♂, KAM-F, N.8328-1, *Ph. antennalis* Kasparyan, 1988, syninclusions — a) Diptera, Ceratopogonidae, b) Plantae, large pollens; 1 ♂, KAM-F, N. 8379, *Ph. brischkei* (Brues, 1923), syninclusions — "Stellate hairs" of the oak (*Quercus* spp.); 1 ♂, KAM-F, N.7377, *Ph. kasparyani* Manukyan, 2019, syninclusions — a) Thysanoptera-2, b) Hymenoptera, Formicidae-2, c) Arachnida, Acari-1; 1 ♂, KAM-F, N.7378, *Ph. kraxtepellensis* Manukyan, 2019; 1 ♂, KAM-F, N.29-24.11; 1 ♂, KAM-F, N.82/24.1, Hymenoptera, Ichneumonidae, Cryptinae; syninclusions — a) Arachnida, Acari; b) Hymenoptera, Formicidae-2, c) Pteromalidae; Psocoptera; d) Coleoptera, Scirtidae, e) Coleoptera indet.; f) Diptera, Ceratopogonidae, g) Mycetophilidae, h) Phoridae, i) Dolichopodidae; j) Insecta indet. (more than 100 coprolites); k) Plantae, Bryophyta; l) Angiospermae, 3 flowers, m) *Quercus* spp. (stellate hairs).

Details of the body structure are given according to Broad *et al.* [2018], wing venation according to Spasojevic *et al.* [2018] (Fig. 3). A Canon EOS 6D camera mounted on Leica M60 stereo microscope was used for the photography. All dimensions are given in mm. The stacking of photos was made with Helicon Focus program. Figure 3 was made by M.V. Podolsky (Kaliningrad Amber Museum, KAM).

Taxonomy

Order Hymenoptera Linnaeus, 1758
Family Ichneumonidae Latreille, 1802
Subfamily Pherhombinae Kasparyan, 1988

Furpherhombus Manukyan **gen.n.**

Type species: *Furpherhombus leleji* Manukyan **sp.n.**, by present designation

DIAGNOSIS. Body length about 3.3, forewing length 2.7–2.9. The distal half of the flagellum is not thickened; 18–23). First flagellomere 7–8× as long as maximum width. Areolet closet, rhombic. The length of the pterostigma is 4.5× as long as height. Marginal (radial) cell 2.8–3× as long as wide. Vein 2m-cu almost straight, probably with a single bulla in the anterior third or half. Hind coxa strongly elongated, 2.1–2.5× as long as wide. Tergite 1 more than 4–6× as long as wide, narrow and parallel-sided; tergite 2 transverse, 0.75× as long as wide (*F. parvulus*) or equal (*F. leleji*).

ETYMOLOGY. The genus name is derived from the name of Fur Formation and Baltic amber genus *Pherhombus*. This combination emphasizes the faunal connection of these Lagerstätten.

COMPARISION. *Furpherhombus* differs from the genus *Pherhombus* in its small size — body length of *Furpherhombus* ~3.3 mm, forewing 2.7–2.9 mm, while *Pherhombus* body length 6.7–9 mm, forewing 4.7–9.5 mm. The flagellum is not thickened in its distal half, which is clearly thickened in most species of the genus *Pherhombus*. The number of flagellomeres is reduced: in *Furpherhombus* — 18–23 flagellomeres, while in *Pherhombus* it is always more than 25, mostly 27–30 flagellomeres.

DISTRIBUTION. Only known from Fur formation and Baltic amber.

OTHER SPECIES. *Furpherhombus parvulus* (Meier, Wacker et Klopfstein, 2022), **comb.n.**

Furpherhombus leleji Manukyan **sp.n.**
Figs 1–6.

MATERIAL. Holotype. **Sex unknown**, specimen N.8714, late Eocene Baltic amber (Amber Museum, Kaliningrad). Insect completely intact; there are no syninclusions; Darwin wasp is located in an irregularly rectangular amber piece 1.1 × 0.8 × 0.4 mm (Fig. 1a). The left surface of the body, mandibles and pincers are covered with a white opaque layer (Fig. 1b). The body structure is seen on the right dorsal-lateral and, partly, on the ventral surfaces (Figs 1b, 2a). The distal third of the right wing is partly destroyed because it overlooks the amber, the veins on this place are partially discoloured. The cuticula is discoloured in some places too.

DESCRIPTION. Face narrow (Fig. 3a), with a weak vertical thickening in the middle. Eyes large, converge ventrally, without a notch opposite the antennal sockets. Antenna with 18 flagellomeres, flagellum without tyloids (Figs 3b, c). Flagellomere-1 is more than 8× as long as wide, the second is more than 6×, the third and fourth are 4× greater than the apical width; further, up to the 9th flagellomere the length gradually decreases; after the 9th, their widths are almost equal to the lengths; subapical and apical flagellomeres are clearly demarcated. Temples behind the eyes are sharply narrowed. Gena slightly convex. Clypeus small, evenly convex, without apical tooth, about 2.7× as long as high, clypeal suture deep. Labrum conspicuously exposed, its width equal to the width of

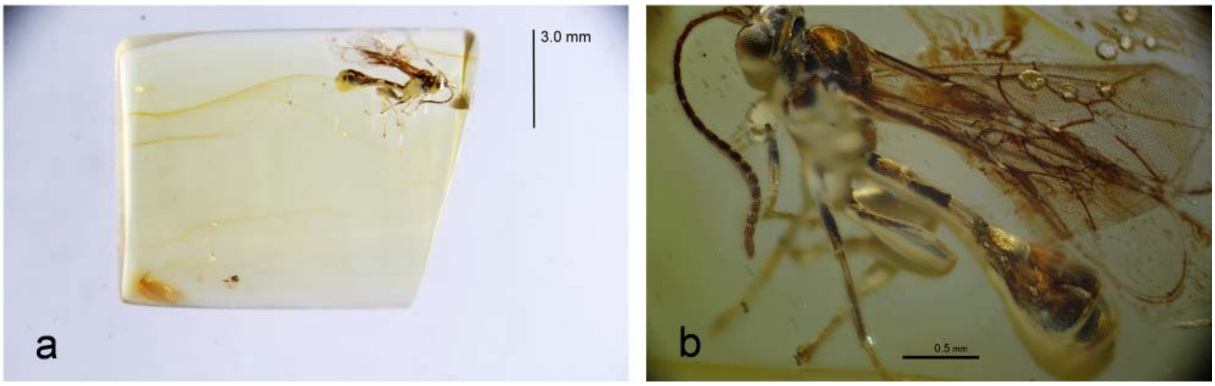

Fig. 1. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, holotype, general view: a — left; b — right.
Рис. 1. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, голотип, общий вид: a — слева; b — справа.

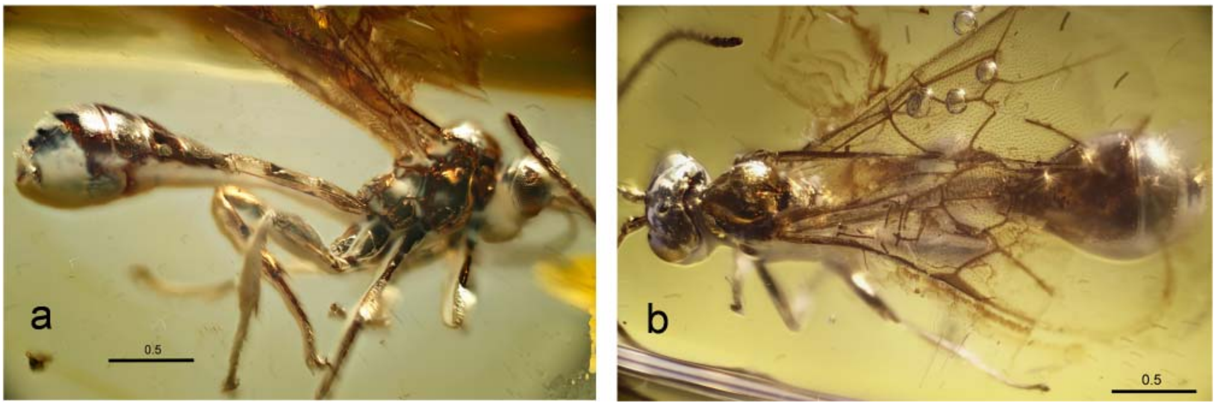

Fig. 2. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, holotype, general view: a — right; b — dorsal.
Рис. 2. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, голотип, общий вид: a — справа; b — сверху.

the clypeus. Mandibles short, not touching, probably without teeth. Palpi not visible. Ocelli enlarged, edges of the antennal sockets raised; distance between the ocelli less than their diameter. Distance from the lateral ocellus to the edge of the eye is 1.8× the diameter of the ocellus; distance from the lateral ocellus to the occipital carina is equal to the diameter of the ocellus. Vertex is depressed. Occipital carina distinct (Fig. 1b, 2b, 4a).

Mesosoma short and tall, its height ~2× its width and equal to its length without the propodeum (Fig. 4a). Pronotal collar and epomia well developed. Mesoscutum strongly narrowed anteriorly, triangular (dorsal view); notauli are absent. Mesopleuron slightly convex; epicnemial (prepectal) carina interrupted in the upper 0.3 part; episternal scrobe and speculum distinct; pleural sulcus without bending towards the episternal scrobe; sternaulus and posterior transverse carina of the mesosternum is absent. Scutellum is noticeably depressed at the base and bordered with carina on the sides. Postscutellum distinct, protruding above propodeum. Metapleuron narrow, slightly convex. Propodeum narrow, elongated posteriorly with sharp carinae; area petiolaris short, approximately 2.5-3× shorter than area superomedia and areola combined. Fore and middle tibiae and tarsi slender. All coxae and trochanters elongated; hind coxae 2.4–2.5× as long as wide. Hind femur 4.4× as long as width. Hind tibia 4.5× as long as width. Tarsal claws of the hind legs large, curved at right angles; arolium considerably extending beyond claw tips (Figs 4b, c).

Fore wings hyaline (Figs 5a, c); pterostigma 4.5× as long as wide; radial cell 2.8× as long as wide; 4-Rs 3.3× as long as r-rs; RA does not reach the apex of the wing. Areolet closed, rhombic, large, its width is almost equal to its height (Fig. 5c); 2m-cu short, straight, extends from the areolet from its middle, with a single bulla in anterior third or half; 1cu-a connected to vein M+Cu opposite vein 1-M+1-rs (nervulus interstitial according to the nomenclature of Townes, 1969); 3-Cu 0.5× as long as 2cu-a (postnervulus is broken in the upper 0.3 part, weakly postfurcal and inclival according Townes, 1969). Ramulus is absent. Hindwing is visible only on the distal half (Fig. 3b); 1-Rs 1.2× as long as rs-m.

Metasoma. First tergite straight (Fig. 6a), narrow, parallel sided, weakly striated, with deep glymmae, more than 6× as long as wide; spiracles located in anterior 0.3; dorsal carina at the base of the tergite distinct up to the spiracles, then weak, not reaching the apex of the tergite. T2 transverse, as long as wide; its length 0.3× length of the T1. T3 0.7× as long as wide (Fig. 6b).

The body smooth, shiny, with very sparse pubescence; predominantly reddish-rusty, legs yellow.

ETYMOLOGY. This species is named in the honor of Professor Arkady Stepanovich Lelej (Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of the

Russian Academy of Sciences; Vladivostok, Russia), a well-known Russian hymenopterist.

DIAGNOSIS. Differs from *F. parvulus* by the proportions of veins, 1-Rs and rs-m in the hind wing — in *F. leleji* 1-Rs 1.2× longer than the vein rs-m, while in *F. parvulus* it is shorter — 0.47× as long as rs-m. Also differs from *F. parvulus* by the absence of ramulus and a few number of flagellomeres, of which there are 18 in *F. leleji*, and 20 in *F. parvulus*, or possibly more. Distinguished by a longer and narrower first tergite of the metasoma – in *F. parvulus* the T1 more than 4× as long as maximum width, in *F. leleji* it is 6×.

TYPE LOCALITY AND HORIZON. Baltic amber; Late Eocene, Prussian Formation, Priabonian range (~33.9–37.2 Ma). Southeast coast of the Baltic Sea, Primorskiy quarry, Yantarnyi, Kaliningrad Province, Russia.

REMARKS. Since the color in amber fades during fossilization [Kopylov, Jouault, 2024], the original color was probably red combined with lemon yellow.

Discussion

The straight, slightly curved first tergite, the tile-like overhanging tergites of the metasoma, the club-shaped top of the metasoma, and many other characteristic features provide us the grounds to classifying the genus *Furpherhombus* in the subfamily Pherhombinae.

When a pherhombine in the Fur formation was found, Meier and co-authors [Meier *et al.*, 2022] believed that there were insufficient grounds for describing a new genus, although they noted that *F. parvulus* was an independent evolutionary line. The discovery of *F. leleji* in Baltic amber changed the situation, and the need for describing the new genus became justified.

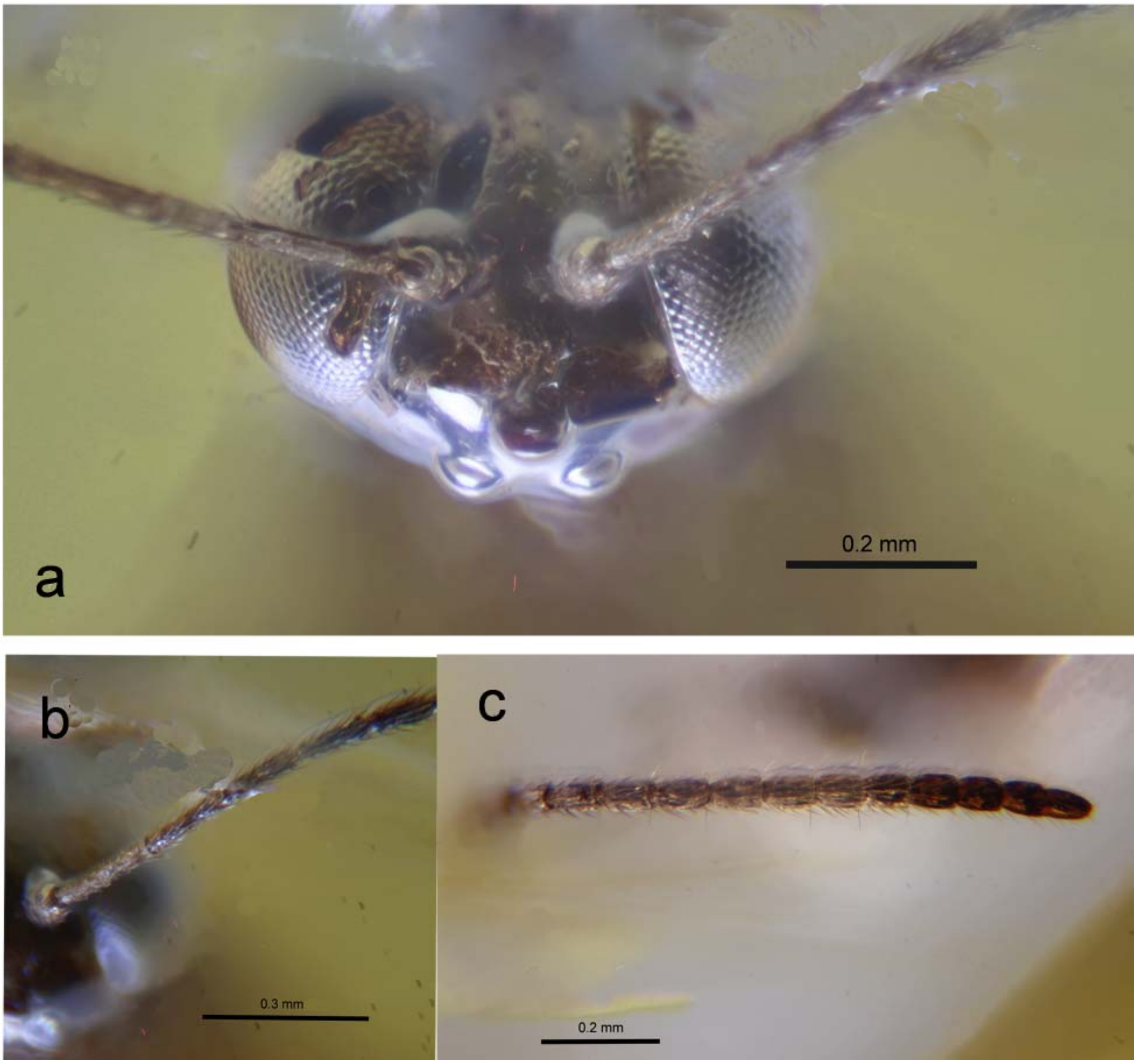

Fig. 3. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, holotype: a — head, anterior view; b — basal part of antenna; c — distal part of antenna.
Рис. 3. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, голотип: a — голова спереди; b — основание антенны; c — вершина антенны.

Can characteristics of the genus Furpherhombus be related to sexual dimorphism?

The studied females of the genus *Pherhombus* show no differences in body size related to their sex, as both sexes of *Pherhombus* have comparable sizes [Manukyan, 2019]. Therefore, we consider the smaller body size of the *Furpherhombus* species to be a primary phenomenon. Meier *et al.* [2022] had the same opinion about *F. parvulus*, and the discovery of *F. leleji* supports this point of view. I can also say that a line of large-sized *Pherhombus* occurred somewhat later than the formation of the "furpherhombus" line. In the Late Eocene (Baltic amber), the "furpherhombus"

Fig. 4. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, holotype: a — head and mesosoma, dorso-lateral view; b, c — hind tarsus and claws.
Рис. 4. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, голотип: a — голова и мезосома, дорсо-латеральная поверхность; b. c. — лапка и коготок задней ноги.

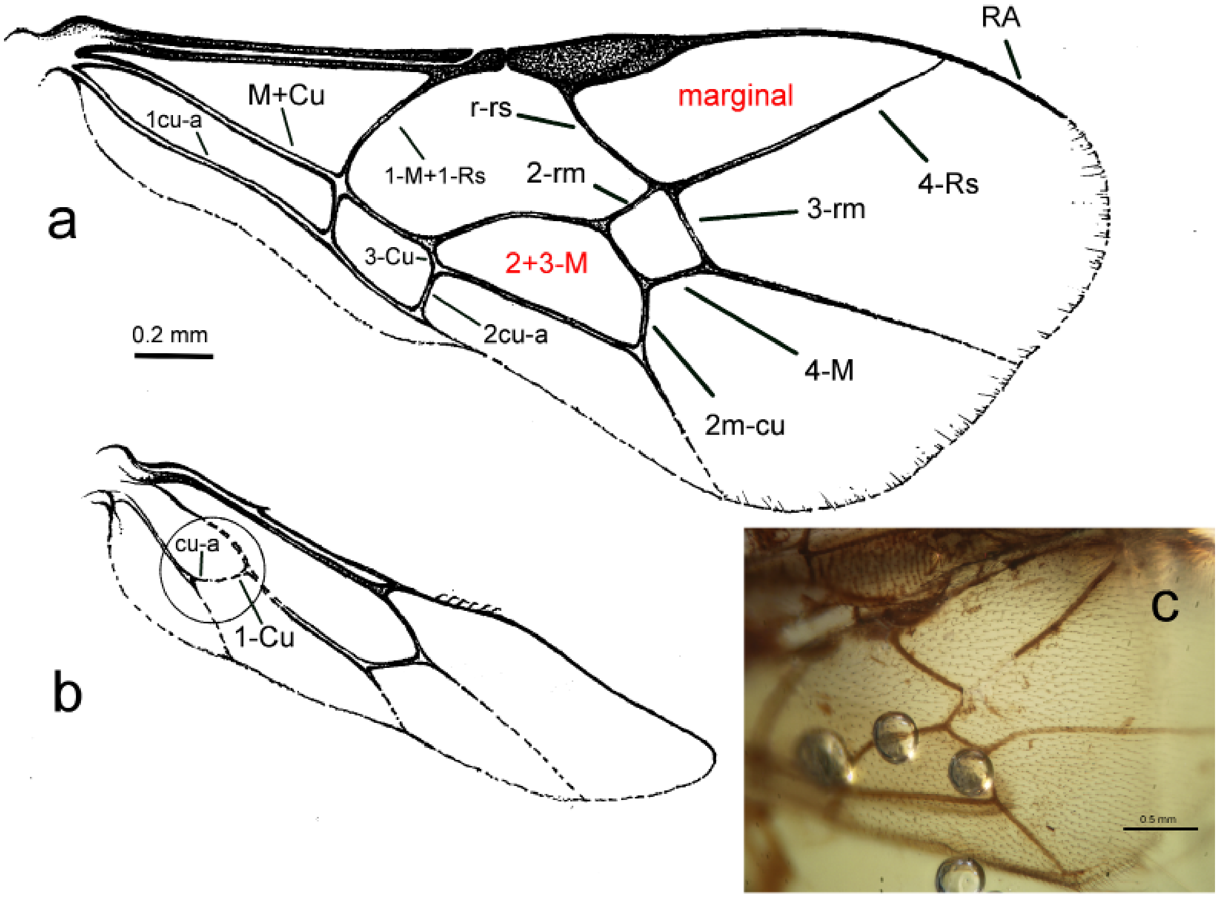

Fig. 5. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, holotype: a — fore wing; b — hind wing, the circle shows the reconstructed area; c — areolet.

Рис. 5. *Furpherhombus leleji* **sp.n.**, KAM-F N.8714, голотип: a — переднее крыло; b — заднее крыло, кругом показано реконструированная часть; c — зеркальце.

line appears to be in the fading state, which explains its exceptionally low occurrence compared to the large-sized ones (genus *Pherhombus*). The sex of *F. leleji* as well as *F. parvulus* is unidentified. The general contours of the structure of the apex of the abdomen give a slight reason to assume that the studied specimen is a female. In our view, a thin, short, needle-shaped ovipositor of *Pherhombus*, which is hardly visible even in amber materials, has a low chance of being detected on imprints. Sexual dimorphism in the pherhombines is extremely low and is expressed by barely perceptible signs. Since the flagella of the two examined females is not thickened dorsally [Manukyan, 2019], it may give us a reason to assume that the holotype *F. leleji* can be a female. However, considering the limited value of this character, it is still necessary for us to acknowledge the undetermined sex of that specimen.

Notes on the taphonomy and biology of pherhombines

F. parvulus was found in rock material, where large insects are known to have a selective advantage. Conversely, the amber, which has a reverse selectivity, is dominated by large pherhombuses, and the small-sized *F. leleji* is known from a single specimen. This does not contradict the established views on insect taphonomy, but rather is a reflection of the evolutionary history of this particular taxon.

The general scheme of insect taphonomy in amber is given by Martínez-Delclòs and co-authors [2004]. Viertler and co-authors [2024] give three taphonomic scenarios for the burial of Darwin wasps in amber. I am providing some additions to these scenarios by taking into account properties and conditions of the primary resin. The initial resin could have a very different consistency, exudes during different seasons, at different temperatures, humidity, etc. This also applies to further fossilization, which also occurred in different temperature conditions, humidity, etc. Various combinations of these circumstances resulted in several ways of inclusion formation in amber. We classify these scenarios below.

1. Liquid resin acts according to the laws of a ***Newtonian fluid***. In this case, the classical, simplest and most frequently presented scheme takes place, when an insect adheres to the resin and subsequently is covered by new layers of resin. According to this scheme, a “layered” amber is formed (Fig. 7), which is characterized by an abundance of small inclusions. The animals are located between the layers and are easily damaged when the amber is processed. In practice, such pieces are impregnated with synthetic resins to strengthen them. In most cases, this gives a positive result, however, there is a risk of resin seeping into the insect's body and making optical interference during the study. A more radical way is to place amber under conditions of high pressure and temperature in an autoclave [Szwedo, Zontag, 2009]. The method is often used when treating amber for commercial uses, as it produces attractive-looking stones, which, however, are unsuitable for the scientific entomological research due to deformation and charring of the insects.

2. Thick resin acts according to the laws of a ***Bingham (non-Newtonian) fluid***. In this case, the efforts of an

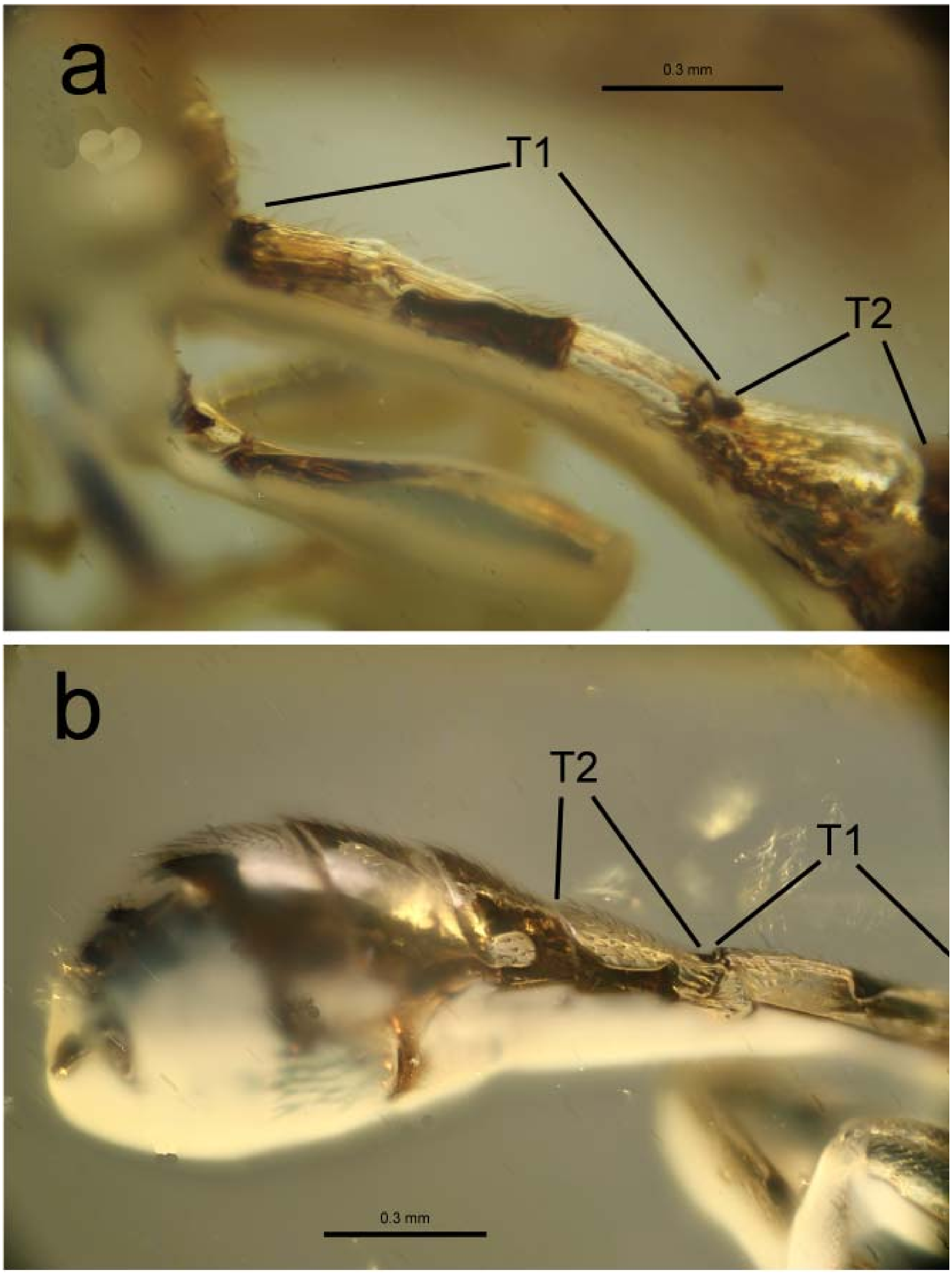

Fig. 6. *Furpherhombus leleji* **sp.n.**, KAM-F 8714, holotype: metasoma, a — first and second metasomal segments; b — lateral view.
Рис. 6. *Furpherhombus leleji* **sp.n.**, KAM-F 8714, голотип: метасома, a — первый и второй сегменты; b — латеральная поверхность.

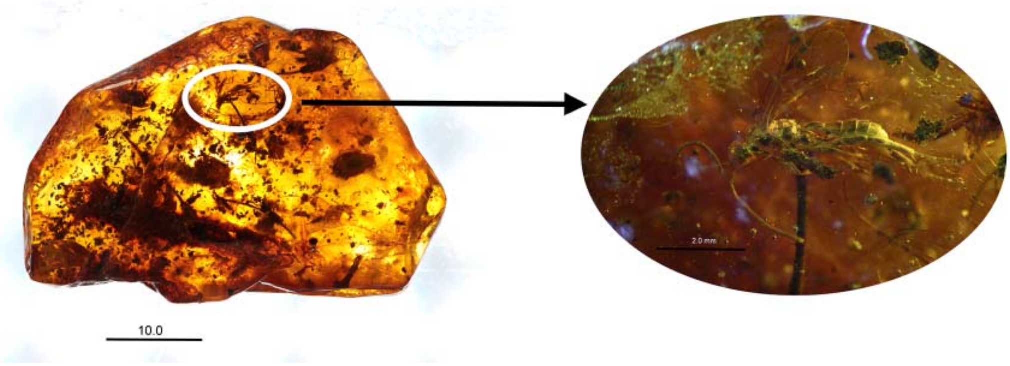

Fig. 7. A piece of amber formed from liquid resin according to the laws of Newtonian fluids, KAM-F 82/24.1, Hymenoptera, Ichneumonidae, Cryptinae (see syninclusions in “Material and methods”).

Рис. 7. Янтарь, образованный из жидкой смолы действующий по законам ньютоновских жидкостей, KAM-F 82/24.1, Hymenoptera, Ichneumonidae, Cryptinae (сининклюзы см. “Материал и методика”).

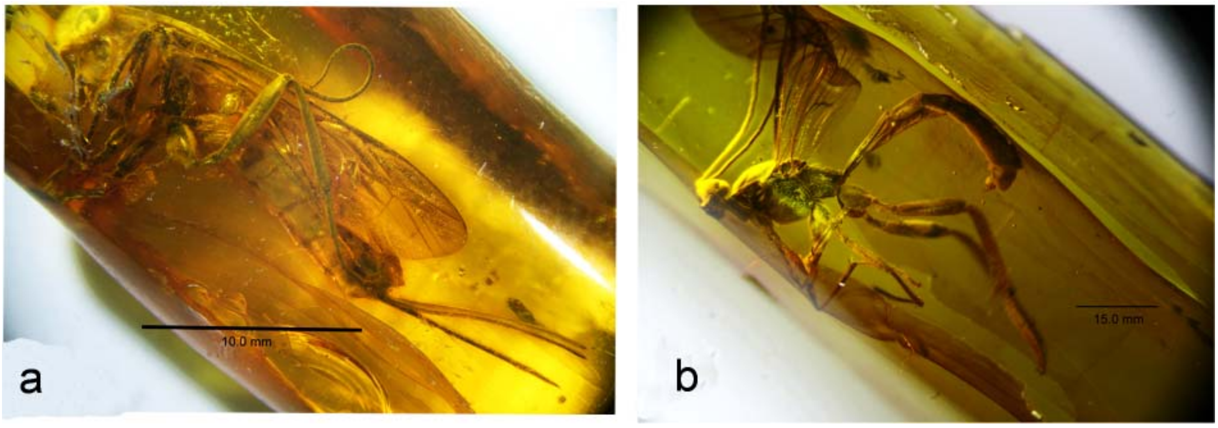

Fig. 8. A piece of amber formed from thick resin according to the laws of Bingham (non-Newtonian) liquids, a — Hymenoptera, Ichneumonidae, Pimplinae sp., KAM-F 8825; b — Pimplinae sp., KAM-F without number.

Рис. 8. Янтарь, образованный из густой смолы действующий по законам бингамовским (не ньютоновских) жидкостей, a — Hymenoptera, Ichneumonidae, Pimplinae sp., KAM-F 8825; b — Pimplinae sp., KAM-F без номера.

insect to free itself and attempts to take off, lead to even greater immersion in the resin. Accepting such a scenario is the only way to explain the ingress of medium and large insects (Fig. 8). In such cases, “high-quality” inclusions are formed in transparent monolithic amber. Usually, these are relatively large or medium-sized insects who have active and strong flight, such as dragonflies (Odonata), horntails (Hymenoptera, Siricidae), long-legged flies (Diptera, Dolichopodidae) and others. Sometimes insects are deformed in such an amber, and the flow of the thick resin breaks the joints of flagella, metasoma, legs, etc.

*3. **Mixed type**,* when one part of the resin has properties of a Newtonian fluid, and another – of a Bingham one.

4. The pressure of the resin in the confined space of a tree leads to its instant release. This mechanism leads to the formation of **teardrop-like amber** specimens without inclusions, as well as icicle-shaped forms of amber. The latter regularly contain insects, including Darwin wasps (Fig. 8B). The inclusions are located between concentrically arranged layers.

We explain the predominance of male pherhombines in amber by their higher flight activity, which led them to getting trapped in amber as the second and third scenarios describe. The biology of pherhombines was previously discussed [Manukyan, 2019], and new materials confirm and add to these hypotheses. The genus *Furpherhombus* is a part of the phylogenetic line Pherhombinae–Townesitinae–Hybrizontinae [Kasparyan, 1988]. Meier and co-authors [2022] applied Bayesian phylogenetic analysis based on a combined morphological and molecular matrix [Spasojevic *et al.*, 2021], which confirmed this point of view. We agree with the conclusions of Meier and co-authors [2022], whose tree converge pherhombines to highly specialized Hybrizontinae and contrasts them with Townesitinae. They indicate a number of characters that support such an alignment, such as reduced mandibles of Townesitinae and Hybrizontinae, which in Townesitinae are bidentate, and Pherhombinae and Hybrizontinae having the posterior basins strongly elongated compared to the ones of Townesitinae [Meier *et al.*, 2022]. The obvious similarity in the structure of the ovipositor, which in Pherhombinae and Hybrizontinae is thin (needle-shaped) and short [Manukyan, 2019: 1328; 2023: 408] in contrast to Townesitinae, in which it is equal in length to the body or even longer [Kasparyan, 1994], should be added to those characters. Morphological similarity and phylogenetic affinity also suggest similarities in their biology. It is known that females Hybrizontinae oviposit into ant pupae when the larvae are transported outside of the nest by worker ants [Komatsu, Konishi, 2010; Gómez Durán, van Achterberg, 2011; Hisasue *et al.*, 2023]. Therefore, for pherhombines, parasitization in ants (Hymenoptera, Formicidae) seems to be the most likely scenario. Although it may seem poorly justified, at this time this hypothesis is the only one supported by some data.

The origin of the Pherhombinae, as already documented, is of Early Eocene. It was probably at that time that specialization was focused on ecologically close, but different-sized hosts — on small-sized ones for the "furpherhombus" line, and on large-sized ones for the "pherhombus" line.

In general, the fauna of Baltic amber has all signs of isolation, as it contains a number of genera with the status "only here" in contrast to other locations. The subfamily Pherhombinae is an example suggesting that this fauna is less unique and has its roots at least in the Early Eocene. In this regard, the discovery of *F. leleji* and other Darwin wasps, in particular Pimplinae of the genus *Crusopimpla* Kopylov, Spasojevic et Klopfstein, 2018 [Manukyan, 2023] are revealing. At the same time, these discoveries indicate the potential of the lagerstätte of Baltic amber for wider extrapolation to Early and Middle Eocene faunas. Baltic amber provides incomparably more fossil material than any other source. Purposeful search and museum collecting of Baltic amber can contribute to solving many problems of the evolution of the biosphere in the Cenozoic.

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