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First Rovno amber species of the genus *Telmatophilus* (Coleoptera: Clavicornia: Cryptophagidae) from Veselukha floodplain

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ABSTRACT. *Telmatophilus sidorchukae* Lyubarsky et Perkovsky sp.n. is described from Priabonian Rovno amber, the first Eocene species of the genus. The amber was collected from the Veselukha floodplain in the north-west Rovno region. The new species is similar to the extant Palearctic *Telmatophilus typhae*, which is an obligate herbivore of *Typha* flowers. The new species differs from all recent congeners by a combination of: comparatively long antenna with the 3rd, 4th and 5th antennomeres more than twice as long as wide, 10th antennomere subquadrate, 11th long-oval; distance between the middle coxae half the diameter of the middle coxae; the distance between the metacoxae about five times greater than between the procoxae and approximately equal to the diameter of the posterior coxae. The origin of the genus is linked to the expansion of the helophyte plants on which *Telmatophilus* species feed, which was apparently facilitated by the appearance of macrophyte lakes in Northern Eurasia after climatic cooling beginning in the second half of the Eocene. Late Priabonian "*Telmatophilus*" *britannicus* Kirejtshuk et Kurochkin, 2019 from the Bembridge Marls of the UK is transferred to Cryptophilinae (Erotylidae) as *Cryptophilus britannicus* (Kirejtshuk et Kurochkin, 2019) comb.n.

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KEY WORDS: Cryptophagidae, *Telmatophilus*, late Eocene, Rovno amber.

Первый ровенский янтарный вид *Telmatophilus* (Coleoptera: Clavicornia: Cryptophagidae) из поймы Веселухи

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РЕЗЮМЕ. Описан новый вид из позднеэоценового ровенского янтаря: *Telmatophilus sidorchukae* Lyubarsky et Perkovsky sp.n. Первый эоценовый вид этого рода описан из поймы р. Веселухи (северо-запад Ровенской области). Новый вид сходен с современным палеарктическим видом *Telmatophilus typhae*, облигатно питающимся на *Typha*. Новый вид отличается от всех современных представителей этого рода комбинацией признаков: относительно длинные усики (3-й, 4-й и 5-й членики усика более чем в 2 раза длиннее ширины, 10-й членик не поперечный, 11-й удлиненно-овальный); расстояние между средними тазиками вдвое меньше, чем диаметр среднего тазика; расстояние между задними тазиками примерно в 5 раз больше, чем между передними тазиками, примерно равно диаметру заднего тазика. Предполагается, что возникновение рода связано с широким распространением полупогруженных растений, на которых питаются *Telmatophilus*, которому способствовало появление макрофитных озёр на севере Евразии после начавшегося во второй половине эоцена похолодания. Недавно описанный из Бембриджа (Великобритания) позднеэоценовый вид *Telmatophilus britannicus* Kirejtshuk et Kurochkin, 2019 перемещен в подсемейство Cryptophilinae (Erotylidae) как *Cryptophilus britannicus* (Kirejtshuk et Kurochkin, 2019) comb.n.

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КЛЮЧЕВЫЕ СЛОВА: Cryptophagidae, *Telmatophilus*, поздний эоцен, ровенский янтарь.

Introduction

Rovno amber is the southern coeval analogue of the famous Baltic amber (Perkovsky *et al*., 2007). Nearly all Rovno amber inclusions from the Rovno region that have been studied so far originated from the Klesov deposit and the Horyn River basin (Perkovsky *et al*., 2010; Perkovsky, 2017), except for new collections from the more western basins of the Styr and Stokhod rivers. These new collections (mostly from Voronki and Velyki Telkovichi) revealed a number of new species of beetles, neuropterans and snakeflies (Perkovsky, Makarkin, 2019; Jałoszyński, Perkovsky, 2019; Legalov *et al*., 2019; Makarkin, Perkovsky, 2020), and also some Hymenoptera previously recorded from Baltic amber (Perkovsky, Olmi, 2018; Martynova *et al*., 2019) or from Baltic and Bitterfeld amber (Radchenko, Perkovsky, 2018, 2020).

These new collections include the first silken fungus beetles (Coleoptera: Cryptophagidae) from these localities, which we here determine to be a new species of *Telmatophilus.* All previous fossil silken fungus beetles are known from the Cretaceous and Eocene. Two Lower Cretaceous monotypic genera were previously described from South China (in shale, Cai, Wang, 2013; Lyubarsky, Perkovsky, 2018a) and Spain (in late Albian El Soplao amber, Peris *et al*., 2017). Almost all other Cretaceous cryptophagids have been recorded from late Santonian Taimyr amber (*Baeomorpha* Realm: Gumovsky *et al*., 2018): Atomariinae *Nganasania khetica* Zherikhin, 1977 and *N. taymyrica* Lyubarsky et Perkovsky, 2014 (Lyubarsky, Perkovsky, 2017a) and Cryptophagini *Microticus* (Lyubarsky, Perkovsky, 2015) and *Ennoticus* (Lyubarsky, Perkovsky, 2017b). Moreover, *Lebanophytum* Kirejtshuk et Azar (Kirejtshuk, Azar, 2008) (originally placed in Cerophytidae, later in Lebanophytidae Kirejtshuk in Kirejtshuk et Azar, 2013), was removed from Elateroidea and placed in the Cryptophagidae by Yu *et al*. (2019).

Some representatives of subfamily Atomariinae have been recorded in Priabonian Baltic amber, viz. *Atomaria* Stephens, 1829, *Ephistemus* Stephens, 1829, and subfamily Cryptophaginae, viz., *Antherophagus* Dejean, 1821, *Cryptophagus* Herbst, 1792, *Micrambe* Thomson, 1863, and *Telmatophilus* Heer, 1841 (Klebs, 1910; Kubisz, 2001); the latter genus is also reported from Bitterfeld amber (Hieke, Pietrzeniuk, 1984). Four atomariines and four cryptophagines have been reported so far from Priabonian ambers (Spahr, 1981; Hieke, Pietrzeniuk, 1984; Lyubarsky, Perkovsky, 2010, 2011, 2012, 2013, 2014, 2018, 2019a; Perkovsky, Lyubarsky, 2014), including the first extinct Eocene monotypic genus *Spaniophagus* Lyubarsky et Perkovsky, 2019 (Lyubarsky, Perkovsky, 2019b).

Recently a new late Priabonian species was described: “*Telmatophilus*” *britannicus* Kirejtshuk et Kurochkin, 2019 (Kirejtshuk *et al*., 2019) from the Bembridge Marls, UK (see below).

Materials and methods

The amber was collected in the floodplain of the Veselukha River, specifically from the amber-bearing zone 12 km long and 5–6 km wide that starts 8 km north of the village of Ozertsy (Vladimirets district) and reaches the village of Rudki (Zarechnoye district). The sample was cut from the larger, clear piece of amber LKV-8 75 × 39 × 31 mm, weighing 34.2 g, which also included stellate hairs.

Photographs were taken at the Paleontological Institute, Russian Academy of Sciences (Moscow) by A.P. Rasnitsyn using a Leica MZ 16 microscope and by D.D. Vorontsov using a Nikon E-800 microscope; brightfield and incident illumination were combined. Stacks of images, comprising multiple focal planes, were obtained with Olympus OM-D E-M10II digital camera. Images were corrected for colour, brightness and noise with Adobe Lightroom. Figures herein contain layered (multifocal) images from 10 to 40 focal planes processed with Helicon Focus 7.5.8 using algorithm B.

Amber pieces were cut and polished by the protocols of Sidorchuk (2011, 2013) with tools described by E.A. Sidorchuk and D.D. Vorontsov (Sidorchuk, Vorontsov, 2018). All of the material is housed in the amber collection of the Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine (SIZK) .

Systematic paleontology

Family Cryptophagidae Kirby, 1826
Subfamily Cryptophaginae Kirby, 1826
Tribe Cryptophagini Kirby, 1826
Genus ***Telmatophilus*** Heer, 1841

Telmatophilus sidorchukae **sp.n.**
Figs 1, 2.

MATERIAL. Holotype, SIZK No LKV-35, Rovno amber, Priabonian. Sex of the holotype: unknown. Syninclusions SIZK No LKV-32: 2 Diptera (Phoridae, Sciaroidea); SIZK No LKV-33: 2Collembola, Symphypleona; SIZK No LKV-34: Coleoptera, Collembola (Entomobryomorpha); SIZK No LKV-36: Collembola (Symphypleona); SIZK No LKV-37: Coleoptera, Collembola (Entomobryomorpha); SIZK No LKV-38: 2 Acari; SIZK No LKV-39: Collembola (Entomobryomorpha); SIZK No LKV-40: Collembola (Symphypleona), Acari; SIZK No LKV-41: 2Collembola (Symphypleona), 2Acari; SIZK No LKV-42: Acari; SIZK No LKV-43: Diptera (Keroplatidae); SIZK No LKV-44: Acari (Oribatei); SIZK No LKV-45: Psocoptera.

DIAGNOSIS. This new fossil species differs from extant congeners by a combination of: small body size; comparatively long antenna, 3rd, 4th and 5th antennomeres more than twice as long as wide, 10th antennomere not transversal, 11th long-oval; distance between middle coxae half diameter of middle coxae; distance between metacoxae about five times as wide as between procoxae, approximately equal to diameter of posterior coxa.

DESCRIPTION. 1.7 mm long. Body black, elongate oval, parallel-sided, moderately convex dorsally, subflattened ventrally; covered with confused puncturation; short, decumbent pubescence (Figs 1A, 2).

Head with slightly convex anterior margin, comparatively large and prominent eyes, without frontoclypeal suture. Antennae about one

Fig. 1. *Telmatophilus sidorchukae* sp.n. (photo).
A — total view, dorsal; B — total view, ventral; C — total view, lateral; D — meso- and metathorax.
Рис. 1. *Telmatophilus sidorchukae* sp.n., фото.
A — общий вид, дорзально; B — общий вид, вентрально; C — общий вид, латерально; D — средне- и заднегрудь.

Fig. 1 (continued).
Рис. 1 (продолжение).

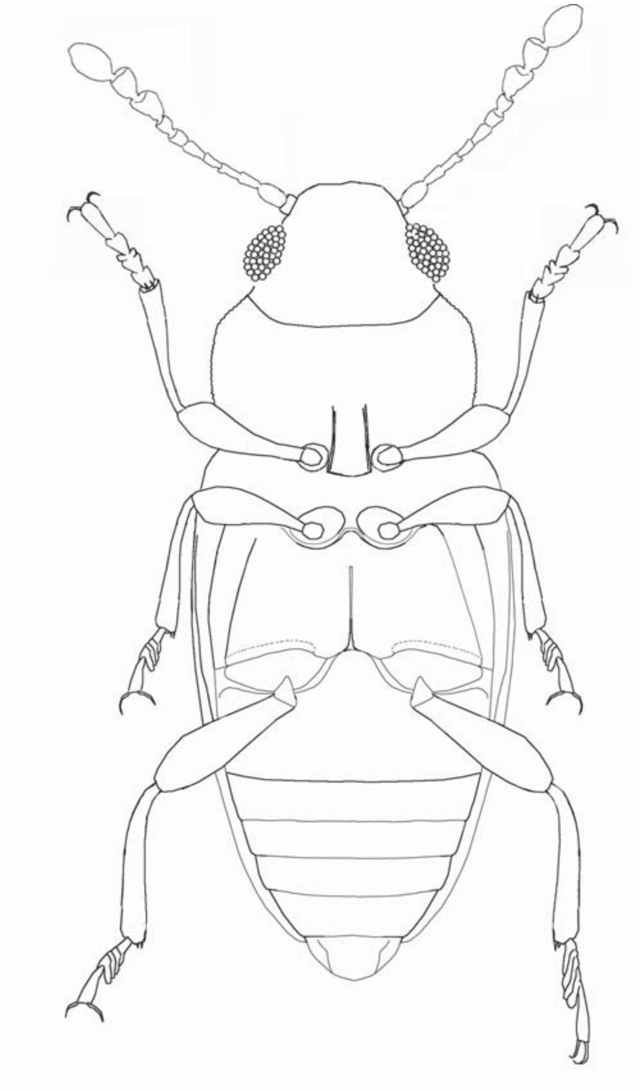

Fig. 2. *Telmatophilus sidorchukae* sp.n.
Total view, ventral, line drawings.
Рис. 2. *Telmatophilus sidorchukae* sp.n.
Общий вид, вентрально.

and a third as long as head width, about 2.5 times as long as antennal club, reaching base of pronotum. 1st antennomere oval, 1.6 times as long as wide, 2nd, in 1.4 times as long as wide, 3rd, 4th, and 5th, 2 times as long as wide, 6th, 1.7 times as long as wide, 7th, 1.5 times as long as wide, 8th subquadrate, club 3-segmented, elongate, slightly loose, consisting of comparatively large, not transverse segments: 9th antennomere elongated trapezoid, 1.3 times as long as wide, 10th antennomere subquadrate, 11th elongated oval, 1.8 times as long as wide (Fig. 1B).

Pronotum about 1.7 times as wide as long, greatest width at posterior third of its length, arcuately narrowing both anteriorly and posteriorly, gently sloping at sides, anterior margin straight, anterior angles rounded, lateral margin evenly weakly serrate, posterior angles almost pointed, posterior margin slightly concave, with weak median lobes. Pronotum without sublateral lines, median fold. Pronotal basal pits present, connected by a groove. Prosternum moderately long, with process comparatively wide, somewhat narrower than antennal club, subparallel-sided, truncate, slightly widened at apex. Procoxae closed posteriorly, oval and slightly transverse. Metasternal projection almost reaching middle of length of middle coxa. Distance between middle coxae twice less than diameter of middle coxa (Fig. 1B,D). Metasternum with median longitudinal line. Metaventrite about as long as prosternum, mesoventrite combined, its posterior edge between coxae angulate. Distance between metacoxae about five times as wide as that between procoxae, approximately equal to diameter of posterior coxa (Fig. 1D). Tarsomeres distinctly lobed, tarsal formula 555.

Elytra about 1.6 times as long as wide combined, slightly arcuate at sides, slightly wider than pronotum, apparently gently sloping at sides, their apices seeming to together forming a single arc. Epipleura moderately narrow, reduced, almost reaching 1st ventrite of abdomen.

Ventrite 1 almost as long as ventrites 2–4 combined (Fig. 1C); hypopygidium widely rounded at apex. Hypopygidium protrudes from under the elytra; this sometimes occurs in *Telmatophilus*, especially often in females.

ETYMOLOGY. The new species is named in honor of Ekaterina A. Sidorchuk.

REMARKS. In one species of the genus (*T. americanus* LeConte), there is sexual dimorphism in leg morphology, in particular in the hind tibia. However, European species of the genus developing on cattails do not have this dimorphism precluding determination of the sex of the amber specimen.

Discussion

The genus *Telmatophilus* has been previously reported in Baltic and Bitterfeld ambers (Klebs 1910; Barthel, Hetzer, 1982; Hieke, Pietrzeniuk 1984); however, these specimens were never named and these determinations need to be confirmed. Recently "*Telmatophilus*" *britannicus* Kirejtshuk et Kurochkin, 2019 (Kirejtshuk *et al*., 2019) was described from Priabonian Bembridge Marls (Bembridge, 34 Mya), a bit younger than the Priabonian amber deposits (Ross, Self 2014; Tolkanits *et al*. 2018 and references therein). "*T.*" *britannicus* as described (Kirejtshuk *et al*., 2019) is yellow and has a full epipleuron reaching the apex of the elytra ("Epipleura moderately narrow, slightly narrowing apically and almost reaching apices of elytra": Kirejtshuk et Kurochkin, 2019: 67). These diagnostic characters place the specimen in the family Erotylidae (Leschen, 2003: 29). This species also has a prosternum with a relatively short space in front of the coxa; elytral epipleuron complete to the apex of the elytron; prothorax parallel-sided and widest at middle; small body; light coloration; pronotal anterior angles angular and slightly protruding; and the lateral edges of pronotum are arcuate. By these character states, we transfer *Telmatophilus britannicus* Kirejtshuk et Kurochkin, 2019 to Erotylidae Latreille 1802, tribe Cryptophilini Casey, 1900, genus *Cryptophilus* Reitter, 1874: *Cryptophilus britannicus* (Kirejtshuk et Kurochkin, 2019) **comb.n.**

Telmatophilus sidorchukae sp.n. is then the first species of the genus *Telmatophilus* described from Eocene.

The new species looks most like *T. typhae* (Fallén, 1802) because of its comparatively long 9th and 10th antennomeres, but differs by the length of its 3–5th antennomeres and the structure of its meso- and metathorax.

As already mentioned, the new fossil species differs from recent congeners by a combination of small body size, comparatively long of antenna, the 3rd antennomere more than twice as long as wide, the 10th antennomere not transverse 11th long-oval, and the distance between the middle coxae half the diameter of the middle coxa.

Extant Holarctic species of this genus are associated with aquatic plants, particularly *Typha* and *Sparganium*. The transition to obligatory feeding on flowers is rather infrequent in Cryptophagidae (Leshen, 1996); besides *Telmatophilus*, this is only known in one genus of

Atomariinae from the South Hemisphere (Leshen, 1996). A transition to phytophagy from mycetophagy may sometimes occur within a genus: among the many species of *Atomaria*, nearly all are mycetophagous, but *Atomaria linearis* Steph. feeds on sugar beet. Episodic feeding on flowers is also known for a number of other genera, including *Mnioticus* (Leshen, 1996) from the mountains of East Africa. *Mnioticus* is related to *Telmatophilus* (Leshen, 1996), as well as to the Santonian genus *Microticus* from the Kheta Formation of Taimyr. The distribution of angiosperms in the Santonian of Taimyr appears to have been rather limited (Nadein, Perkovsky, 2018), and angiosperm pollen is relatively rare there (less than 10%, according to Kara-Murza, 1960). Therefore, it seems highly unlikely that *Microticus* fed on flowers.

Species of *Telmatophilus* are found in quite different habitats: in flowers of marsh marigold, *Caltha palustris* (Ranunculaceae); in the flowers of Umbelliferae; in the reed *Phragmytes*; under bark; on willow; or on sedge. The seasonal history and habits of *T. typhae* was summarized by Hoebecke & Wheeler (2000). *T. typhae* in N. America is found on *Typha latifolia* and *Typha angustifolia* (introduced from Europe). Both larvae and adults of *Telmatophilus* feed on the semi-aquatic plants *Sparganium* (Sparganiaceae) and *Carex* (Cyperaceae) as well as *Typha* (Typhaceae). Overwintered females of *T. typhae* lay eggs on the outer surface of immature male *Typha* inflorescences in late May (Hoebecke, Wheeler, 2000). The eggs hatch in about 3–4 days and the emerging larvae burrow into the flowers to feed. Larval development requires approximately 16–19 days. The first two larval stages feed on immature, succulent stamens and pollen. The final instar larva and adults feed on mature pollen grains. Larvae of all three instars, pupae, and adults are all found on mature male flower clusters. When male flower clusters break up from the central column of the plant, they fall into the standing water along with the beetle larvae and pupae. Pupation occurs by the end of July, requiring about five days, and new adults begin to emerge by mid-August. The life cycle of *Telmatophilus* (the of *T. typhae* is the best known) coincides with that of its host plant. This implies that the flowers of *Typha* are a stable and widespread resource.

The spread of semi-submerged helophyte plants (cattail, bur-reed, sedge) on which *Telmatophilus* species feed appears to have been facilitated by the appearance of macrophyte lakes during climatic cooling in the second half of the Eocene (Ponomarenko, 2010). Cattails and the other helophyte plants mentioned above have a near-global geographical distribution, while the *Telmatophilus* species are found only in the Holarctic, and *Telmatophilus* feeding on *Typha* (disregarding recent invasions), are only known in the Palearctic. The connection between the ancestors of *Telmatophilus* switching to feeding on flowers and the geological record of their host plants has been made possible by the publication of a recent revision of the phylogeny and historical biogeography of *Typha* (Zhou *et al*., 2018).

Typha is a relatively ancient genus. Both *Typha* and *Sparganium* have extensive and distinctive fossil records dating back to the Paleogene, as well as two Maastrichtian records (Zhou *et al*., 2018). The respective crown ages of *Typha* and *Sparganium* were estimated to be 39.03 Mya (95% HPD: 22.64–57.60 Mya) and 18.03 Mya (5.79–36.69 Mya), respectively (Zhou *et al*., 2018). The Late Cretaceous and Paleogene fossils differ somewhat from extant *Typha* species, however, and Zhou *et al*. (2018) didn’t rule out the possibility that these are part of its stem lineage. It appears reasonable that the time of appearance of *Telmatophilus* matches that of the *Typha* crown-group, close to Priabonian Baltic, Rovno and Bitterfeld ambers. Molecular dating indicates that the origin of crown-group *Typha* occurred in Bartonian (middle Eocene); and that it most likely originated in East Eurasia and then dispersed into other areas (Zhou *et al*., 2018). It may be that the reproductive cycle of the ancestors of *Telmatophilus* that fed on semi-submerged helophyte plants became connected to colder winters, which prevented the genus from spreading beyond the boundaries of the Holarctic.

The genus *Telmatophilus* was revised by Otero (2012), confirming the status of *Telmatophilus brevicollis* Aubé, 1862, *T. caricis* (Olivier, 1790) and *T. typhae* (Fallén, 1802). In this work, he established two new synonymies: *Cryptophagus sparganii* Ahrens, 1812 = *Telmatophilus caricis* (Olivier, 1790) and *Cryptophagus schonherrii* Gyllenhal, 1808 = *Telmatophilus typhae* (Fallén, 1802). The larvae of *Telmatophilus brevicollis* depend on the seeds of *Sparganium erectum* L.; *Telmatophilus caricis* lives on *Typha* sp. and *Sparganium* sp., in which they grow during June and July. *Telmatophilus typhae* lives on *Typha latifolia* L., *T. angustifolia* L. and other aquatic plants and feeds on pollen.

Occurrences of *Telmatophilus* in the Palearctic include *T. brevicollis* (S Europe – Caucasus – Kazakhstan); *T. caricis* (S Europe – N Africa – Caucasus – Uzbekistan – Siberia – Mongolia); *T. orientalis* Sasaji, 1987 (Kanto (Honshu), Japan); and *T. typhae* (S Europe – N Africa – Caucasus – Kazakhstan – Uzbekistan – Kyrgyzstan – Siberia – Russian Far East – Hebei (China) – Hokkaido (Japan) – N Korea).

The sole native American species *T. americanus* feeds only on transboreal species of *Sparganium* and the arecid *Peltandra*, while cattails in the Eastern part of North America are fed on by the introduced *T. typhae* (Hoebecke, Wheeler, 2000). *T. americanus* does not range south beyond the states of Colorado, Indiana and New York (Majka, Langor, 2010); unlike the Palearctic species, *T. americanus* does not penetrate to the subtropics. Combined with the Priabonian findings of *Telmatophilus* in E. and N. Europe and its Palearctic range, this supports the notion of a European or, less likely, extratropical Asian origin of the genus, with a rather late migration into North America (probably via Beringia) of just one boreal species feeding on *Sparganium*. The lack of other Nearctic species, together with the broad distribution of *Typha latifolia* in the Nearctic, suggests that at least in Europe the genus first appeared only after the 'De Geer' and 'Thulean' routes through Greenland and Iceland (Archibald *et al*., 2011) ceased to exist.

The finding of *Telmatophilus* in the floodplain of the Veselukha (between the Styr and Stokhod basins) rather than in Klesov is further evidence of more extensive wetlands there (as well as in Horyn basin: Perkovsky , Vlaskin, 2005) compared to Klesov. The first amber species of *Sphagnum* was described from the Styr basin (Ignatov *et al*., 2019), upon which also various diatoms were found. The occurrences of a number of species shared between Rovno amber from the Styr, Veselukha and Stokhod basins and Baltic amber might be explained by some similarities of their paleoclimates (Martynova *et al*., 2019). High humidity at the locality of the holotype is further indicated by an unusually large number of collembolans from various suborders (9 specimens) among the syninclusions. Combined with the large size of the amber sample, this abundance of collembolans suggests burial of the resin bearing the holotype near the base of the trunk (Perkovsky *et al*., 2012 at references therein). It is probable that the wet forest litter near a water body was the habitat of the imago after the end of flowering period of the semi-aquatic host plants near a water body.

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