

An extraordinary spittlebug nymph (Homoptera: Cercopoidea) from mid-Cretaceous Burmese amber

Необычайная нимфа пенницы (Homoptera: Cercopoidea) из средне мелового бирманского янтаря

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КЛЮЧЕВЫЕ СЛОВА: Hemiptera, Auchenorrhyncha, Cicadomorpha, пенницы, морфология, мокрицеобразные нимфы, восковые пластинки, скрытый образ жизни.

ABSTRACT. *Aidanympa thompsoni* **gen. et sp.n.** from Burmese amber is the first fossil find of nymphal Cercopoidea. This nymph, with a flat crown, outstretched prothoracic paranota and wingpads, and over thirty wax plates on the head, legs, thoracic and abdominal tergites, is more primitive than all other known cercopoid nymphs. The morphology of the new nymph indicates that these nymphs produced spittle, and likely lived in confined spaces, such as leaf axils or between cone scales. *Aidanympa* **gen.n.** is assigned to the Mesozoic family Sinoalidae and tentatively associated with adults of the genus *Makrosala* Chen et Wang, 2020. Two monotypic Cretaceous families are transferred from Cercopoidea to Membracoidea and synonymized under the family Cicadellidae (= Cercopionidae Hamilton, 1990, **syn.n.**) or its subfamily Ledrinae (= Myanmalidae Chen, 2026, **syn.n.**).

РЕЗЮМЕ. *Aidanympa thompsoni* **gen. et sp.n.** из бирманского янтаря — первая находка ископаемых нимф надсемейства Cercopoidea. Эта нимфа (с плоской теменной стороной головы, распростертыми переднегрудными паранотами и крыловыми зачатками, и более чем тридцатью восковыми пластинками на голове, ногах, грудных и брюшных тергитах) более примитивна, чем все другие известные нимфы Cercopoidea. Особенности строения указывают на то, что эти нимфы выделяли пену и, вероятно, обитали в замкнутых пространствах, например, в пазухах листьев или между чешуями шишек. *Aidanympa* **gen.n.** отнесен к мезозойскому семейству Sinoalidae и предварительно сопоставлен с имago рода *Makrosala* Chen et Wang, 2020. Два монотипных меловых семейства перенесены из Cercopoidea

в Membracoidea и синонимизированы с семейством Cicadellidae (= Cercopionidae Hamilton, 1990, **syn.n.**) или его подсемейством Ledrinae (= Myanmalidae Chen, 2026, **syn.n.**).

Froghoppers and spittlebugs constitute the superfamily Cercopoidea known since the Early Jurassic, with five extant families and over 3,000 described species [Hamilton, 2001; Thompson, 2026]. Cercopoid nymphs do not jump and live hidden inside the protective foam nests; Machaerotidae nymphs build calcareous dwelling tubes on twigs, while Cercopidae nymphs usually feed on roots at or below the soil surface. The nymphs imbibe xylem sap that is 99% or more water, excrete large amounts of excess water, and produce spittle by grasping external air with the last laterotergites and then releasing it as bubbles into the surrounding soapy excretions. Malpighian tubule products and/or wax from the abdominal glands act as surfactants (their roles remain poorly understood) [Rakitov, 2002]. To breathe in this foamy or liquid medium, cercopoid nymphs use a so-called respiratory tube, formed by abdominal laterotergites directed medially and closing the ventral space into which the spiracles open [Šulc, 1912]. Considering this lifestyle of cercopoid nymphs, it is not surprising that they have not been recorded as fossils.

An extraordinary nymph of Cicadomorpha (more precisely, its exuvium) was discovered in Burmese amber. Its body plan has no analogues in Hemiptera. In psyllids and Coleorrhyncha, as well as in basal Hemiptera (Archescytinidae) and the Permian Cicadomorpha, the nymphs are oval, dorsoventrally flattened, their head and all thoracic and abdominal segments bearing side lobes directed laterally [Shcherbakov, 1996, 2002]. This body

design is termed onisciform or oniscoid (wood louse-like). Among modern Cicadomorpha, such nymphs are found only in Ledrinae. The new nymph has a unique design, with only its head and thorax oniscoid, so it can be termed 'semi-oniscoid'. The abdomen is narrow, and its laterotergites are folded onto the ventral side, forming a breathing tube. There are four pairs of large and two pairs of small wax plates on the abdominal tergites; surprisingly, wax plates are also present on the crown, thoracic nota, and dorsal side of the femora and tibiae. Abdominal wax plates combined with a breathing tube are found only in Cercopoidea nymphs. Extant families of this group have three (Machaerotidae [Evans, 1940; Maa, 1963]) or two pairs of abdominal wax plates and no wax plates on the thorax, head, or legs, which proves that the new nymph belongs to some extinct cercopoid family. In a distinctive pentagonal head shape, the new nymph is similar to adults of the genus *Fangyuania* Chen, Szwedó et Wang, 2018 and is therefore assigned to the same family Sinoalidae [Chen *et al.*, 2018, 2019b, 2023]. Based on the relatively large size of this middle instar nymph, it can be tentatively associated with another sinoalid genus, *Makrosala* Chen et Wang, 2020. However, this preliminary association requires confirmation. The new nymph is described below as a new genus and species. It is the first fossil find of nymphal Cercopoidea.

The fossil was photographed using a Leica DFC425 camera coupled to a Leica M165C stereomicroscope, and the images were z-stacked with Helicon Focus 7.0.2. The holotype is deposited in the collection of Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN).

Superfamily Cercopoidea Leach, 1815
Family Sinoalidae Wang et Szwedó, 2012
Aidanympa **gen.n.**

TYPE SPECIES. *Aidanympa thompsoni* **sp.n.**

DIAGNOSIS. Small, dorsoventrally flattened Cicadomorpha nymph with unusual semi-oniscoid design: head and thorax wide, flattened; abdomen narrow, subconical, convex dorsally. Crown flat, pentagonal; eyes small; antennae short, setaceous, with slender tapered flagellum; postclypeus large; rostrum short. Prothoracic paranota and wingpads large, rugose, directed laterally; prothoracic paranotum with semicircular sinus around eye. Legs short, stout; all three pairs similar, hind legs not modified; tibiae subclavate, curved at base, widened before apex, with sparse strong setae on outer margin, apical pecten of short teeth narrower than maximum tibia width; tarsi two-segmented; claws large, hooked. Abdominal segments I–VII wide, VIII–IX narrow; laterotergites directed medially, concealing sternites and forming respiratory tube. Thoracic nota and abdominal tergites II–VII with one pair of wax plates each; femora and tibiae on dorsal side with one wax plate each; head with large median and two small lateral wax plates. Sides of abdomen with long, strong setae.

COMPOSITION. Type species.

COMPARISON. A unique combination of characters distinguishes the new genus from all known hemipteran nymphs. It differs from Psyllomorpha and other Sternorrhyncha in the large prothoracic paranota and short setaceous antennae with a slender flagellum tapered apically, from Fulgoromorpha in the absence of carination and the structure of antennae, and

from Coleorrhyncha and Heteroptera in the structure of the head and antennae. Within Cicadomorpha, the new genus is reliably placed in Cercopoidea based on the combination of the abdominal wax plates and the breathing tube. It differs from all known cercopoid nymphs by a larger number of abdominal wax plates (6, not 2–3 pairs), as well as the presence of wax plates on the head, thorax and legs. Distinct from oniscoid nymphs of primitive extinct groups of Cicadomorpha, such as Upper Permian *Aleuromypha* Riek, 1974, in the elongate abdomen with last segments narrow and laterotergites folded ventrally. In the distinctive pentagonal shape of the crown, the nymph is similar to the adult of the monotypic Burmite genus *Fangyuania*, a member of the Late Mesozoic cercopoid family Sinoalidae, and it is therefore assigned to this family (see Discussion).

REMARKS. *Aleuromypha bibulla* Riek, 1974 from the uppermost Permian (Changhsingian) of Mooi River, Karoo Basin, South Africa, originally assigned to whiteflies, is in fact similar to various undescribed nymphs from the Permian of Russia; all of them have a large pronotum with well-developed paranota and a dorsal anus and belong to the basal families of Cicadomorpha.

The only other fossil nymph for which cercopoid affinities were assumed, *Jascopus notabilis* Hamilton, 1971 from the Upper Cretaceous (Upper Campanian) Cedar Lake amber, Manitoba, Canada, was singled out into the family Jascopidae as combining features of Cicadellidae and Cercopidae s.l., i.e., Cercopoidea [Hamilton, 1971]. However, Evans [1972] revised the systematic position of this fossil and transferred it to Cicadellidae (for more details, see Shcherbakov [1992]). The genus *Jascopus* Hamilton, 1971 differs from *Aidanympa* **gen.n.** in having the body not flattened; crown subtriangular; wingpads directed ventrolaterally; tibiae straight; fore and middle tibiae with two dense rows of setae on outer margins; hind tibia elongated, with apical pectens flared; tarsi three-segmented; basitarsus, especially hind, elongated; claws small.

ETYMOLOGY. From Russian *ay da...!* (interjection expressing admiration; cf. *Well, what a ...!*), and *nymphe*, a minor female nature deity in ancient Greek folklore (literally, *What a nymph!*); gender feminine.

Aidanympa thompsoni **sp.n.**
Figs 1–7.

MATERIAL. Holotype nymphal exuvium PIN 5608/600a—Burmese amber, Hukawng Valley, Kachin State, Myanmar; mid-Cretaceous (Albian–Cenomanian). Syninclusion: Diptera Ceratopogonidae PIN 5608/600b.

DESCRIPTION. Exuvium of middle (II–III) instar nymph. Body flattened dorsoventrally, oblong (1.9:1), 4.3 mm long, 2.3 mm wide, widest at mesothorax. Head and thorax wide, their dorsal surface nearly flat, outer margins foliaceous; abdomen subconical, 1.7x as long as wide, of seven wide and two narrow segments, widest at segment III. Body and appendages brownish, tergites of abdomen gradually become darker towards its apex. Dorsum sparsely covered with minute setae.

Head rounded pentagonal, broad shovel-shaped, half thorax width; crown 1.2x as wide as long. Ecdysial line along crown and thorax, on crown Ψ-shaped: median stem reaching head apex, two lateral arms running anterolaterad. Eyes small, oblong, twice longer than scape width, mostly ventral. Antennal ledges foliaceous, produced before eyes; antennae inserted ventrally, half as long as head width, setaceous; scape wide; pedicel elongate, subclavate, twice narrower than scape; flagellum slender, 7-segmented, 1st flagellomere longest, thrice narrower than scape, 2nd to 6th of similar length, 7th shortest,



Figs 1–3. *Aidanympa thompsoni* Shcherbakov, **gen. et sp.n.**, holotype nymphal exuvium, habitus, dorsal (1, 3) and ventral view (white arrows, wax plates on head).

Рис. 1–3. *Aidanympa thompsoni* Shcherbakov, **gen. et sp.n.**, голотип, экзувий нимфы, габитус, вид сверху (1, 3) и снизу (белые стрелки, восковые пластинки на голове).

subconical. Postclypeus broad, widest before antennae, shallowly convex, with faint muscle striations, occupying most of face and reaching head apex, but not extended onto crown. Anteclypeus narrow triangular, 0.6x as long as pronotum medially. Rostrum short and wide, shorter than antenna, not reaching apices of middle coxae, seemingly two-segmented, widest beyond midlength of first segment; first segment (probably undivided 1+2nd) pear-shaped, twice as long as barrel-shaped terminal (3rd?) segment.

Pronotum width 2.6x its sublateral length (within paranotum); paranota subtriangular, their outer margin convex, anterior margin concave around eye and strengthened with sclerotized rib. Fore and hind wingpads nearly equal, oblique quadrangular, covered (as well as prothoracic paranota) with

coarse oblique reticulated wrinkles; metanotum transversely rugose near posterior margin. Mesosternal furca small, slender, on short stalk. Legs very short, stout, all pairs subequal and similar in their structure and armature; hind coxae not enlarged, hind tibiae not elongated. Fore and middle femora narrowed apically, shorter than antenna; hind femora with dorsal margin arched, almost as long as antenna. Tibiae shorter than femora, subclavate, curved near base, thickened before apex; outer margin with 6–7 strong dark setae, distal ones in pairs; apical pecten C-shaped, of 8–10 short wide dark teeth (inner strongest) in two irregular rows. Tarsi 2-segmented, 1st segment small triangular, 2nd twice longer than 1st, widened before apex; claws strong, narrow, hooked, diverging at right angle; no pretarsal lobes or setae visible.

Abdomen convex dorsally, arcuate in cross section, concave ventrally (as preserved in exuvium), tapered, with convex lateral margins. Segments II–VI of subequal length, I twice shorter, VII 1.5x longer. Posterior parts of lateral margins of tergites III–VI with dense rows of long (up to 1/3 tergite length), stout, dark setae. Posterior margins of tergites I–II nearly straight, of tergites III–VI concave, of tergite VII strongly convex. Segment VIII twice narrower than VII, preserved drawn into it and only slightly protruding, with two apical lobes, apex of left lobe torn off, as well as greater part of segment IX. Laterotergites directed medially, on segments II–IV nearly meeting, on V–VIII meeting at midline, closing breathing tube.

Complete set of dorsal wax plates, matt silvery in incident light and grey in transmitted light (especially large plates on abdomen), each plate with dark rim (likely edge of wax gland

concealed by unmodified cuticle); small clumps of tangled wax threads visible on some plates. Three plates on crown: large, rounded subtriangular median plate subequal to postclypeus and superimposed on it, but wider posteriorly and shorter anteriorly (not reaching head apex); pair of adjacent smaller plates, obliquely elongated, laterally superimposed on medial parts of eyes. Pair of concave plates on each thoracic notum, obliquely elongated, superimposed on coxae, but smaller. Plate on distal part of flattened dorsal side of each femur and tibia. Pair of depressed plates in lateral thirds of abdominal tergites II–VII: plates of tergites III–V rounded quadrangular, large, subequal to tergite length, anteriorly covered by preceding tergite; plates of tergite VI twice smaller, in its anterior half; plate of tergite V at its posterolateral corner with small subtriangular accessory plate, separated by narrow cuticular bridge; plates of tergites II and VII very small, rounded, subequal to scape diameter,



Figs 4–7. *Aidanympha thompsoni* Shcherbakov, **gen. et sp.n.**, holotype nymphal exuvium, dorsal (4, 7) and ventral view: 4 — right antenna and eye; 5 — left side of thorax with legs (white arrows, wax plates on legs and thoracic notum); 6 — rostrum; 7 — abdomen (short white arrows, wax plates on right side; long arrows, accessory wax plates on tergite V; blue arrows, anomalies in wax plate arrangement on left side; black arrows, laterotergites).

Рис. 4–7. *Aidanympha thompsoni* Shcherbakov, **gen. et sp.n.**, голотип, экзuvий нимфы, вид сверху (4, 7) и снизу; 4 — правые усик и глаз; 5 — левая сторона груди и ноги (белые стрелки, восковые пластинки на ногах и грудных нотах); 6 — хоботок; 7 — брюшко (короткие белые стрелки, восковые пластинки на правой стороне; длинные стрелки, добавочные восковые пластинки на тергит V; голубые стрелки, аномалии в расположении восковых пластинок левой стороны; черные стрелки, латеротергиты).

on tergite II concealed by posterior margin of hind wingpad, on tergite VII in basal third. This pattern is observed on the right side of the abdomen, while on the left side there are some anomalies: plate on tergite II absent; small additional plate medial to large plate on tergite IV; accessory plate of tergite V oblong, shifted medially; two very small plates instead of one on tergite VII, proximal one connected to plate of tergite VI by subcuticular structure (both tergites IV and VII with three plates). Total number of plates 36 (should be 35 in normal specimens).

ETYMOLOGY. Named after spittlebug expert Dr. Vinton Thompson.

Discussion

Four extinct families are classified within Cercopoidea: Procercopidae, Cercopionidae, Sinoalidae, and Myanmalidae. Three of them are known from Burmese amber. The fourth, monotypic family Cercopionidae, based on a single specimen from the Lower Cretaceous (Upper Aptian) Crato Formation of Brazil, was described as differing from other cercopoids in the structure of the head and hind wing [Hamilton, 1990]. Later, a second specimen from the same beds, very similar to the first in structure and size (body with folded tegmina ~11 mm long), but more completely preserved, was assigned to this family [Menon *et al.*, 2007, fig. 11.43e]. In the elongate tegmen, narrowly rounded apically, with the costal margin shallowly convex near the base, costal space narrow, and venation reticulate distally, in the very elongated hind legs with the tibia slender, half the length of the body, 1st tarsomere weakly flared, and 2nd not flared apically (second specimen), as well as in the head and hind wing structure, *Cercopion reticulata* Hamilton, 1990 fits the megadiverse family Cicadellidae (superfamily Membracoidea). This genus and species may belong to the tribe Proconiini of the subfamily Cicadellinae or to an extinct group within the family Cicadellidae. Therefore, a new synonymy is proposed: Cicadellidae Latreille, 1802 = Cercopionidae Hamilton, 1990, **syn.n.**

The monotypic family Myanmalidae, recently described from Burmese amber [Chen *et al.*, 2026a], was erroneously placed in Cercopoidea. In the spatulate head with two close-set ocelli, narrow postclypeus, shape of pronotum, venation of tegmen and hind wing, and the structure of hind legs, including transversely enlarged hind coxae, *Myanmala zireni* Chen, 2026 corresponds to the extant subfamily Ledorinae of the family Cicadellidae. Ledorinae is a primitive and the oldest known extant leafhopper subfamily, recorded since the Early Cretaceous (Late Aptian) [Hamilton, 1983; Shcherbakov, 1992, 2025] and represented in Burmite by two specimens belonging to two endemic genera [Chen *et al.*, 2019a, 2021]. Therefore, a new synonymy is proposed: Ledorinae Fairmaire, 1855 = Myanmalidae Chen, 2026, **syn.n.**

The large and widespread Mesozoic family Procercopidae, very rare in Burmite (known from only two specimens belonging to two endemic genera) [Fu *et al.*, 2020], is quite similar to modern cercopoids, especially Aphrophoridae, so procercopid nymphs may have resembled those of living froghoppers.

The family Sinoalidae, known from the Middle Jurassic to the mid-Cretaceous, comprises 32 species in 21 genera, classified into two subfamilies and four tribes. Half of this diversity is known from the Jurassic of China (Callovian of Daohugou), the other half from Burmese amber [Chen *et al.*, 2023, 2026b; Paleobiology Database, 2026]. In most sinoalids, the anterior head margin is smoothly rounded or triangularly produced, except for the monotypic Burmese amber genus *Fangyuania* showing a broadly pentagonal head with foliaceous margins, closely resembling that of the new nymph.

The holotype of *Aidanympa thompsoni* **sp.n.** is considered to be a middle (II or III) instar due to its two-segmented tarsi and the fore wingpads equal to hind wingpads. If this nymph, with the body 4.3 mm long, is the III instar nymph, then the V instar would be about 8.4 mm long, and the adult over 10 mm long, since each subsequent instar is approximately 1.4x larger than preceding one [Emeljanov, Shcherbakov, 2018]. *Fangyuania xiai* Chen, Szwedó *et al.*, 2018 has the body length with folded tegmina of only 7.2–7.8 mm [Chen *et al.*, 2018, 2019b]. Most other Burmite sinoalids have similar or smaller sizes (5.3–7.4 mm long), except for *Shuixiua yuchena* Chen *et al.*, 2026 (9.6 mm long), *Makrosala venusta* Chen *et al.*, 2020 (~12 mm) and *M. elegans* Chen *et al.*, 2020 (14.5 mm) [Chen *et al.*, 2020]. This means that *Aidanympa* **gen.n.** corresponds to adults of some other genus of Sinoalidae with larger body sizes, possibly *Makrosala* Chen *et al.*, 2020. The head shape of *Aidanympa* **gen.n.** differs from that of adults of *Makrosala* spp. — parabolic with small angles just before eyes (such head shape is found also in some other genera, e.g. *Paraornatialis* Fu *et al.*, 2019). However, it is quite possible that the head shape was different in sinoalid adults and nymphs due to differences in their lifestyles, as in some leaf- and treehoppers with cryptic (sub)oniscoid nymphs (e.g. Stenocotini, some Ledorini, Nicomiinae): spatulate, sometimes subquadrangular or pentagonal heads of nymphs, in contrast to short, rounded or triangular heads of adults. In this case, *Fangyuania* represents a rare instance of the nymphal head shape retained in adult Sinoalidae (among Ledorinae, spatulate heads in adults are quite common).

Aidanympa **gen.n.** has a well-developed breathing tube, formed by abdominal laterotergites directed medially and meeting along the midline, which indicates that these nymphs produced foam. Small eyes, outstretched rugose prothoracic paranota and wingpads, powerful legs with hooked claws, strong tibial pectens (in a non-jumping nymph), and stiff setae on the outer side of all tibiae, as well as along the sides of the abdomen, suggest that this creature lived in narrow, confined spaces on host plants, such as leaf axils, stem folds, deep crevices between cone scales, etc., and could anchor itself to or between the walls of its shelter. When reconstructing this lifestyle for the new nymph, we should explain the presence of numerous wax plates on its dorsal side. Among modern spittlebugs, the highest number of wax plates (three pairs instead of two) is characteristic of nymphs of Machaerotidae, which spend most of their lives in

narrow tubes head downwards immersed in excreted liquid. However, to moult, they exit their tubes and build temporary foam nests. By analogy, we hypothesize that sinoalid nymphs moulted outside their deep retreats — on the surface of host plants — and that the secretions from the numerous wax plates enabled them to rapidly construct a foam nest and protected them against adverse factors such as heat, intense light, desiccation, and adhesion to the host plant's resin or gum. The holotype cast skin could have been carried by the wind from the moulting site into the resin in the Burmese amber forest.

Most modern cercopoids live on stems or roots, though some feed on gymnosperm cones or angiosperm inflorescences [Bales, Furniss, 1984; Pramanik, Liang, 2020]. Two species of the Neotropical genus *Mahanarva* Distant, 1909 often inhabit water-filled flower bracts of *Heliconia* spp. and are the only Auchenorrhyncha that are aquatic (although facultatively) [Fish, 1977; Thompson, 1997]. In nymphs of these and certain other Cercopidae, abdominal segments VIII and IX are conspicuously narrowed, and the posterior margin of tergite VII is convex [Foieri *et al.*, 2016], just as in the new genus.

The wax plates of *Aidanympa* **gen.n.** look exactly the same as the wax plates of planthopper nymphs preserved in amber, e.g., like the medial plates on tergites VI–VIII of *Alicodoxa* Emeljanov et Shcherbakov, 2011 (Dictyopharidae) from Eocene Rovno amber [Emeljanov et Shcherbakov, 2011, figs 1, 3]. The structure of the wax plates on the head and fifth tergite of the new nymph — with closely adjacent plates separated by narrow cuticular bridges — is reminiscent of the condition in nymphs of some Fulgoroidea (e.g. Cixiidae, Fulgoridae, Dictyopharidae), in which the wax plates are subdivided into parts by similar cuticular bridges [Emeljanov, 2009].

The presence of wax plates on the head, thorax and legs in the new genus is of outstanding interest. Wax-secreting areas are found all over the dorsal body surface in many nymphal and nymph-like adult Sternorrhyncha (aphids, coccids, whiteflies). However, in Auchenorrhyncha, namely frog hopper and planthopper nymphs, wax production is concentrated on the rear, and specialized wax plates are developed only on the posterior abdominal tergites. A rare exception is the Burmite adult (female) *Inoderbe* Shcherbakov et Emeljanov, 2021 from the extinct planthopper family Inoderbidae, which possesses numerous wax plates on the thorax and abdomen, as well as wax filaments on the legs and other appendages [Shcherbakov, Emeljanov, 2021]. The new nymph is another, even more remarkable exception. Wax-secreting areas over the entire dorsum were probably characteristic of at least some oniscoid nymphs among basal Hemiptera and primitive Cicadomorpha.

In conclusion, it can be said that Sinoalidae are very primitive and unusual cercopoids, and the discovery of their nymphs only emphasizes their uniqueness. Spittlebugs evolved two primary defensive adaptations: the foam nests in nymphs and the unsurpassed jumping ability in adults [Thompson, 2026]. *Aidanympa* **gen.n.** indicates that spittle production was already present in sinoalid nymphs, however, unlike the relatively short

and robust adult hind legs of modern frog hopper families, the hind legs of Sinoalidae were quite long and very slender, although they bore the characteristic cercopoid armature. Apparently, the jumping mechanism of sinoalids was either not yet as advanced as that of present-day spittlebugs, or its efficiency was somewhat reduced due to unknown aspects of the adult's lifestyle.

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