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THE LONGEST-NOSED MESOZOIC FULGOROIDEA (HOMOPTERA): A NEW FAMILY FROM MID-CRETACEOUS BURMESE AMBER

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Summary. *Dorytocus ornithorhynchus* **gen. et sp. n.**, based on nymphs of three different instars from mid-Cretaceous Burmese amber, represents a new family Dorytocidae **fam. n.**, which is similar to Cretaceous Perforissidae in the unique structure of the pronotum and abdominal segments IX and X, but differs from it in the presence of a long (especially in late instars) head process, long rostrum, flattened fore and mid tibiae, asetigerous hind tibial pecten, and highly carinate abdomen. Structural features and relative abundance of Dorytocidae **fam. n.** imply that they dwelt on the bark of amber-producing trees. The new genus is the longest-snouted Mesozoic planthopper known so far – its slender head process is one-quarter as long as the body in the last instar nymph, and more than one-third as long in the adult (known to us from photos). These hoppers were likely thorn mimics, and their elaborate crypsis protected them from increased visual predation during the rise of modern-type birds in the mid-Cretaceous.

Key words: planthoppers, Perforissidae, Mimarachnidae, Neazoniidae, nymphs, adult, fossil, crypsis, birds, visual predation.

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Резюме. *Dorytocus ornithorhynchus* **gen. et sp. n.** описан по личинкам трех различных возрастов из средне мелового бирманского янтаря и выделен в семейство Dorytocidae **fam. n.** Новое семейство сходно с меловыми Perforissidae по уникальному строению переднеспинки и IX–X сегментов брюшка, отличаясь развитым головным отростком (очень длинным на старших возрастах), уплощенными передними и средними голенями, отсутствием субапикальных щетинок на вершинных зубцах задних голеней и сильным развитием килей на брюшке. Строение и сравнительная многочисленность доритоцид позволяют предполагать, что они обитали на коре янтароносных деревьев. Новый род – самый длинноносый среди известных в мезозое фулгороидов, его головной отросток составляет четверть длины тела у личинки последнего возраста и более трети у имаго (известного нам по фото). Криптический облик доритокусов, выглядевших как колючки на ветке, мог скрыть их от зорких хищников вроде птиц современного типа, появившихся в середине мела.

INTRODUCTION

Several fossil fulgoroid families have been described from the Cretaceous: Lalacidae (Hamilton, 1990), Neazoniidae (Szwedo, 2007), Perforissidae (Shcherbakov, 2007a) and Mimarachnidae (Shcherbakov, 2007b). Lalacids are known, as adult stages, exclusively from rock fossils, while the other families (including mimarachnids; Shcherbakov, 2017) are also known from amber (perforissids as adults and early instar nymphs, neazoniids as nymphs, mimarachnids as adults). In some characters these families are more primitive than the extant planthopper families. Another peculiar fulgoroid family found in mid-Cretaceous Burmese amber is described below.

The Burmese amber contains the richest insect fauna including 284 families, 449 genera, and 524 species already described (Ross, 2017). It is collected from mines in the Hukawng Valley, Kachin State, Myanmar. The amber-containing rock has been dated early Cenomanian (Shi *et al.*, 2012), however, an ammonite of the Albian genus *Mortoniceras* Meek, 1876 was found in the sandstone above the amber layer (Cruickshank & Ko, 2003). The amber was formed at a low paleolatitude (~12°N) under wet tropical conditions (Grimaldi & Ross, 2017). The Burmese amber tree was similar to *Agathis* (Araucariaceae), and the amber forest was a tropical-subtropical rainforest resembling the kauri forest in Northern New Zealand (Poinar *et al.*, 2007; Poinar & Buckley, 2008).

The type material is deposited in A. A. Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera and processed with Helicon Focus 5.1.

DESCRIPTIONS OF NEW TAXA

Order Homoptera

Suborder Auchenorrhyncha

Infraorder Fulgoromorpha

Superfamily Fulgoroidea Latreille, 1807

Family Dorytocidae Emeljanov et Shcherbakov, fam. n.

Type genus: *Dorytocus* Emeljanov et Shcherbakov, gen. n.

DIAGNOSIS. Small planthoppers. Eumetope without intermediate carinae (for planthopper cranium nomenclature, see Anufriev & Emeljanov, 1988; Emeljanov, 1996, 2001). Rostrum long. Pronotum inverted V-shaped, its disc much displaced anteriorly and deeply incised posteriorly. Legs slender; hind tibia without lateral teeth, with asetigerous apical pecten; hind tarsal pectens setigerous. In nymphs: median carina of pronotum double; lateral carinae of mesonotal disc running along posterior pronotal margin; disc of meso- and metanotum with sensory pits; fore and mid tibia foliaceous; dorsum of abdomen carinate, without wax-pore plates, with long segments IX and X not retracted between lateral lobes of segment VIII.

COMPOSITION. Type genus.

REMARKS. In many characters similar to Cretaceous Perforissidae, being distinct in the longer legs and rostrum, asetigerous hind tibial pecten, at nymphal stage in the carinate dorsum of abdomen and foliaceous tibiae, and in the elongated head of the type (and only known) genus. In Perforissidae the head, rostrum and legs are short, tibiae not foliaceous, the hind tibial pecten is setigerous; in perforissid nymphs the median carina of pronotum is single, and the dorsum of abdomen ecarinate. The abdominal segments IX–X are well developed, not retracted between lateral lobes of the segment VIII in nymphs of Perforissidae and Dorytocidae fam. n., whereas in nymphs of other fulgoroid families the segment X is reduced or absent, and the segment IX is often retracted.

Genus *Dorytocus* Emeljanov et Shcherbakov, gen. n.

Type species *Dorytocus ornithorhynchus* Emeljanov et Shcherbakov, sp. n.

DIAGNOSIS. Head with long process, especially at late instars. Coryphe narrow triangular, distally tapered up to double carina. Lateral areas of head process (halves of acrometope – on homology, see Discussion) faced laterodorsally.

COMPOSITION. Type species.

REMARKS. The head is produced into a long process in some genera of many extant planthopper families, but such elongation is never characteristic of all genera of any family.

ETYMOLOGY. From the Greek *dory* (spear) and *tocos* (offspring); gender masculine.

***Dorytocus ornithorhynchus* Emeljanov et Shcherbakov, sp. n.**

Figs 1–22

MATERIAL. Holotype PIN 5608/3, nymph of supposed instar V (right hind leg broken off distal to mid-tibia); paratypes PIN, nymphs: 5608/4, supposed instar III (translucent, eyes transparent, but not exuvium; abdomen telescoped and upcurved, tergite I hidden under metanotum, apex of abdomen polished away; right side adjacent to a level of debris; gas bubbles on left side), likely sucked out by a spider or predatory bug; 5608/5, supposed instar II — Burmese amber, Hukawng Valley, Kachin State, Myanmar; mid-Cretaceous, Albian–Cenomanian.

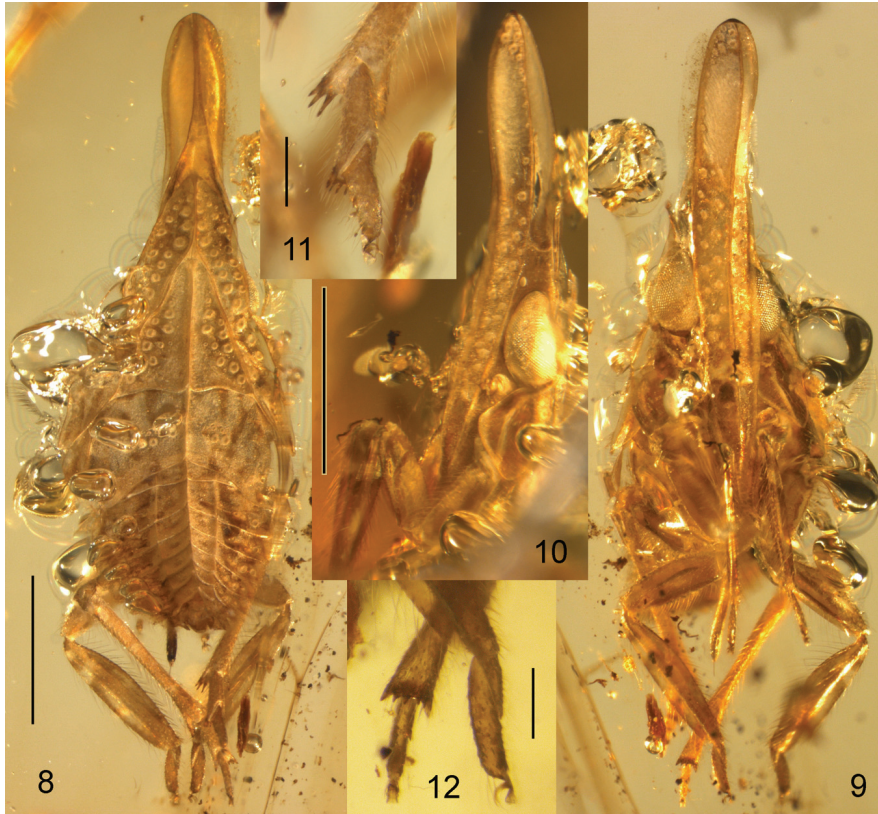


Figs 1–7. *Dorytocus ornithorhynchus* sp. n., holotype instar V nymph: 1 – dorsal view; 2 – ventral view; 3 – head, ventrolateral view; 4 – end of abdomen and distal part of hind leg, dorsal view; 5 – distal part of hind leg, ventral view; 6 – fore and mid leg; 7 – hind tarsus, laterodorsal view. Scale bars, 1 mm (1–3), 0.5 mm (4–6), and 0.2 mm (7).

DESCRIPTION. Nymphs. Rather slender, resembling long-headed Dictyopharinae such as *Dictyophara (Chanithus) pannonica* (Germar, 1830), *Scolops* Schaum, 1850 etc.

All nymphal instars (based on supposed V, III and II instar). Head produced into anteriorly directed process (degree of elongation, shape of head process and some

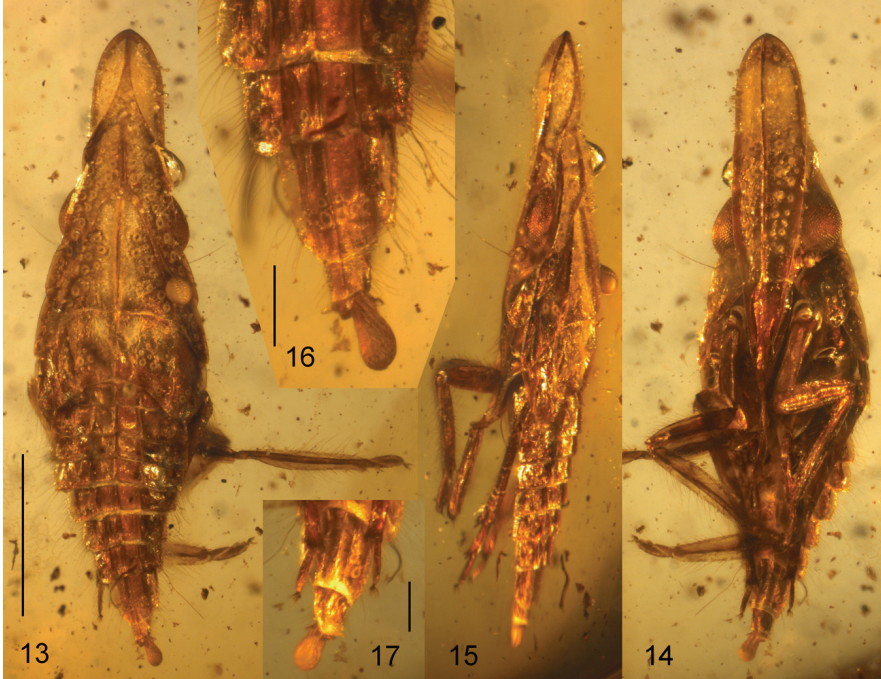
other characters change with instar – see below). Coryphe arrowhead shaped, basally triangular, distally tapered up to narrow stripe separating lateral areas of head process (halves of acrometope) that are faced laterodorsally and nearly meet along midline. Lateral area at base separated from preocular area by carina. Coryphe depressed towards median line, V-shaped in cross-section, with vestigial Y- or T-shaped carina in basal part. Carina between eumetope and lateral areas forming apical callus at head apex. Eumetope parabolic rounded at apex, widest anterior to



Figs 8–12. *Dorytocus ornithorhynchus* sp. n., paratype instar III nymph: 8 – dorsal view; 9 – ventral view; 10 – head and prothorax, lateral view; 11 – distal part of hind leg, dorsolateral view; 12 – mid and hind tarsus. Scale bars, 1 mm (8–10) and 0.2 mm (11–12).

eye, with simple median carina, without intermediate carinae (represented only by lateral areas with sensory pits). Eumetope in profile shallowly concave anterior to eyes and convex distally, in cross-section tectiform, especially towards apex; head process distally diamond-shaped in cross-section. Boundary of eumetope and postclypeus (epistomal suture) nearly straight. Postclypeus with carinae as sharp as on eumetope, slightly tapered apically, about twice as long as wide. Anteclypeus

elongate, about as long as postclypeus. Rostrum long, slender, dark and acuminate at apex, reaching at least abdominal segment VII; apex of middle segment far beyond mid coxae. Eys not much projecting laterally, mostly concealed by pronotum from above. Antennae small; pedicel twice longer than scape.



Figs 13–17. *Dorytocus ornithorhynchus* sp. n., paratype instar II nymph: 13 – dorsal view; 14 – ventral view; 15 – lateral view; 16 – end of abdomen, dorsal view; 17 – end of abdomen and hind tarsi, ventral view. Scale bars, 1 mm (13–15) and 0.2 mm (16–17).

Pronotum inverted V-shaped in dorsal view. Disc of pronotum produced forwards up to level much anterior to eyes, forming angulate pronotal ledge to conceal posterior margin of coryphe. Pronotum bounded anteriorly with jugal carina. [In nymphs, this “primary carina of pronotal dorsum” was termed either lateral (Yang & Yeh, 1994) or jugal (Emeljanov, 2001). The former term is inappropriate, because this carina is rather oblique-transverse, not developed as a whole in adults, and does not fit into accepted nomenclature of adult pronotal carinae, including the version proposed and corrected by Emeljanov (1980, 1996). In nymphs of many families, the jugal carina is developed as integral carina uniting the anterior carina of disc, postocular carina, and main portion of the adult lateral carina.] Lateral margin of pronotal dorsum sinuate above eye. Posterior angles of pronotum reaching beyond midlength of mesonotal disc. Posterior margin of pronotum deeply angulately incised, incision reaching level of anterior orbitae or nearly so and occupying more than half of pronotal length.

Median carina of pronotum double. Pronotal paranota more or less rhomboidal, with horizontal and vertical carinae, the latter joining lower margin before posterior angle of pronotum. Disc of mesonotum for most of its length embraced between paradiscal parts of pronotum; median and lateral carinae of mesonotal disc sharp; lateral carinae of the disc running along margins of pronotal incision, continuing their direction caudally, and continued with inner margins of forewing pads; posterior margin of mesonotal disc transverse, wavy. Metanotum sinuate posteriorly, with sharp median carina.

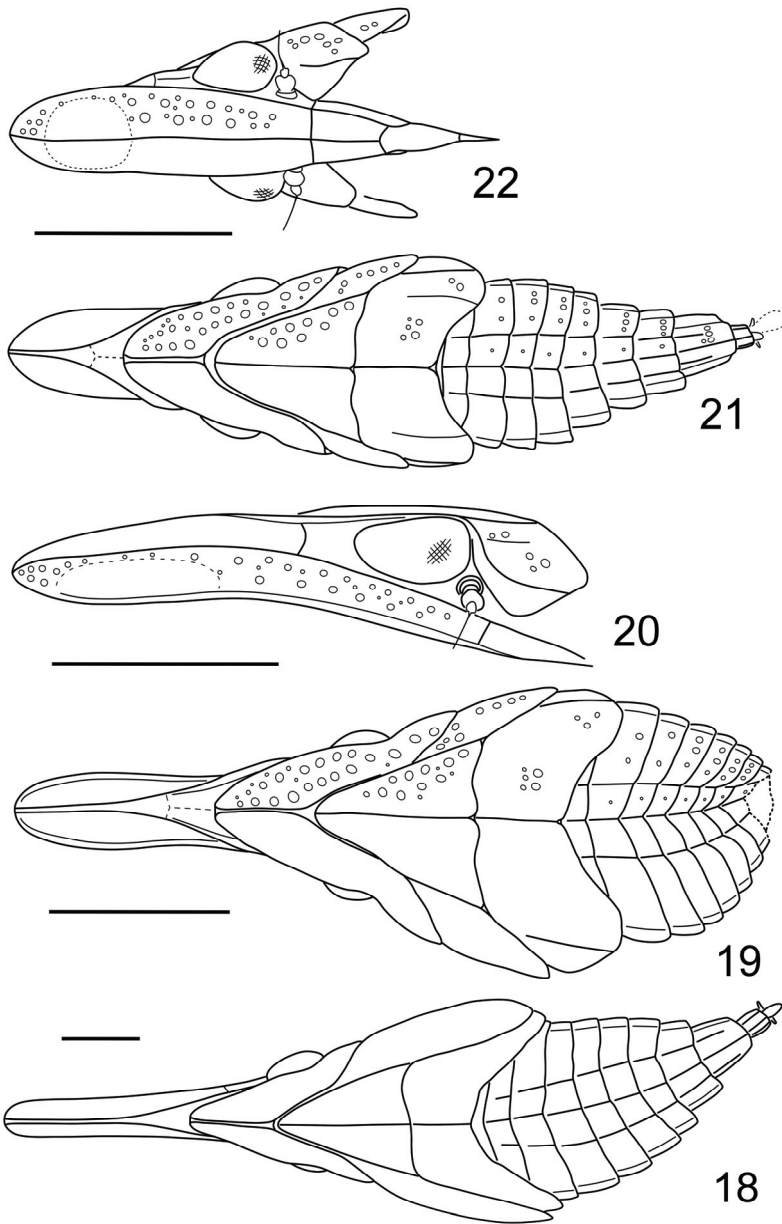
Legs rather slender. Fore and mid tibiae flattened, with foliaceous dorsal (outer) and ventral (inner) edges. Hind tibiae thin, terete, without lateral teeth; apical pecten aseptigerous, i.e. without subapical setae on dorsal sides of apical teeth, but with long setae on plantar surface. Fore and mid tarsi 2-segmented, with 2nd tarsomere twice longer than 1st. Hind tarsus 3-segmented (instar V) or 2-segmented, in instar III with lateral teeth on apical tarsomere. Pretarsus with powerful, curved claws and relatively narrow, pear-shaped arolium.

Abdomen from segment IV gradually tapered posteriorly. Very short tergite I and shortened tergite II not reaching lateral margins of abdomen; slightly elongated tergite III longer than each of subequal tergites IV–VI; elongate tergites IX and X not retracted between lateral lobes of tergite VIII. Tergites II–X with sharp median and intermediate carinae; tergites III–X with lateral carinae, on III–IX foliaceous. Laterotergites faced ventrally. Segment IX longer than VIII or X. Segment X longer than wide, at apex with long tongue-like dorsal sclerite (epiproct) and subtriangular lateral sclerites (paraprocts), sometimes (instar II paratype) with everted rectum.

Sensory pits (based mainly on the paratypes, III and II instar; less well preserved pits in the holotype instar V conform the pattern; the description is given for one side only). Eumetope at each side with 2 longitudinal rows, lateral and median; pits of lateral row smaller than those of inner row and generally alternating with them; between eyes additional intermediate row of minute pits; few minute extraserial pits. Pronotum dorsally with 2 somewhat irregular, oblique longitudinal rows of pits varying in size, 12 pits in posterior (inner) row, 8 in anterior (outer) row; 4 posteriormost pits without counterparts in anterior row; several minute extraserial pits anteriorly and posteriorly. Disc of mesonotum with two pit rows medial to laterodiscal carina (5 pits along carina and 5 medial to former row); paradiscal area with 2–4 pits; forewing pad with 4 pits. Metanotum with group of 5 pits (3 small in anterior row and 2 large posteriorly) in discal area and 2–3 pits on hind wing pad. Abdominal tergites III–VIII with 1 minute medial pit, 1 small intermediate pit, and 2 or 1 lateral pits (smaller outer pit absent on tergite III and sometimes on tergite IV); tergite IX with 3 pits and 1 small pit anterior to inner pit.

Lateral carinae of postclypeus, carinae of coxae, femora, tibiae and tarsi, and lateral carinae of abdomen with long hairs.

Nymphal instars differ in proportions, head shape, degree of tibia flattening, hind leg armature, number of tarsomeres etc. Each next instar is ca. 1.4 times longer than the preceding one, which is consistent with the assumption that all the studied instars are conspecific.



Figs 18–22. *Dorytocus ornithorhynchus* sp. n.: 18 – holotype instar V nymph, body, dorsal view; 19–20 – paratype instar III nymph: 19 – body, dorsal view; 20 – head and pronotum, lateral view; 21–22 – paratype instar II nymph: 21 – body, dorsal view; 22 – head, pro- and mesonotum, ventral view. Scale bars, 1 mm.

Instar V. Head process nearly straight and parallel-sided, very narrow, $\times 6.5$ as long as wide, $1/4$ of body length and 0.85 of thorax length. Eumetope without pale oval area, in apical $1/4$ darker and without discernible pits except near apex. Thorax $\times 1.9$ as wide as head. Fore- and hind wing pads acuminate, almost reaching posterior margin of abdominal tergite III; metanotum without laterodiscal carinae. Fore and mid tibia foliaceous (thrice as wide as middle part of hind tibia), fore lanceolate, mid nearly so, dorsal edge with long, ventral edge with long and distally with shorter, stronger setae, 3–4 of which grouped comb-like at apex anteroventrally. Hind tibial pecten of 6 asetigerous teeth, 3 in medial and 3 in lateral group. Hind tarsus 3-segmented; 1st tarsal pecten of 8 setigerous teeth, 2nd of 6 setigerous teeth. Claws with 3 setae in basal third. Abdomen widest at segment III. Bilobed genital rudiment beyond posterior margin of sternite VIII. Segment IX about as long as wide, much longer than VIII, slightly tapered distally. Segment X slightly longer than wide, as long as VIII, twice narrower than IX. Cuticle dark, mottled with pale. Body 10.5 mm long.

Instars II–III. Coryphe in profile straight basally and convex distally. Eumetope before head apex with pale oval area devoid of sensory pits; pits near head apex smaller and denser. Cuticle pale with dark markings, including dark streaks on thoracic nota, abdominal tergites, and flattened tibiae. Dorsum with fine cover of microscopic wax particles.

Instar III. Head process widest about midlength, slightly constricted near base, rather narrow, $\times 2.5$ as long as wide, about $1/5$ of body length and 0.6 of thorax length. Thorax $\times 1.6$ as wide as head. Forewing pads reaching midlength of metanotum, hind wing pads poorly projecting backwards; metanotum without laterodiscal carinae. Fore and mid tibiae as in instar V — foliaceous (thrice as wide as middle part of hind tibia), lanceolate, with short setae grouped comb-like at apex. Hind tibial pecten of 6 asetigerous teeth: 3 long inner, 1 long outer, and 2 shorter in between. Hind tarsus 2-segmented. 1st tarsal pecten of 6 teeth, with narrow diastema, teeth (possibly except for outermost) with long subapical seta. 2nd tarsomere about midlength with a pair of teeth at sides, inner (posterior) tooth double. [Taking into account the presence of subapical setae, this pattern corresponds to instar III in the tribe Ranissini (Dictyopharidae Orgeriinae); all the same in Dictyopharinae, but their nymphs have no subapical setae (Emeljanov, 1995, 2001).] Claws with 1 seta in basal third. Abdomen widest at segment III. Body 4.2 mm long as preserved; reconstructed body length (based on head+thorax length) ca. 5.3 mm.

Instar II. Head process widest at base, tapered towards apex, short, $\times 1.4$ as long as wide, $1/8$ of body length and 0.37 of thorax length. Thorax $\times 1.4$ as wide as head. Forewing pads not reaching midlength of metanotum, hind wing pads poorly projecting backwards; metanotum with faint laterodiscal carinae. Fore and mid tibiae less flattened than in instar III (twice as wide as middle part of hind tibia). Hind tibial pecten of 6 asetigerous teeth. Hind tarsus two-segmented; 1st tarsomere large, wider and longer than 2nd, with pecten of 6 setigerous teeth (setae not visible on two inner teeth); apical tarsomere terete, without lateral teeth marking apex of future middle tarsomere. Claws without setae, less curved than in instar III. Abdomen widest at segment IV. Body 3.8 mm long.

REMARKS. From one of amber dealers, several photographs of an adult were obtained, probably the same species. Habitually somewhat similar to leafhoppers *Adelungia* Melichar, 1902 (Cicadellidae Adelungiinae). Head process very long, constituting more than 1/3 of the body length (with wings), ensiform, acuminate, deflected dorsally. Pronotum inverted V-shaped, with deep triangular incision posteriorly. Tegmina leathery, as long as the head process, not much projecting beyond the apex of abdomen; (SC+)R forked basally, CuA forked before wing mid-length, M much later. Legs slender. Body mottled with dark. About 20 mm long.

ETYMOLOGY. From the Greek *ornis* (bird) and *rhynchos* (snout); alluding to the head process as in the duckbill).

DISCUSSION

Systematic position of the new family

Plesiomorphies of Dorytocidae **fam. n.**:

1. Eumetope with primary median carina and, respectively, without median area(s), like e.g. in Cixiidae, many Delphacidae, and Perforissidae.

2. Hind tibia without lateral teeth.

3. Hind tarsal pectens setigerous.

In nymphs:

4. Sensory pits on disc of meso- and metanotum, like in Delphacidae, Cixiidae, Meenoplidae (nymphs of Kinnaridae remain undescribed), some Derbidae, Perforissidae and Neazoniidae.

5. Well-developed, elongate abdominal segments IX and X, like in Perforissidae (not retracted between lateral lobes of segment VIII as in other Fulgoroidea).

6. Abdomen without wax-pore plates, like in Delphacidae and nymphs of Meenoplidae, Perforissidae and Neazoniidae.

7. Sensory pits in median area of abdomen, like in some Delphacidae (*Achorotile* Fieber, 1866 – Emeljanov, 1996).

Apomorphies of Dorytocidae **fam. n.**:

1. Pronotum inverted V-shaped, its disc much displaced anteriorly and deeply incised posteriorly, like in Perforissidae and nymphs of some Derbidae (*Losbanosia* Muir, 1917; *Parapeggia* Yang et Wu, 1994 – Yang & Yeh, 1994).

In nymphs:

2. Lateral carinae of mesonotal disc running along posterior pronotal margin, like in Perforissidae.

3. Fore and mid tibia foliaceous (help masking shadow in hoppers living on plants).

4. Median pronotal carina doubled (like in Neazoniidae; retention of nymphal condition — see Kennedy & Bartlett, 2015).

Apomorphy of *Dorytocus* **gen. n.**:

1. Head with long process, its lateral areas visible from above, and narrow arrow-head shaped coryphe, not unlike some Delphacidae (see Fennah, 1964; Asche, 1985; Bartlett, 2010) and Fulgoridae (e.g. *Capenopsis minos* Fennah, 1962; Strongylodematinae belong to Fulgoridae – Emeljanov, 1979, 2007).

In above-mentioned plesiomorphies 1–6 and apomorphies 1 and 2, Dorytocidae are similar to Cretaceous Perforissidae (Shcherbakov, 2007a), and in some of these characters also to Cretaceous Neazoniidae known only from nymphs (Szwedo, 2007, 2009). Possibly Dorytocidae retained nymphal sensory pits at the adult stage (we cannot ascertain this from available photographs), like Perforissidae and some other Fulgoroidea.

Dorytocidae are similar to Perforissidae in many characters, including unique structure of their pro- and mesonotum (apomorphies 1–2), so we suggest that their head carinae followed the same pattern, and homologize elongate lateral areas of the head process in *Dorytocus* gen. n. with the halves of acrometope separated with the very narrow apex of coryphe. An intermediate configuration of the head carinae is found e.g. in *Burmissus* Shcherbakov, 2017 (Mimarachnidae): the head is short like in perforissids, but unlike the latter the acrometope is shaped not as a continuous narrow stripe, but as a pair of elongate triangular areolets (trigons, that correspond to lateral areas of *Dorytocus*) with touching apices. The pattern of head carinae with two contiguous trigons visible from above occurs also in some Cixiidae (e.g. *Cixiosoma* Berg, 1879; head short), Achilidae (e.g. *Parargeleusa* Fennah, 1950; head short), Dictyopharidae (e.g. *Cleotyche* Emeljanov, 1997; head slightly elongate), and Delphacidae (e.g. *Tumidagena* McDermott, 1952; head elongate). It is modified in *Dorytocus* due to an extreme elongation of the head and distal narrowing of the coryphe.

Therefore we consider Dorytocidae as descendants of Perforissidae, and the superficial resemblance of the new family to some Delphacidae, Dictyopharidae, and Fulgoridae as an evolutionary parallelism. In turn, Perforissidae have been hypothesized to be neotenous descendants of the Jurassic Fulgoridiidae, both families belonging to the pre-cixioid group (Shcherbakov, 2007a). Apparently, Dorytocidae also fit into this group, being somewhat more derived than Perforissidae in having asetigerous tibial pectens and a ‘modern-looking’ snout.

Biology

The foliaceous fore and mid tibiae and edges of the abdomen of dorytocid nymphs, their long rostra, and dark-mottled, cryptic colouration, as well as their abundance in Burmese amber, are consistent with the assumption that Dorytocidae were corticolous and dwelt on the bark of amber-producing trees. The extremely long and slender rostra are common among Mesozoic Auchenorrhyncha indicating that feeding on trees with thick and rough bark was then more widespread than in recent biota (e.g. in Palaeontinidae, Tettigarctidae, Fulgoridiidae, Mimarachnidae – Shcherbakov & Popov, 2002; Shcherbakov, 2017).

So far, an elongated head was recorded among Mesozoic planthoppers only in some mid-Cretaceous adult Lalacidae: in *Protodelphax rhinion* Hamilton, 1990, the head process is less than 1/10 of the total body length (Hamilton, 1990). The extremely long and slender head process of *Dorytocus* gen. n., constituting a quarter of the total length in the last instar nymph and more than a third in the adult (known to

us from photos), is comparable only to the longest noses of modern lanternflies (Fulgoridae, e.g. *Pyrops* Spinola, 1839 and *Zanna* Kirkaldy, 1902). The new genus is a worthy candidate for *The Guinness Book of Records!*

The shape of this enormous snout suggests that *Dorytocus* gen. n. was a thorn mimic like various treehoppers. Dark-mottled colouration and the carinate dorsum contributed to its cryptic habitus. In the nymphs, the foliaceous tibiae and sides of the abdomen, fringed with setae, eliminated shadows. The camouflage of Dorytocidae appears to be more elaborate than that of the pre-Cretaceous, e.g. Triassic hoppers (Shcherbakov, 2011).

During the Middle to Late Cretaceous biotic crisis (or Cretaceous Terrestrial Revolution: Rasnitsyn, 1988; Zherikhin, 2002; Lloyd *et al.*, 2008; Katz, 2017), angiosperms, herbivorous and social insects, mammals, squamates, and birds (Brusatte *et al.*, 2015) diversified rapidly. Birds, which are among the key visual predators nowadays, had actively preyed on insect galls and mines already by the Turonian (Krassilov, 2008). In the Late Cretaceous, the modern biota started to emerge, and *Dorytocus* gen. n. seems to be a first glimpse of luxurious life of tropics, a predecessor of living lanternflies with their fantastic head processes, such as the alligator-like *Fulgora* Linnaeus, 1767 mimicking arboreal lizards and snakes (Hogue, 1984).

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