

New Dymorphoptilidae (Cicadomorpha) from the end-Permian and Middle Jurassic of Siberia: earliest evidence of acoustic communication in Hemiptera and the latest find of the family

Новые Dymorphoptilidae (Cicadomorpha) из терминальной перми и средней юры Сибири: древнейшее свидетельство акустической коммуникации у Hemiptera и самая поздняя находка семейства

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KEY WORDS: Homoptera, Auchenorrhyncha, Prosboloidea, morphology, stridulation, plastron, mimicry, Permian–Triassic boundary.

КЛЮЧЕВЫЕ СЛОВА: Homoptera, Auchenorrhyncha, Prosboloidea, морфология, стридуляция, мимикрия, пластрон, граница перми и триаса.

ABSTRACT. Two new monotypic genera of Dymorphoptilidae are described. *Unturella truncata* gen. et sp.n. with a preserved stridulatory area from the end-Permian of the Tunguska Basin is the earliest conclusive evidence of acoustic communication in Hemiptera. *Eumorphoptila pritykinae* gen. et sp.n. from the Middle Jurassic (Bathonian) of Kubekovo near Krasnoyarsk is the latest record of the family.

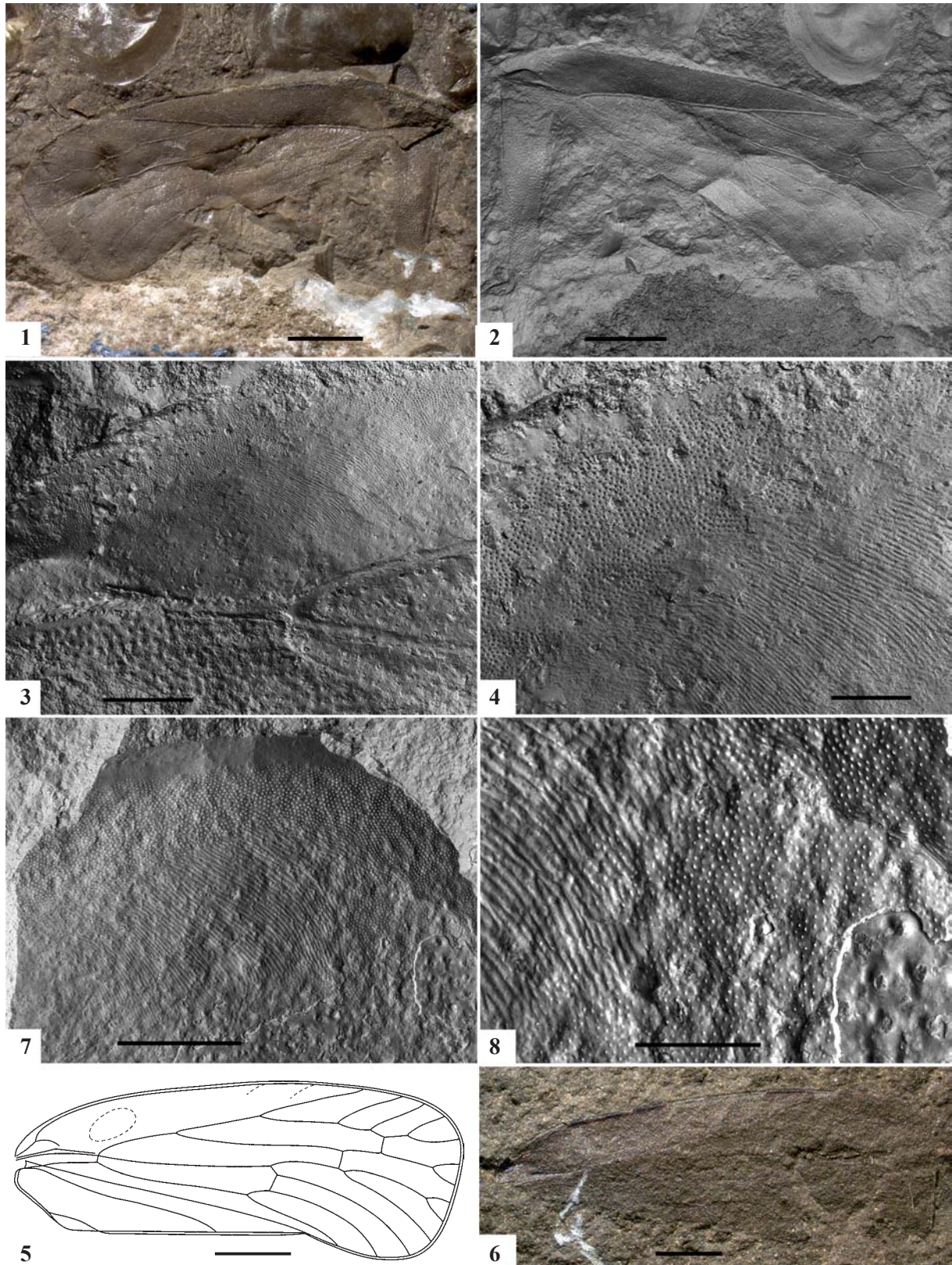
РЕЗЮМЕ. Описаны два новых монотипических рода Dymorphoptilidae. *Unturella truncata* gen. et sp.n. с сохранившимся стридуляционным полем из терминальной перми Тунгусского бассейна — древнейшее неопровержимое свидетельство акустической коммуникации у Hemiptera. *Eumorphoptila pritykinae* gen. et sp.n. из средней юры (бат) Кубеково близ Красноярска — самая поздняя находка семейства.

The family Dymorphoptilidae was established for the genus *Dymorphoptila* Handlirsch, 1906 with the tegmen emarginate (postnodal part produced tongue-like) from the latest Triassic of England [Handlirsch, 1906–1908]. Evans [1956] described another family Eoscarterellidae for Australian Late Triassic genera with tegmina of a less unusual shape, and assigned both families to Cercopoidea. Later he discovered a stridulatory device in Triassic eoscarterellids, with a strigil on the underside of costal area of tegmina [Evans, 1961]. Shcherbakov [1984, 2000] united these families and

Permian Fulgoringruidae and included Dymorphoptilidae s.l. in Prosboloidea. Dymorphoptilids are quite common and diverse in the Triassic, and in the Permian and Jurassic they are represented by only a few genera.

Two new monotypic genera are described below. *Unturella truncata* gen. et sp.n. with a preserved stridulatory area from the end-Permian of the Nizhnyaya Tunguska River basin is the earliest evidence of acoustic communication in Hemiptera. Several specimens were collected in the intertrappean beds traditionally dated to the Early Triassic, although there is growing evidence that at least the lower of these strata lie below the Permian–Triassic boundary (PTB) of the International Stratigraphic Scale [Sadovnikov, 2015]. The paratypes were found at the Khungtukun-2 locality in the Bugarikta Formation (slightly below PTB, ~252 Ma) [Shcherbakov et al., 2021], and the holotype at the Untun-2 locality (about 60 km from the previous locality), which is attributed either to the Bugarikta Formation or the overlying Nidym Formation [Novojilov, 1970], or to the next Kochechumo Formation [Kazakov et al., 2002]. These two localities are considered to be synchronous or nearly so based on the presence of the index fossil conchostracan *Echinolimmadia mattoxi* [Novojilov, 1970; Orlova, 1999]. Dymorphoptilids are quite common and moderately diverse in the PTB beds of the Nizhnyaya Tunguska River basin.

Eumorphoptila pritykinae gen. et sp.n. from the Middle Jurassic of Kubekovo is the latest record of the



Figs 1–8. *Unturella truncata* gen. et sp.n.: 1–5 — holotype right tegmen, Untuun-2, terminal Permian or basal Triassic: 1 — negative impression (next to two conchostracan shells); 2–4 — positive impression: 2 — tegmen; 3 — base of costal area with strigil; 4 — part of strigil and adjacent area; 5 — venation (dotted oval, strigil); 6–8 — paratypes, Khungtukun-2, terminal Permian: 6 — PIN 5382/98, left tegmen, positive impression (mirrored); 7–8 — PIN 5382/100, right tegmen, negative impression (mirrored): 7 — part of costal area with strigil; 8 — part of strigil and adjacent area; 2–4, 7–8 — SEM. Scale bars: 1, 2, 5, 6 — 2 mm; 3, 7 — 0.5 mm; 4, 8 — 0.2 mm.

family. The only known specimen was collected among about 2000 fossil insects near the village Kubekovo on the left bank of Yenisey River downstream of Krasnoyarsk, in the reference section of the Upper Itat Subformation (Bathonian, ~168 Ma) [Nikulov et al., 2015].

The material is deposited at Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera. Scanning electron images of uncoated specimens were obtained with TESCAN VEGA microscope using back-scattered electron detector. The vein nomenclature is after Shcherbakov [1984, 1996].

Superfamily Prosboloidea Handlirsch, 1906
Family Dymorphoptilidae Handlirsch, 1906

Unturella Shcherbakov, **gen.n.**

Unturella: Kazakov et al., 2002: 160 (nomen nudum)

Unturella: Varganov et al., 2015: 127 (nomen nudum)

TYPE SPECIES. *U. truncata* Shcherbakov, **sp.n.**

DIAGNOSIS. Tegmen elongate, not emarginate, broadly truncate apically (with distinct apex and tornus), entirely finely punctate. Costal margin smoothly convex, costal area broad, flat, without distinct prenodal R branches. RA to dSc as long as R stem. Both dSc (distal part of Sc) and postnodal RA branches long, oblique. CuA fork long; M forked distal to CuA. Apical cells narrow. Strigil wide, densely microscopically striate. Ambient vein smooth. Claval veins widely separated.

COMPOSITION. Type species.

COMPARISON. Similar to the Late Permian genera *Belmontocarta* Evans, 1958 (Changhsingian, Sydney Basin) and *Permocixiella* Becker-Migdisova, 1961 (Wuchiapingian, Kuznetsk Basin) and the Middle Permian genus *Linglunxiellus* Szwedo et Huang, 2019 (Capitanian, South China) in the elongate, not emarginate tegmen with narrow apical cells. *Belmontocarta* differs from *Unturella* **gen.n.** in the CuA fork shorter, and punctation coarser and confined to veins in the postnodal part of tegmen (the costal margin is smoothly convex in *Belmontocarta*, see photo in Jell [2004]). *Permocixiella* and *Linglunxiellus* differ from *Unturella* **gen.n.** in the punctation limited to the tegmen base (and apparently claval), *Permocixiella* also in the tegmen rounded apically and the ambient vein corrugated, and *Linglunxiellus* in the tegmen broader and distal vein branches more numerous and close-set.

ETYMOLOGY. From Untuun River (type locality) and *Eoscarterella*; gender feminine.

Unturella truncata Shcherbakov, **sp.n.**

Figs 1–8.

Unturella truncata Shcherb.: Kazakov et al., 2002: 160 (nomen nudum)

Unturella truncata Shcherb.: Varganov et al., 2015: 127 (nomen nudum)

MATERIAL. Holotype PIN 2989/1±, complete tegmen (clavus separated; M-CuA area crumpled, so that apical margin seems oblique), Untuun-2, left bank of Untuun R. (left tributary of Kochechumo R.) against mouth of Khoktokon R., Evenkiysky District,

Krasnoyarsk Krai; Bugarikta, Nidym or lower Kochechumo Formation (Agitkan Horizon), terminal Permian (Changhsingian) or basal Triassic; paratypes PIN 5382/98±, 100±, 101±, 104±, incomplete tegmina (clavus missing), Khungtukun-2, right bank of Nizhnyaya Tunguska R. 4.9 km ESE from mouth of Khungtukun R., Evenkiysky District, Krasnoyarsk Krai; Bugarikta Formation (Khungtukun Horizon [Sadovnikov, 2015]), terminal Permian (Changhsingian).

DESCRIPTION. Tegmen 12.0–13.5 mm long, elongate (2.7:1), transversely truncate apically, with distinct apex and tornus (posterior apical angle). Costal margin convex near base, nearly straight (not concave) distally; precostal carina narrow except near base; CP long, strong; bSc long, low arched. R stem arched forwards proximally, as long as RA to dSc. dSc very long, slanting, continuing proximal RA. RA with 2–3 postnodal branches less oblique than dSc; prenodal branches barely visible or absent. RP with small fork. M forked distal to CuA, pectinate backwards, with 3 main branches, M1 with small fork. Basal cell long, closed with arculus. CuA fork long, CuA1 arched forwards, CuA2 joining margin distant from claval apex. Three crossveins. Claval veins widely separated, nearer to sides of clavus; Pcu gently curved, joining margin about 2/3 clavus length. Tegmen entirely covered with fine punctures on upperside (coarser on clavus) and stub-like microtrichia on underside (apparently forming plastron). In costal area near base these microtrichia merge into closely packed microscopic ridges covering elongate oval fingerprint-like area (strigil) about 1.3 x 0.6 mm; ridges more dense in proximal part of strigil (10 per 100 µm) than in its distal part (6.5 per 100 µm) Ambient vein not corrugated; marginal membrane narrow. Tegmen brownish, more so towards base, especially in costal area and on clavus; precostal carina dark brown.

ETYMOLOGY. Latin *truncatus* (truncated).

Eumorphoptila Shcherbakov, **gen.n.**

TYPE SPECIES. *Eumorphoptila pritykinae* Shcherbakov, **sp.n.**

DIAGNOSIS. Tegmen small, elongate, convex, entirely coarsely punctate; postnodal part short and narrow, emarginations very slight. Veins thick, subcarinate, with few short distal branches. Costal margin convex, costal area narrow. RA to dSc more than twice as long as R stem, with strong prenodal branches. CuA fork very short, distal to claval apex. CuA stem and Pcu close to claval furrow, claval veins close-set. Commissural margin with several small tubercles.

COMPOSITION. Type species.

COMPARISON. Distinct from other genera in the elongate convex tegmen with a small postnodal part and raised veins with few short distal branches. Similar to *Dymorphoptila notodon* Shcherbakov, 1988 (Bajocian, southern Mongolia) in the strong prenodal branches on RA and presence of prominences on the commissural margin, but in the latter the postnodal part is much longer, limited by distinct emarginations, distal vein branches are more numerous, and prominences are larger and spine-like. Two other dymorphoptilid genera known from the Jurassic differ from *Eumorphoptila* **gen.n.** in the more developed postnodal part with longer vein branches and CuA fork (*Mesoatraxis reducta* Becker-Migdisova, 1949, Toarcian, Kyrgyzstan), or the sinuate costal mar-

Рис. 1–8. *Unturella truncata* **gen. et sp.n.**: 1–5 — голотип, правое переднее крыло, Унтуун-2, терминальная пермь или базальный триас: 1 — обратный отпечаток (рядом две раковинки конхострак); 2–4 — прямой отпечаток: 2 — переднее крыло; 3 — основание костального поля со стригилом; 4 — часть стригила с примыкающим участком; 5 — жилкование (пунктирный овал — стригил); 6–8 — паратипы, Хунгтукун-2, терминальная пермь: 6 — ПИН 5382/98, левое переднее крыло, прямой отпечаток (отражено зеркально); 7–8 — ПИН 5382/100, правое переднее крыло, обратный отпечаток (отражено зеркально): 7 — часть костального поля со стригилом; 8 — часть стригила с примыкающим участком; 2–4, 7–8 — СЭМ. Длина масштабных линеек: 1, 2, 5, 6 — 2 мм; 3, 7 — 0,5 мм; 4, 8 — 0,2 мм.

gin, broader costal area, and longer R stem (*Stigmocercopsis parvis* Lin, 1986, Bajocian, South China).

ETYMOLOGY. From Greek *eu-* (true, good) and *Dysmorphoptila*; gender feminine.

Eumorphoptila pritykinae Shcherbakov, **sp.n.**

Figs 9–10.

MATERIAL. Holotype PIN 1255/1608±, complete tegmen; Kubekovo near Krasnoyarsk, Emel'yanovo district, Krasnoyarsk Krai; upper Itat Formation, Middle Jurassic (Bathonian).

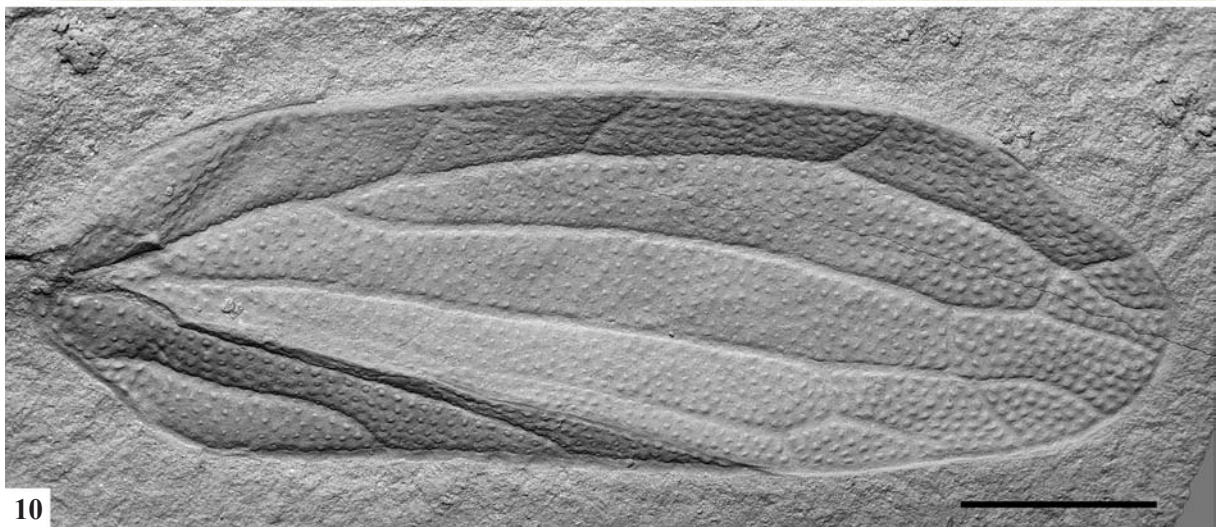
DESCRIPTION. Tegmen 6.0 mm long, elongate (3.0:1), acutely rounded at apex; postnodal part short (about 1/4 tegmen length); emarginations distal to dSc and at CuA1 very slight. Costal margin convex, more so at base; precostal carina narrow; CP faint, bSc short, high arched. Costal area narrow, with oblique swelling in strigil area, but strigil not detected. RA to dSc more than twice as long as R stem; one weak prenodal R branch before R fork and two strong on RA. RA and anterior M branch with short forks; posterior M branch fused with CuA1 for half of its length. Basal cell very short, closed with short M+CuA anastomosis. CuA stem

weak proximally, close to claval furrow; CuA2 crossvein-like. Claval veins close-set and displaced anteriorly, 1A bisinuate. Commissural margin with 10 regularly spaced small tubercles. Narrow marginal membrane posterior to tegmen apex. Tegmen and veins pale; membrane entirely punctate, coarser in postnodal part (appearing almost areolate); veins with bases of setae, larger on RA and claval veins.

ETYMOLOGY. Named after Lyudmila N. Pritykina, a Russian paleoentomologist who collected many fossils at Kubekovo.

Discussion

Five subfamilies were proposed in Dysmorphoptilidae [Szwedo, Huang, 2019], but such classification seems premature. The end-Permian *Unturella* **gen.n.** is similar to the Late Permian *Belmontocarta* and *Permocixiella* and Middle Permian *Linglunxiellus*, and all four likely form a natural group. However, these genera are divided



Figs 9–10. *Eumorphoptila pritykinae* **gen. et sp.n.**, holotype left tegmen, negative impression, Kubekovo, Middle Jurassic: 9 — photo; 10 — SEM. Scale bars: 1 mm.

Рис. 9–10. *Eumorphoptila pritykinae* **gen. et sp.n.**, голотип, левое переднее крыло, обратный отпечаток, Кубеково, средняя юра: 9 — фото; 10 — СЭМ. Длина масштабных линеек: 1 мм.

between two subfamilies, Permocixiellinae and Eoscarterellinae in the key of Szwedó and Huang [2019], based on a single character, the extent of the tegminal punctation (limited to the tegmen base and apparently clavus, which remains unknown, in the former, covering most of the tegmen in the latter). Other characters used in the key to differentiate these subfamilies (position of dSc apex, relative width of postnodal part, shape of postclaval margin) are the same for all four genera. In remaining three dysmorphoptilid genera known from the Permian, the tegminal punctation is absent on the postnodal membrane (*Dysmorphoscartella* Riek, 1973, Changhsingian, Karoo Basin and *Sinomorphoptila* Fu et Huang, 2020, Capitanian, South China; both placed in Dysmorphoptilinae) or limited to the tegmen base and clavus (*Fulgoringruo* Pinto, 1990, Kungurian, Parana Basin; *Fulgoringruinae*). It suggests that the tegminal punctation evolved in parallel in more than one lineage within Dysmorphoptilidae. More studies are needed to develop a natural classification of the family.

The oldest animal sound-producing devices have been recorded in the forewings of Early Permian, and possibly Carboniferous, orthopteroids [Béthoux et al., 2003; Schubnel et al., 2021]. Stridulation is a mechanism of producing sound by rubbing together certain body parts, usually one structure with a well-defined ridge or nodules (plectrum) moving across a finely-ridged surface (strigil or stridulitrum) or vice versa. Grasshoppers are well known for stridulating when their hind femora rub against the forewings. Hemiptera, especially Auchenorrhyncha, also use airborne sounds and substrate vibrations to communicate [Claridge, 1985; Virant-Doberlet, Cokl, 2004; Liao et al., 2019]. Stridulatory devices of the “forewing-hindleg” type, with a strigil on the costal margin of hemelytron and a plectrum on the hind femur, occur in several groups of Heteroptera (some Schizopteridae, Saldidae, Lygaeidae, Alydidae) [Leston, 1957; Ashlock, Lattin, 1963; Polhemus, 1976; Schaefer, Pupedis, 1981] and some fossil Auchenorrhyncha (e.g. Dysmorphoptilidae) [Evans, 1961]. In modern Auchenorrhyncha, stridulation is a rare mode of sound production [Boulard, 2006] and “forewing-hindleg” stridulators are unknown.

The strigil discovered on the underside of the costal area in the tegmina of *Unturella* **gen.n.** is the earliest evidence of acoustic communication in Hemiptera. This new genus is the oldest known dysmorphoptilid with entirely punctate tegmina, and sclerotization of the costal area was probably a prerequisite for the strigil development. The excellent preservation of *Unturella* **gen.n.** allows to see that the fine ridges of this strigil are formed from rows of fused microtrichia. Non-wettable covering of stump-like microtrichia on the underside of dysmorphoptilid tegmen trapping a thin layer of air (plastron) was apparently an adaptation for life on shore vegetation, especially helophytes, like in Scytinopteroidea, another group of Permian–Triassic Cicadomorpha with heavily punctate tegmina [Shcherbakov, 1996].

The tegmina are oddly shaped in many, mostly Triassic, dysmorphoptilids, with the postnodal part pro-

jecting tongue-like and/or a row of lobes or tubercles on the commissural margin (e.g. *Dysmorphoptila*; *Dysmorphoptiloides* Evans, 1956; *Tennentsia* Riek, 1976) [Lambkin, 2015]. Projections of the apical and commissural margins are developed in many species of the related Triassic family Maguviopseidae, which likely imitated thorns or bracts of their host plants [Shcherbakov, 2011], and the same type of crypsis is assumed in Dysmorphoptilidae [Szwedó, Huang, 2019]. The late Middle Jurassic *Eumorphoptila* **gen.n.** shows these traits in a reduced state: the postnodal projection short and indistinctly separated, commissural tubercles small and inconspicuous. This kind of plant-part mimicry may have become ineffective against predators by the mid-Jurassic.

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References

- Ashlock P.D., Lattin J.D. 1963. Stridulatory mechanisms in the Lygaeidae, with a new American genus of Orsillinae (Hemiptera: Heteroptera) // *Ann. Entomol. Soc. Am.* Vol.56. P.693–703. <https://doi.org/10.1093/aesa/56.5.693>.
- Béthoux O., Nel A., Lapeyrie L., Gand G. 2003. The Permostridulidae fam. n. (Panorthoptera), a new enigmatic insect family from the Upper Permian of France // *Eur. J. Entomol.* Vol.100. P.581–585. <https://doi.org/10.14411/eje.2003.087>.
- Boulard M. 2006. Acoustic signals, diversity and behaviour of cicadas (Cicadidae, Hemiptera) // S. Drosopoulos, M.F. Claridge (eds.). *Insect Sounds and Communication: Physiology, Behaviour, Ecology, and Evolution.* New York: Taylor & Francis. P.331–349.
- Claridge M.F. 1985. Acoustic signals in the Homoptera: behavior, taxonomy, and evolution // *Annu. Rev. Entomol.* Vol.30. P.297–317.
- Evans J.W. 1956. Palaeozoic and Mesozoic Hemiptera (Insecta) // *Aust. J. Zool.* Vol.4. P.165–258. <https://doi.org/10.1071/ZO9560165>.
- Evans J.W. 1961. Some Upper Triassic Hemiptera from Queensland // *Mem. Queensl. Mus.* Vol.14. No.1. P.13–23.
- Handlirsch A. 1906–1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen.* Leipzig: Wilhelm Engelmann. ix+1430 S. <https://doi.org/10.5962/bhl.title.34145>.
- Jell P.A. 2004. The fossil insects of Australia // *Mem. Queensl. Mus.* Vol.50. P.1–124. <https://doi.org/10.1082/j.2204-1478.50-1.2004.2004.01>.
- Kazakov A.M., Konstantinov A.G., Kurushin N.I., Mogutcheva N.K., Sobolev E.S., Fradkina A.F., Yadryonkin A.V., Devyatov V.P., Smirnov L.V. 2002. [Stratigraphy of Oil and Gas Basins of Siberia. Triassic System]. Novosibirsk: Department “GEO”, Siberian Branch, Russian Academy of Sciences. 322 pp. [in Russian].
- Lambkin K.J. 2015. Revision of the Dysmorphoptilidae with emarginate tegmina (Hemiptera: Auchenorrhyncha: Cicadomorpha: Prosboloidea) of the Queensland Triassic // *Zootaxa.* Vol.3936. P.357–374. <http://dx.doi.org/10.11646/zootaxa.3936.3.3>
- Leston D. 1957. The stridulatory mechanisms in terrestrial species of Hemiptera Heteroptera // *Proc. Zool. Soc. Lond.* Vol.128. P.369–386. <https://doi.org/10.1111/j.1096-3642.1957.tb00331.x>
- Liao Y.C., Wu Z.Z., Yang M.M. 2019. Vibrational behavior of psyllids (Hemiptera: Psylloidea): functional morphology and

- mechanisms // *PLoS one*, Vol.14. e0215196. <https://doi.org/10.1371/journal.pone.0215196>.
- Nikulov L.P., Babkin A.N., Kolyamkin V.M., Leshchinski S.L., Serzhantov N.F., Rachmatullin R.N. 2015. [State geological map of Russian Federation]. Scale 1:200000. 2nd ed. Series Yeniseyskaya. Sheet O-46-XXXIV (Sosnovoborsk). Explanatory report. Moscow: VSEGEI. 248 pp. [in Russian].
- Novojilov N.I. 1970. [Extinct Limnadioidea (Conchostraca-Limnadioidea)]. Moscow: Nauka. 237 pp [in Russian].
- Orlova E.F. 1999. Permian-Triassic conchostracan faunas from the north of central Siberia // *Stratigr. Geol. Correlation*. Vol.7. P.465–472.
- Polhemus J.T. 1976. Shore bugs (Hemiptera: Saldidae, etc.) // Cheng L. (ed.). *Marine Insects*. New York: North-Holland–Elsevier. P.225–262.
- Sadovnikov G.N. 2015. Paleocological characterization of the Middle Siberian trappean plateau during the middle period of its formation (terminal Permian) // *Paleontol. J.* Vol.49. P.438–447.
- Schaefer C.W., Pupedis R.J. 1981. A stridulatory device in certain Alydinae (Hemiptera: Heteroptera: Alydidae) // *J. Kans. Entomol. Soc.* Vol.54. P.143–152.
- Schubnel T., Legendre F., Roques P., Garrouste R., Cornette R., Perreau M., Perreau N., Desutter-Grandcolas L., Nel A. 2021. Sound vs. light: wing-based communication in Carboniferous insects // *Commun. Biol.* Vol.4. P.1–11. <https://doi.org/10.1038/s42003-021-02281-0>.
- Shcherbakov D.E. 1984. Systematics and phylogeny of Permian Cicadomorpha (Cimicida Cicadina) // *Paleontol. J.* No.2. P.87–97.
- Shcherbakov D.E. 1996. Origin and evolution of the Auchenorrhyncha as shown by the fossil record // C.W. Schaefer (ed.). *Studies on Hemipteran Phylogeny*. Lanham (Maryland): Entomological Society of America. P.31–45.
- Shcherbakov D.E. 2000. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permo-Triassic crisis // *Paleontol. J.* Vol.34. Suppl.3. P.S251–S267.
- Shcherbakov D.E. 2011. New and little-known families of Hemiptera Cicadomorpha from the Triassic of Central Asia — early analogs of treehoppers and planthoppers // *Zootaxa*. Vol.2836. P.1–26. <http://dx.doi.org/10.11646/zootaxa.2836.1.1>
- Shcherbakov D.E., Vinn O., Zhuravlev A.Y. 2021. Disaster microconchids from the uppermost Permian and Lower Triassic lacustrine strata of the Cis-Urals and the Tunguska and Kuznetsk basins (Russia) // *Geol. Mag.* Vol.158. P.1335–1357. <https://doi.org/10.1017/S0016756820001375>.
- Szwedo J., Huang D. 2019. First Dysmorphoptilidae from the Permian of China (Hemiptera: Cicadomorpha: Prosbolomorpha), with notes on the fossil record of the family // *Palaeoentomol.* Vol.2. P.148–170. <https://doi.org/10.1134/S0031030113070010>.
- Varganov A.S., Popova N.N., Sosnovskaya A.V., Smokotina I.V., Glushkov V.M., Kazhaeva O.D., Mikryukova L.N. 2015. [State Geological Map of the Russian Federation, Scale 1:1 000 000 (third generation). Angara-Yenisey Series. Sheet P-47 — Baik. Explanatory Note]. Saint Petersburg: Kartograficheskaya fabrika VSEGEI. 359 pp. [in Russian].
- Virant-Doberlet M., Cokl A. 2004. Vibrational communication in insects // *Neotrop. Entomol.* Vol.33. P.121–134. <https://doi.org/10.1590/S1519-566X2004000200001>.