

## Mesozoic spider mimics — Cretaceous Mimarachnidae fam.n. (Homoptera: Fulgoroidea)

## Мезозойские имитаторы пауков — меловые Mimarachnidae fam.n. (Homoptera: Fulgoroidea)

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КЛЮЧЕВЫЕ СЛОВА: подражание паукам, Mimarachnidae, Fulgoroidea, Auchenorrhyncha, носатки, филогения, ископаемые, меловой период, Забайкалье, Байса.

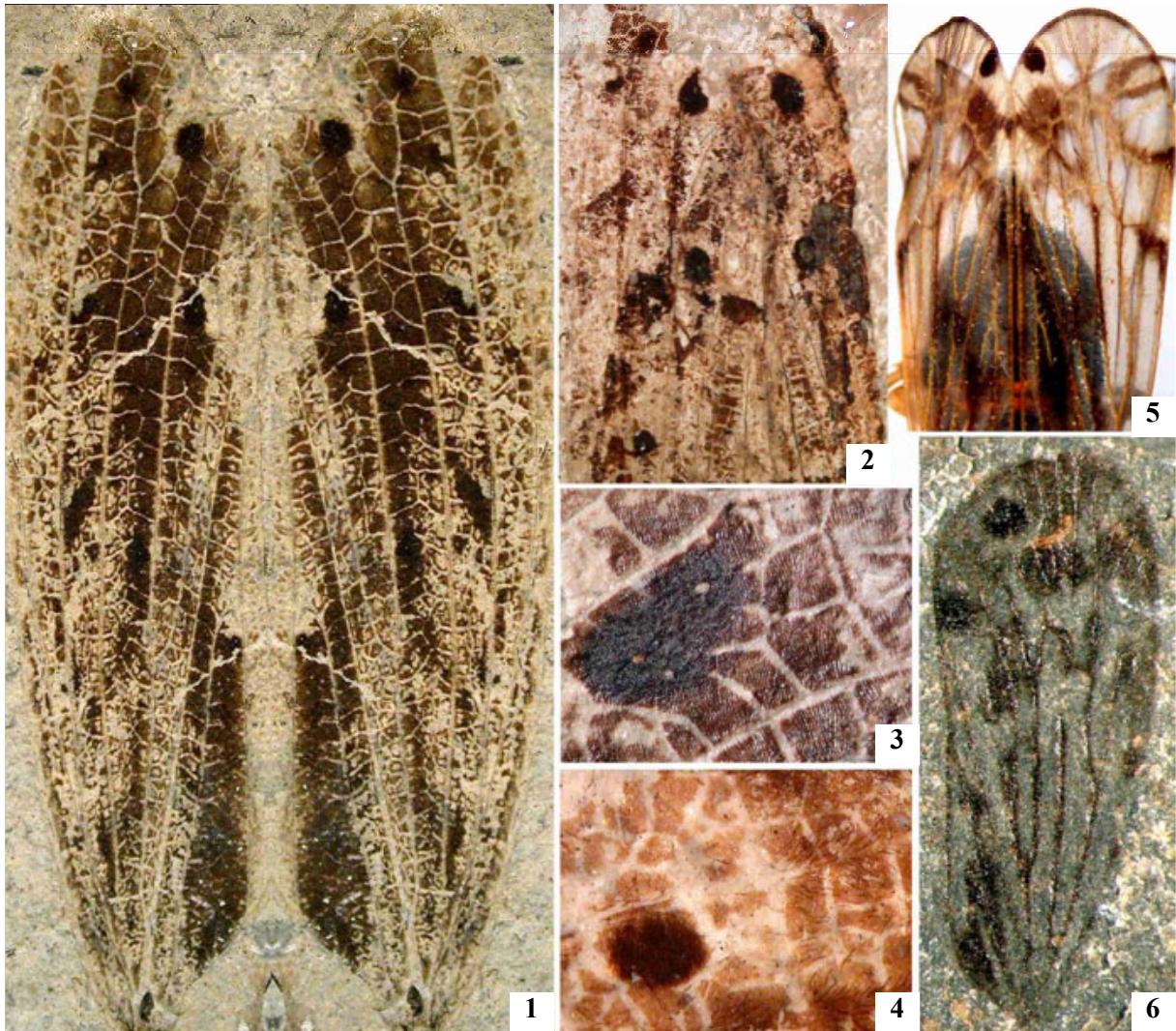
ABSTRACT. A new family of primitive (pre-cixioid) Cretaceous planthoppers, Mimarachnidae **fam.n.** is described, comprising two new genera and species, *Mimarachne mikhailovi* **gen. et sp.n.** and *Saltissus eskovi* **gen. et sp.n.**, from the Early Cretaceous of Baissa, Transbaikalia. With the spider-like dark silhouette and several small black eyespots with pupils on rear parts of their folded tegmina *M. mikhailovi* **sp.n.** could be a perfect spider mimic. The arrangement of eyespots is discussed in light of possible taxonomic affinity of the spider model. Similar colour patterns found in some modern Cixiidae and Jurassic Fulgoridiidae allow hypothesizing that spider mimicry originated about 200 million years ago.

РЕЗЮМЕ. Описано новое семейство примитивных (до-циксиидных) меловых носаток, Mimarachnidae **fam.n.** с двумя новыми родами и видами, *Mimarachne mikhailovi* **gen. et sp.n.** и *Saltissus eskovi* **gen. et sp.n.** из раннего мела Забайкалья (Байса). Напоминавший паука темный силуэт и изображавшие его глаза черные со светлыми зрачками пятнышки на задней части сложенных передних крыльев *M. mikhailovi* **sp.n.** давали этим носаткам возможность имитировать пауков. Расположение глазчатых пятен обсуждается в свете возможной таксономической принадлежности пауков-моделей. Сходная окраска некоторых современных Cixiidae и юрских Fulgoridiidae позволяет предположить, что подражание паукам возникло около 200 млн. лет назад.

Predator mimicry is rather uncommon subtype of Batesian mimicry. Jumping spider (salticid) mimics are known in Diptera (Tephritidae) [Mather & Roitberg, 1987], diverse Microlepidoptera [Rota & Wagner, 2006] and various Fulgoroidea: Derbidae [Floren & Otto, 2001], nymphal Fulgoridae [Zolnerowich, 1992], brachypterous Caliscelidae [O'Brien, 1967], and adult Eury-

brachyidae (*Gelastopsis insignis* Kirkaldy, 1906); other eurybrachyids, *Platybrachys* spp. mimic huntsman spiders (Sparassiidae) [Chew, 2007]. The movements imitating spider gait or displays are an important part of this mimicry syndrome as the “spider pattern” itself [Greene et al., 1987; Rota & Wagner, 2006]. Some of these insects mimic the spider head with their fore end (e.g. *G. insignis* and *Caliscelis* spp.), but most others with their rear end (*Platybrachys* spp. bearing eyespots on the tips of their tegmina and moving mostly backwards [Chew, 2007], various moths). The “salticid pattern” in moths includes contrasting bands on forewings (“spider’s legs”) and clustered eyespots at their rear end (“spider’s eyes”). Jumping spider mimicry helps escaping predation not only by salticids and smaller predators, but also by large predators (e.g. birds) through evasive prey mimicry [Rota & Wagner, 2006]. Numerous cases of spider mimicry in unrelated lineages show that Salticidae and possibly some other spider families with acute vision were an important factor in the evolution of their insect prey.

Now the spider mimicry pattern is first recognized in fossils. Several structural features contributed to such a pattern in the Cretaceous planthoppers from the well known Baissa locality [Zherikhin et al., 1999] described below as *Mimarachne* **gen.n.** (Figs 1–3). These features were especially pronounced in agile males, while comparatively broad-winged females more relied on their cryptism. (1) Dark silhouette (half of spider on each tegmen), with four reclined bands in anterior half of the tegmen imitating spider’s legs. (2) Dark abdomen, visible through translucent posterior (commissural) zones of folded tegmina and complementing to the silhouette (like in some modern Cixiidae — Fig. 5). (3) Perfect imitation of spider’s eyes — nearly black ocellar spots with a small, pale central pupil (possibly producing white wax at life) that mimicked a speck of light in the



Figs 1–6. Tegminal patterns: 1–3 — *Mimarachne mikhailovi* gen. et sp.n.: 1 — pair of male(?) tegmina, composite photograph based on holotype PIN 3064/4614; 2 — distal parts of folded female tegmina, paratype PIN 1989/3575; 3 — apical eyespot (doubled), crossveins and microsculpture, paratype female(?) tegmen PIN 3064/4615; 4 — *Saltissus eskovi* gen. et sp.n., paratype PIN 1668/1693, eyespot, crossveins and hairs; 5 — *Myndus musivus* (Germar, 1825), Cixiidae, folded tegmina, recent; 6 — *Fulgoridium* sp., Fulgoridiidae, tegmen, Early Jurassic of Germany.

Рис. 1–6. Окраска передних крыльев: 1–3 — *Mimarachne mikhailovi* gen. et sp.n.: 1 — пара передних крыльев самца(?), фотомонтаж на основе голотипа ПИН 3064/4614; 2 — дистальные части сложенных передних крыльев самки, паратип ПИН 1989/3575; 3 — апикальное глазчатое пятно (удвоено), поперечные жилки и микроскульптура, переднее крыло самки(?), паратип ПИН 3064/4615; 4 — *Saltissus eskovi* gen. et sp.n., паратип ПИН 1668/1693, глазчатое пятно, поперечные жилки и волоски; 5 — *Myndus musivus* (Germar, 1825), Cixiidae, сложенные передние крылья, современный; 6 — *Fulgoridium* sp., Fulgoridiidae, переднее крыло, ранняя юра Германии.

eye (similar design is found in living *G. insignis* bearing a pair of large black spots with white pupil on the metope [Chew, 2007]). Two main eyespots, apical and subapical, were accentuated with adjacent pale crescents. (4) Gradations from more to less dark-speckled background plus meshwork of pale crossveins, imitating the camouflage of an ambush predator. (5) Antiglare cover of fine transverse wrinkles on the surface of tegmina (probably also with some grayish wax coating at life), masking their true outline and prominent main veins, imitating the cover of scales over the spider's body, and contrasting with more minute, rather granu-

late microsculpture of the eyespots that enhanced their deep black tone. Apparently this spider pattern had some counterpart in the behaviour, e.g. sideways or backward movements so widespread in planthoppers.

The pair of apical (rearmost) eyespots of *Mimarachne* gen.n. imitates the frontal eyes of a spider, and the pair of slightly smaller subapical eyespots (near claval apices) presumably corresponds to its posterior eyes, all four main spots forming an elongate rectangle some 3 mm long. Such eye arrangement, with posterior eyes well developed and displaced far backwards is now characteristic of Salticidae, the family still unknown

from the Mesozoic [Penney, 2004]. There are other, less conspicuous eyespots in *Mimarachne* **gen.n.**, but if the arrangement of four main eyespots indeed reflects that of the spider model, it may indicate that the earliest salticids or their predecessors (or at least their structural and behavioural analogues) of quite large size were already in existence by the Early Cretaceous, at least 125 Ma.

In a related genus, *Saltissus* **gen.n.** from the same locality, the colour pattern of tegmen is similar but less obvious (Fig. 4) — single eyespot, two obscure dark bands (more distinct in males) — and the antireflective cover is made of hairs, not microsculpture (possibly imitating more hairy, less scaly spider). These two genera sharing many distinctive characters are assigned to Mimarachnidae **fam.n.** described below.

Simple spider patterns with dark bands and 1–2 apical eyespots on the tegmen are known in other living (e.g. some Cixiidae — Fig. 5) and Mesozoic planthoppers, including some Jurassic Fulgoridiidae (Fig. 6). Formerly these patterns were interpreted as distractive (“false head” turning predator’s attention to the rear end of prey instead of its head) [Shcherbakov & Popov, 2002], but now it seems probable that already in the Early Jurassic (almost 200 Ma) some planthoppers mimicked their visual predators, some spiders, such as Cretaceous Lagonomegopidae which lacked prominent posterior eyes and occupied a niche similar to Salticidae [Penney, 2005].

The Baissa section comprising 18 insect-bearing beds (numbered from top to bottom) is tectonically faulted (“uppermost” beds 9–2 are uplifted lower beds) and reflects gradual transition from humid climate (oldest, ‘cold’ beds 37–31) to the more arid one (youngest, ‘warm’ beds 25–13) [Vršanský et al., 2002]. In the ‘cold’ beds both mimarachnid species known from Baissa are collected, whereas in the ‘warm’ beds the smaller one (*S. eskovi* **sp.n.**) becomes more common (in the bed 15 all finds belong to this species), presumably due to less rich vegetation at drier conditions.

Mimarachnidae **fam.n.** resemble another Cretaceous planthopper family, Perforissidae [Shcherbakov, 2007], but most of their similarities appear homoplastic, reflecting their parallel descent from Jurassic Fulgoridiidae (or related forms). These three families along with Mesozoic Lalacidae and Permo-Triassic Surijokocixiidae constitute the most primitive, pre-cixioid section of Fulgoroidea, characterized by setigerous metatibial pecten and at least in part by retention of sensory pits in adult. Mimarachnidae **fam.n.** was first mentioned (as undescribed family) in [Shcherbakov, 1988]. All specimens of the new taxa are deposited in the Paleontological Institute, Russian Academy of Sciences, Moscow (PIN).

#### Mimarachnidae Shcherbakov, **fam.n.**

TYPE GENUS. *Mimarachne* Shcherbakov, **gen.n.**

DIAGNOSIS. Medium-sized or larger (12–25 mm), elongate planthoppers with little vein branching and meshwork of crossveins, superficially resembling some Fulgoridae. Tegmina obliquely truncate apically, with narrow costal area, R and CuA deeply forked, R fork narrow, RA, CuA1 and CuA2

simple, RP and M with terminal forks, anterior margin of R–RA grooved, RP more raised than RA, weak or indistinct arculus [basal *m-cu*], clavus open [claval furrow not entering margin], stalk of claval Y-vein [Pcu+1A] ending at truncate claval apex, beyond claval apex membranized and sometimes with narrow marginal membrane. Hindwing with R and CuA deeply forked and M simple. Head unmodified (neither produced nor widened and shortened), lateral ocelli developed, coryphe longer than wide, eumetope tricarinate, eumetope+clypeus evenly convex in profile, rostrum long. Pronotum inverted V-shaped, shallowly incised posteriorly. Mesonotum with median carina doubled, lateral carinae converging anteriorly. Legs rather long; apical pecten of hind tibia setigerous, straight, uniserial, of at least 8 teeth; metatarsal pectens concave, uniserial(?), of at least 10 teeth. Ovipositor apparently ensiform. Head and thorax (including most of mesonotal disc) with numerous small sensory pits persisting in adult.

COMPOSITION. Two genera described below.

COMPARISON. Similar to Cretaceous Perforissidae [Shcherbakov, 2007] in simplified venation, tegmen with costal area narrow, clavus open, and (type genus only) narrow marginal membrane, metatibial pecten setigerous, and sensory pits retained in adult (including mesonotum medially of lateral carinae), but easily distinguishable by the deeply forked R, less deeply forked CuA, abundant irregular crossveins, head and pronotum unmodified, mesonotum carinate along midline, smaller and more numerous sensory pits (covering most of mesonotal disc), and larger size.

REMARKS. Several other, yet undescribed fossils belonging to this family are found in the Early Cretaceous (earliest Cretaceous of Turga, Chita Region; Aptian of Bon-Tsagan, Mongolia; Albanian of Khetana, Khabarovsk Region) and Late Cretaceous (Turonian of Kzyl-Zhar, Kazakhstan; on the localities see [Rasnitsyn & Zherikhin, 2002]), up to now all in Asia. Some of these fossils, indeterminate to the genus, show important details (structure of mesonotum and hind legs, Figs 16–17).

#### KEY TO THE GENERA AND SPECIES OF MIMARACHNIDAE (TEGMEN)

1. CuA forked before midlength of tegmen; CuA2 distinct basally, arched forwards apically. RP and M forked near apices (M forked level with CuA2 apex). Medial and commissural area not widened. Stalk of Y-vein shorter than its arms, joins commissural margin. Narrow marginal membrane beyond claval apex. Commissural carina extremely narrow. Precostal carina narrow, subhorizontal. At least 3 dark eyespots with pale pupil. Tegmina bare, shallowly tectiform in repose, more elongate (>3:1), 15–19 mm long ..... *Mimarachne mikhailovi* **gen. et sp.n.**
- CuA forked near claval apex; CuA2 indistinct basally, not arched apically. RP and M forked more proximally (M forked nearer to claval apex). Medial and commissural area widened. Stalk of Y-vein longer than its arms, joins claval furrow. No marginal membrane. Commissural carina prominent, wavy. Precostal carina widened and deflected dorsad at base. Single apical dark eyespot, usually without pale pupil. Tegmina hairy, steeply tectiform in repose, less elongate (<3:1), 9.5–13 mm long ..... *Saltissus eskovi* **gen. et sp.n.**

#### *Mimarachne mikhailovi* Shcherbakov, **gen. et sp.n.**

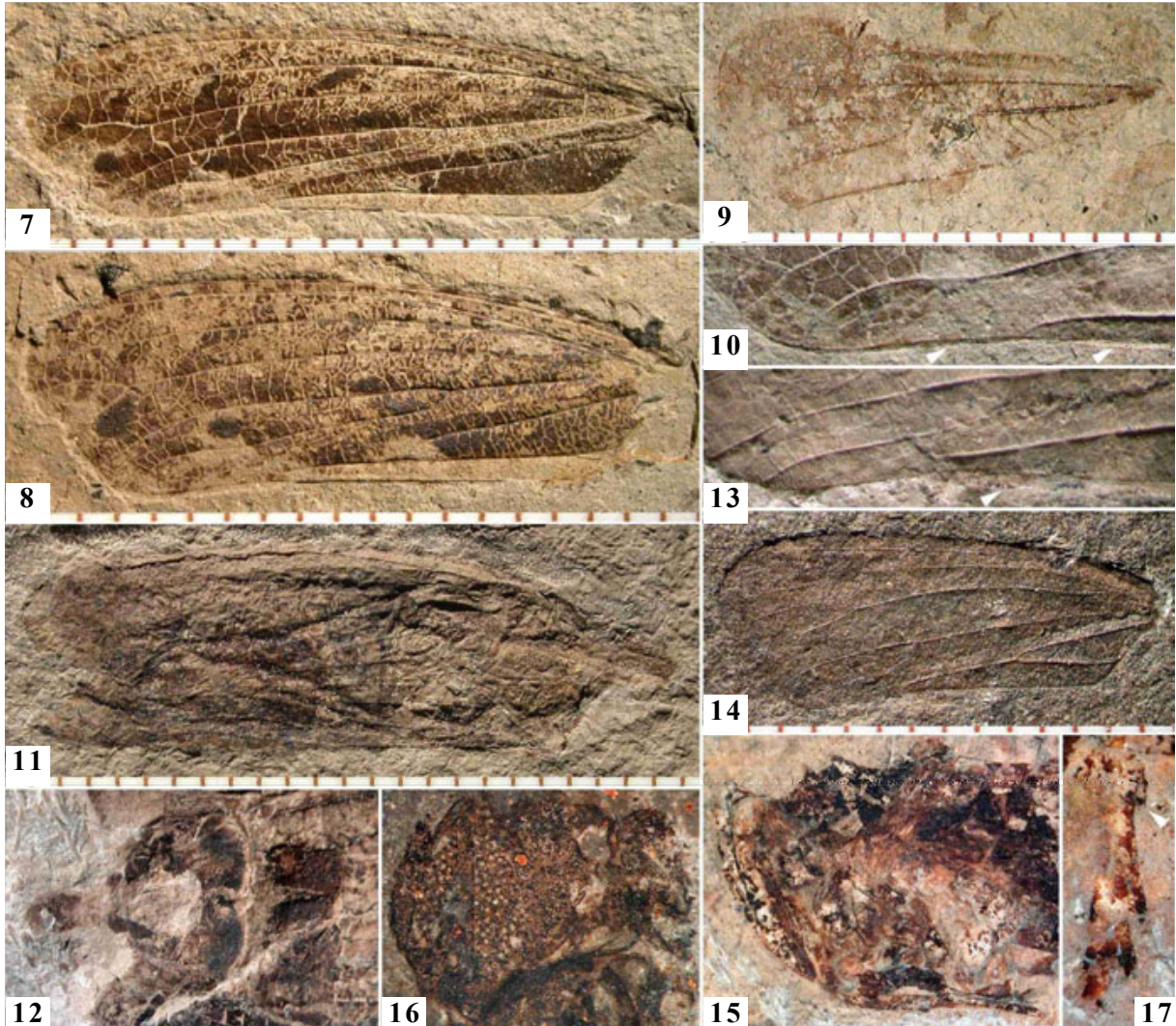
Figs 1–3, 7–12, 18

MATERIAL. Holotype: male(?) tegmen PIN 3064/4614 (bed 31); paratypes: female(?) tegmina PIN 1668/1685, 3064/4615,

hindwing 3064/4621 (bed 31), tegmen 3064/4583 (bed 26), complete female 1989/3575 (bed 19), incomplete male 3064/4018 and clavus 4210/1086 (bed 2) — Baissa, Vitim R., Buryatia, Russia; Zaza Fm., Lower Cretaceous, Neocomian (Berriasian–Barremian, ca. 145–125 Ma) [Zherikhin et al., 1999].

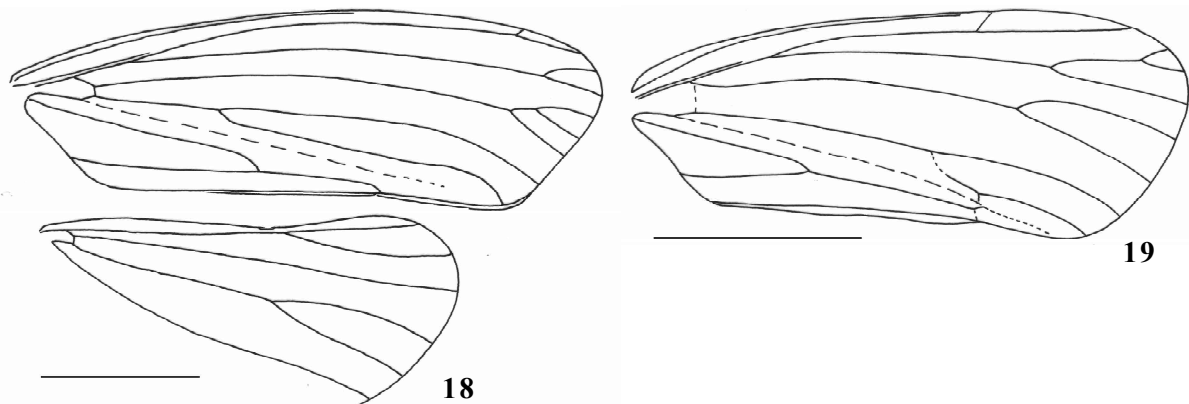
DIAGNOSIS — see the key above.

DESCRIPTION. Body with wings up to 24 mm long. Tegmina shallowly tectiform (complete insects dorsoventrally preserved). Tegmen (15) 18–19 mm long, 5–6 mm wide, more elongate in supposed male (3.7:1) than in supposed females (3.1–3.2:1). Precostal carina narrow, rather horizontal. R stem about as long as R+M stem; RA sometimes with short oblique



Figs 7–17. Mimarachnidae fam.n.: 7–12 — *Mimarachne mikhailovi* gen. et sp.n.: 7 — male(?) tegmen, holotype PIN 3064/4614; 8 — female(?) tegmen, paratype PIN 3064/4615; 9 — hindwing, paratype PIN 3064/4621; 10 — commissural carina (right arrow), claval apex, marginal membrane (left arrow) and lanceolate cell, female(?) tegmen, paratype PIN 1668/1685; 11 — female habitus, paratype PIN 1989/3575; 12 — male genitalia, paratype 3064/4018; 13–15 — *Saltissus eskovi* gen. et sp.n.: 13 — commissural carina (arrow), claval apex and lanceolate cell, female(?) tegmen, holotype PIN 1989/3590; 14 — female(?) tegmen, paratype PIN 3064/4146; 15 — male(?) forebody, paratype PIN 3064/449; 16–17 — Mimarachnidae gen.sp. indet.: 16 — mesothorax (note sensory pits and carinae on mesoscutum), PIN 3800/1601; Khetana (outcrop 2/27), Khabarovsk Region; Emanra Fm., Albian; 17 — distal part of hind leg (note macrosetae of tibial pecten — arrow), PIN 1742/608; Turga, Chita Region; Turga Fm., earliest Cretaceous. Scale interval 1 mm.

Рис. 7–17. Mimarachnidae fam.n.: 7–12 — *Mimarachne mikhailovi* gen. et sp.n.: 7 — переднее крыло самца(?), голотип ПИН 3064/4614; 8 — переднее крыло самки(?), паратип ПИН 3064/4615; 9 — заднее крыло, паратип ПИН 3064/4621; 10 — комиссуральный киль (правая стрелка), вершина клавуса, краевая кайма (левая стрелка) и ланцетовидная ячейка, переднее крыло самки(?), паратип ПИН 1668/1685; 11 — общий вид самки, паратип ПИН 1989/3575; 12 — гениталии самца, паратип ПИН 3064/4018; 13–15 — *Saltissus eskovi* gen. et sp.n.: 13 — комиссуральный киль (стрелка), вершина клавуса и ланцетовидная ячейка, переднее крыло самки(?), голотип ПИН 1989/3590; 14 — переднее крыло самки(?), паратип ПИН 3064/4146; 15 — голова и грудь самца(?), паратип ПИН 3064/449; 16–17 — Mimarachnidae gen.sp. indet.: 16 — среднегрудь (видны сенсорные ямки и кили среднеспинки), ПИН 3800/1601; Хетана (обн. 2/27), Хабаровский край; еманринская св., альб; 17 — дистальная часть задней ноги (видны макрохеты тибияльного гребня — стрелка), ПИН 1742/608; Турга, Читинская обл.; тургинская св., низы мела. Деление шкалы — 1 мм.



Figs 18–19. Venation of Mimarachnidae fam.n., schematized: 18 — tegmen (female?) and hindwing; 19 — tegmen (female?). Scale bars 5 mm.

Рис. 18–19. Жилкование Mimarachnidae fam.n., упрощено: 18 — переднее крыло (самка?) и заднее крыло; 19 — переднее крыло (самка?). Масштабные линейки 5 мм.

anterior branch near apex; RP with very short apical fork. M area [between M and CuA–CuA1] slightly wider than RP area; basal cell narrow; weak arcus between bases of M and CuA. M forked (often 3-branched) level with CuA2 apex. CuA forked before midlength of tegmen; CuA2 distinct basally, arched forwards distally (lanceolate cell beyond claval apex wider than preceding intercubital area). Arms of Y-vein [Pcu and 1A] longer than its stalk, their junction almost equidistant between claval furrow and commissural margin, the stalk clearly joining commissural margin at claval apex. Narrow marginal membrane traceable from claval apex up to beyond CuA2. Commissural carina extremely narrow. Tegmen bare, finely transversely wrinkled, in anterior half dark-speckled with four reclined dark bands, in posterior half mostly dark (excluding commissural area and lanceolate cell; dark pattern less distinct in females), with 3 black, minutely granulate ocellar spots with pale pupils (in medial area apically –doubled in PIN 3064/4615, Fig. 3 — and discally and in intercubital area subapically) and usually also fourth, small one without pupil at M1. Hindwing 14 mm long, costal margin convex proximally, R fork slightly distal to CuA fork, widened intercubital area with series of oblique crossveins. Head much narrower than thorax, eumetope tricarinate. Mesonotum with median carina doubled, lateral carinae converging anteriorly. Head and thorax with small numerous sensory pits. Male genitalia — Fig. 12. Ovipositor rather short (ca. 3 mm long) and slender, upcurved.

ETYMOLOGY. Greek *mimos* (imitator) and *arachne* (spider); gender feminine. The type species is named after my fellow colleague, arachnologist Kirill Mikhailov.

*Saltissus eskovi* Shcherbakov, **gen. et sp.n.**

Figs 4, 13–15, 19

MATERIAL. Holotype: female(?) tegmen PIN 1989/3590 (bed 31); paratypes: tegmina PIN 1668/1693, 3064/4618, 4628, 5190, 4210/1091 (bed 31), 1668/2550, 1989/3336(3339) (bed 19), 3064/4104(4148), 4146, 4152(4160), 4159, 4167 and male(?) 3064/449 (bed 15), incomplete insect 3064/447 (bed 6), clavus 1668/1669 (bed 2) — Baissa, Vitim R., Buryatia, Russia; Zaza Fm., Lower Cretaceous, Neocomian (Berriasian–Barremian, ca. 145–125 Ma).

DIAGNOSIS — see the key above.

DESCRIPTION. Tegmina steeply tectiform (complete insects laterally preserved). Tegmen 9.5–13 mm long, 3.8–5.3 mm wide, more elongate in supposed male (2.9:1) than in supposed females (2.4–2.6:1). Precostal carina widened ba-

sally, deflected dorsad. R stem longer than R+M stem; RA sometimes with short oblique anterior branch distally; RP forked (rarely 3-branched) before CuA2 apex. M area much wider than RP area; basal cell wide; indistinct arcus at R+M bifurcation. M forked nearer to claval apex. CuA forked near claval apex, CuA–CuA1 in almost straight line; CuA2 indistinct basally, passing close to claval furrow and almost straight apically (lanceolate cell narrow). Arms of Y-vein shorter than its stalk, their junction much nearer to claval furrow, the stalk joining claval furrow at claval apex (sometimes the furrow connected there to CuA2 and continued by faint vein appearing as CuA3 — e.g. PIN 3064/4146, Fig. 14). No marginal membrane. Commissural carina prominent, wavy (carinae of both tegmina put together in repose formed a crest along claval commissure). Tegmen with quite long, variously directed, adpressed dark hairs, finely granulate, rather uniformly dark-marbled, with two obscure reclined dark bands in anterior half (more distinct in supposed male) and one black ocellar spot (usually without pale pupil, with dense microsculpture, often with adjacent pale crescent) in medial area apically. Coryphe rather short, eumetope+clypeus evenly convex in profile, lateral ocellus ventral to eye, rostrum reaching beyond hind coxae.

REMARKS. Differences of two genera in the structure of commissural and precostal carinae, claval apex, and presence of marginal membrane all result from their different habitus, compressed laterally in *Saltissus* **gen.n.** and rather dorsoventrally in *Mimarachne* **gen.n.**

ETYMOLOGY. The genera *Salticus* and *Issus*; gender masculine. The type species is named after my fellow colleague, arachnologist Kirill Eskov.

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