

Review of the fossil and extant genera of the cicada family Tettigarctidae (Hemiptera: Cicadoidea)

Обзор вымерших и современных родов цикад семейства Tettigarctidae (Hemiptera: Cicadoidea)

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KEY WORDS: Hemiptera, Cicadomorpha, Cicadoidea, Tettigarctidae, fossil, phylogeny, venation, Mesozoic, Jurassic, Cretaceous, Paleogene.

КЛЮЧЕВЫЕ СЛОВА: Hemiptera, Cicadomorpha, Cicadoidea, Tettigarctidae, ископаемые, филогения, жилкование, мезозой, юра, мел, палеоген.

ABSTRACT. Tettigarctidae, the most primitive family of Cicadoidea, recorded since terminal Triassic (ca. 200 Myr) and ancestral to singing cicadas (Cicadidae), is briefly characterized. Seventeen described fossil tettigarctid genera are keyed and compared to the only extant genus (hairy cicadas); some fossil taxa are commented. Based on tegminal venation, the family is divided into two subfamilies, Cicadoprosobolinae with tribes Cicadoprosobolini **stat.n.**, Architettigini **trib.n.** and Turutanoviini **trib.n.**, and Tettigarctinae with tribes Protabanini **stat.n.**, Meunierini and Tettigarctini. *Sunotettigarcta kudryashevae* **sp.n.** (Upper Jurassic of Karatau) and *Magrebarcta* **gen.n.** for *Liassotettigarcta africana* Nel, Zarbout, Barale et Philippe are described. *Liassocicada* Bode, 1953 = *Liassotettigarcta* Nel, 1996, **syn.n.** *Shaanxiarcta* **nom.n.** is proposed for *Involuta* Zhang, 1993, non Cox, 1931. The hindwing from the Middle Eocene of Eckfeld, Germany is tentatively placed in the extant tribe Tettigarctini. Eleven fossil genera are excluded from the family.

РЕЗЮМЕ. Дана краткая характеристика Tettigarctidae, самого примитивного семейства Cicadoidea, известного начиная с терминального триаса (около 200 млн. лет назад) и предкового для певчих цикад (Cicadidae). Приведены ключи для семнадцати описанных вымерших родов теттигарктид и единственного современного; даны замечания по некоторым вымершим таксонам. По жилкованию передних крыльев семейство разделено на два подсемейства, Cicadoprosobolinae с трибами Cicadoprosobolini **stat.n.**, Architettigini **trib.n.** и Turutanoviini **trib.n.**, и Tettigarctinae с трибами Protabanini **stat.n.**, Meunierini и Tettigarctini. Описаны *Sunotettigarcta kudryashevae* **sp.n.** (верхняя юра Каратау) и *Magrebarcta* **gen.n.** для *Liassotettigarcta africana* Nel, Zarbout, Barale et Philippe. *Liassocicada* Bode, 1953 = *Liassotettigarcta*

Nel, 1996, **syn.n.** Предложено название *Shaanxiarcta* **nom.n.** для *Involuta* Zhang, 1993, non Cox, 1931. Заднее крыло из среднего эоцена Экфельда (Германия) предположительно отнесено к современной трибе Tettigarctini. Одиннадцать вымерших родов исключены из состава семейства.

Introduction

Tettigarctidae is a relict family, comprising the only extant genus of hairy cicadas with two species restricted to the mountains of Tasmania and South-East Australia. *Tettigarcta* is the most primitive living member of the superfamily Cicadoidea, autplesiomorphic in the pronotum expanded posteriorly, venation generalized, male genitalia with harpagones, tarsal empodia present, and thoracic ganglia separated [Evans, 1941; Moulds, 1990, 2005]. Unlike Cicadidae, hairy cicadas (of both sexes) produce only substrate-transmitted vibrational signals [Claridge et al., 1999] and lack auditory tympana. They prefer cool to cold climates and are confined mainly to subalpine forests; adults are active at dusk and after dark (hiding under loose bark during the day), common even in snowy season, and tolerate subzero temperatures [Moulds, 1990]. *Tettigarcta* was separated into a tribe by Distant [1905], raised to subfamily rank by Tillyard [1926] and to a full family by Becker-Migdisova [1947: 448].

Tettigarctidae were first recognized in the fossil record by Zeuner [1944] (Cenozoic of Europe) and Becker-Migdisova [1949] (Mesozoic of Asia); earlier authors described them as Diptera, Megaloptera, or Cicadidae. Becker-Migdisova [1947] first described *Cicadoprosobole* in Prosobolidae, but later transferred it to Tettigarctidae along with three other Mesozoic genera [Becker-Migdisova, 1949]. Evans [1956] separated *Cicadoprosobole* at the family level, and some other authors followed him, placing most or all Mesozoic genera into Cicadoprosobolidae [e.g. Hamil-

Table. Some tegminal characters of tettigarctid tribes and genera compared to the type genera of both subfamilies and to Cicadidae.
 Таблица. Некоторые признаки переднего крыла в трибах и родах Tettigarctidae в сравнении с типовыми родами обоих подсемейств и Cicadidae.

| Character | Cicadoprosobolinae | | | | Tettigarctinae | | typical Cicadidae |
|-------------------------|--------------------|--------------------|--------------------|---------------|----------------|------------|-------------------|
| | <i>Elkinda</i> | <i>Hylaeoneura</i> | <i>Architettix</i> | Turutanoviini | Protabanini | Meunierini | |
| basal cell width | Cc | ? | ? | a | T | T | T |
| RA branches number | a | Cc | i | i or T | i or T | T | T |
| R fork position | T' | ? | a' | Cc or T | T | T | a |
| <i>ir</i> position | C | T | i | Cc or i | T | T | T |
| marginal membrane | C | C | C | Cc | T | T | T |
| costal area width | C | ? | C | Cc | i or T | i or T | T |
| nodal line position | C | ? | i | C | Cc or i | T | T |
| RA branches length | C | C | C | C | C | T | Cc |
| M+CuA junction | a | ? | ? | a | Cc | T | T |
| apical cell behind CuA2 | a | b | T' | d | Cc | T | T |
| M fork position | C | ? | C | C | Cc | i or T | i |
| apical CuA section | T' | ? | a | C | C | Cc or T | T |
| <i>ir</i> inclination | C | a' | C | C | a | Cc | a |

C — as in *Cicadoprosobole*; T — as in *Tettigarcta*; i — intermediate state; a, b, d — aberrant; ? — unknown; a' and T' — homoplastic to 'a' and 'T' of extant cicadoids; Cc — last appearance of 'C' condition in transformation series. First four taxa show more characters in *Cicadoprosobole* state, last two — more characters in *Tettigarcta* condition, and Protabanini are about halfway between the nominate genera of two subfamilies.

C — как у *Cicadoprosobole*; T — как у *Tettigarcta*; i — промежуточное состояние; a, b, d — уклоняющиеся; ? — неизвестно; a' и T' — параллелизм по отношению к 'a' и 'T' современных цикадоидов; Cc — последнее появление состояния 'C' в трансформационном ряду. У четырёх первых таксонов преобладают признаки в состоянии как у *Cicadoprosobole*, у двух последних — в состоянии как у *Tettigarcta*, а Protabanini находятся примерно на полпути между типовыми родами двух подсемейств.

ton, 1990, 1996]. However, it is better to treat these groups as subfamilies [Boulard & Nel, 1990], because diverse Mesozoic forms fill the gap between *Cicadoprosobole* and *Tettigarcta* (Table).

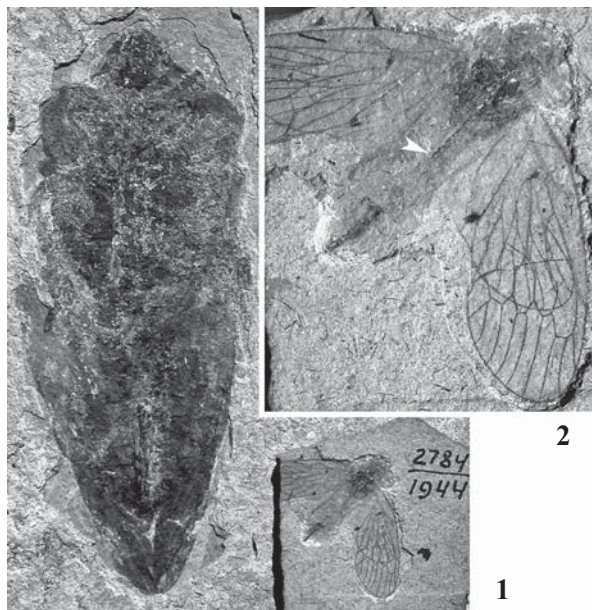
The oldest records of Tettigarctidae s.l. are from the earliest Jurassic and terminal Triassic (ca. 200 Myr) of Eurasia. Jurassic insects of Gondwana are virtually unknown, and fossil tettigarctids in the Southern Hemisphere were found only in the Lower Cretaceous of Brazil [Hamilton, 1990; Menon, 2005] and Tunisia [Nel et al., 1998]. There are no tettigarctids among ten auchenorrhynchan specimens from the well-known Cretaceous locality Koonwarra, Australia. The family persisted in Europe at least until the Middle Eocene (ca. 45 Myr) [Wappler, 2003], whereas the earliest record of Cicadidae is from the Paleocene (ca. 65 Myr) of North America [Cooper, 1941]. Eskov [1987: 98] briefly summarized the former distribution of Tettigarctidae in the Northern Hemisphere. Nel [1996] listed extinct genera which belong to (or are excluded from) the family.

Tettigarctids were structurally diverse and not rare in the Jurassic and Cretaceous, like are singing cicadas in the Cenozoic and nowadays. They varied in size from small forms, with transparent wings less than 15 mm long (*Turutanovia*, *Architettix*) to large cicadas (larger than modern *Tettigarcta*) with dark-patterned wings up to 60 mm long (Figs 1–4). Cretaceous *Elkinda* shows tegminal veins profusely branched, like in some cicadids (e.g. *Polyneura*). Tettigarctids had the beaks usually very long, and hind legs at least sometimes (e.g.

Architettix) [Hamilton, 1990] provided with jumping armature (long laterotibial spines) more developed than in recent cicadoids.

The hair covering in diverse, well preserved tettigarctids was apparently never as long and abundant as in modern hairy cicadas (*Tettigarcta* spp.). A common name of 'Mesozoic hairy cicadas' could rather be applied to another, unrelated family of large, cicada- and even moth-like Auchenorrhyncha, Palaeontinidae, because at least some palaeontinids (as seen in specimens from the Upper Jurassic of Karatau) were extremely hairy, with very long beak and unarmed legs. They presumably were crepuscular and well camouflaged on tree trunks, like living *Tettigarcta*, and the niche partition between Palaeontinidae and Tettigarctidae in the Mesozoic might be analogous to that between *Tettigarcta* and Cicadidae now.

Tettigarcta was contrasted to Cicadidae as the most primitive living genus of the superfamily, and Mesozoic tettigarctid genera permit to trace the ancestry of Cicadoidea even more clearly. All three extant superfamilies of Cicadomorpha Clypeata (Cercopoidea, Cicadoidea, Membracoidea) descended from the fourth, Mesozoic Hylcelloidea [Shcherbakov, 1996]. Cercopoids and cicadoids united by several sound synapomorphies [Emeljanov, 1987] enter the record almost synchronously and possibly represent closely related lineages; membracoids had separated from hylcelloids somewhat later. Phylogenetic position of tettigarctids was also discussed by Hamilton [1996].



Figs 1–2. Tettigarctidae from the Upper Jurassic of Karatau, Kazakhstan: 1 — the largest (specimen PIN 2239/496, 68 mm long, tegmen 55 mm long) and the smallest, *Turutanovia karatavica* Becker-Migdisova (specimen PIN 2784/1944, tegmen 12 mm long), same scale; 2 — same *T. karatavica* specimen, note long rostrum (arrow).

Рис. 1–2. Теттигарктиды из верхней юры Каратау, Казахстан: 1 — самая крупная (экз. ПИН 2239/496, длина 68 мм, длина переднего крыла 55 мм) и самая мелкая, *Turutanovia karatavica* Беккер-Мигдисова (экз. ПИН 2784/1944, длина переднего крыла 12 мм) в одном масштабе; 2 — тот же экз. *T. karatavica*, виден длинный хоботок (стрелка).

The Cenozoic genus *Meuniera*, showing tegminal venation nearest to *Tettigarcta* and Cicadidae, was separated at the tribal level [Boulard & Nel, 1990]. Mesozoic genera (15 of them described) are much more diverse, enough to be classified into four more tribes in two subfamilies, and are distinguishable according to the key below (specimens were examined for genera marked with *; some characters of *Diphtheropsis* and *Turutanovia* are based on additional specimens kept in Paleontological Institute, RAS).

KEY TO THE GENERA OF TETTIGARCTIDAE BASED ON TEGMEN

- 1 Anterior RA branches long, no less than 4 in number and/or some of them forked, totaling at least 4 terminations of RA (not counting one just beyond nodal line); marginal membrane narrow (unknown for *Diphtheropsis*). Costal area broad; basal cell slightly narrowed apically, M and CuA cross-joined or forming short stalk beyond it, CuA base not arched (unknown for *Hylaeoneura*) Cicadoprosobolini **stat.n.** 2
- Anterior RA branch(es) simple, single (rarely two), totaling 2(3) terminations of RA. Basal cell of other shape 5
- 2 Tegmen narrow (clavus length/prenodal width ~1.7), prenodal part coriaceous with weak veins and no distinct punctures. M forked almost at nodal line. Both M and CuA slightly sigmoidal, cross-joined beyond basal cell *Diphtheropsis* Martynov
- Tegmen broader, with stronger veins and/or distinctly punctate. M forked at 0.7–0.8 distance to nodal line ... 3

- 3 All veins profusely branched beyond nodal line; about 30 apical cells. CuA with more than 2 branches; apical cell behind posterior CuA branch much wider than next apical cells. M and CuA forming short stalk beyond basal cell *Elkinda* Shcherbakov
- Less than 15 apical cells. CuA with 2 branches; apical cell behind CuA2 narrower than next apical cell 4
- 4 Transverse *ir* nearer to nodal line than to wing tip. Basal CuA1 section converging to M3+4. Apical cell behind CuA2 short and narrow. RA bent at nodal line. Both M and CuA slightly sigmoidal, cross-joined beyond basal cell *Cicadoprosobole* Becker-Migdisova
- Reclined *ir* nearer to wing tip than to nodal line. Basal CuA1 section subparallel to M3+4. Apical cell behind CuA2 little narrower than and more than 1/2 as long as next apical cell *Hylaeoneura* Lameere et Severin
- 5(1) M3+4 simple. Nodal RA branch distant from nodus. Neither apical CuA section nor CuA2 running along nodal line (the former inclined, the latter reclined and ending at claval apex). Wing margin with torus (angle beyond claval apex); apical cell in CuA fork and next anterior one of similar size and shape. RP separating distally, near nodal line. Costal area broad, prenodal part punctate. Marginal membrane as narrow as ambient vein. Cicadoprosobolinae: *Architettigini trib.n.* *Architettix* Hamilton
- M3+4 forked. Nodal RA branch just at nodus. CuA2 base and often also apical CuA section running along nodal line. Wing margin rounded beyond claval apex; apical cell in CuA fork dissimilar to next anterior one. RP separating proximally, near basal cell 6
- 6 Basal cell narrow, tapered to apex; CuA base arched forwards forming smooth curve with M+CuA stalk beyond basal cell. *ir* no nearer to wing tip than to nodal line; apical cell behind CuA2 very narrow (unknown for *Shuraboprosobole*). Marginal membrane near wing tip as narrow as ambient vein. Costal area wider than intercubital one. Veins often dark but not dark-margined. Cicadoprosobolinae: *Turutanoviini trib.n.* 7
- Basal cell wide, not narrowed to apex; CuA bent at arculus or cross-junction of M and CuA. *ir* nearer to wing tip than to nodal line; apical cell behind CuA2 either moderately narrow or absent. Marginal membrane much wider. Costal area usually no wider than intercubital one. Often some veins broadly dark-margined. Tettigarctinae 9
- 7 Both M+CuA stalk and R stem equally short. Costal margin strongly arched near base. Prenodal part punctate with concolorous veins and few diffuse spots on speckled background. Tegmen more than 30 mm long *Shuraboprosobole* Becker-Migdisova
- M+CuA stalk much shorter than R stem. Costal margin weakly, evenly arched. Tegmen pale with dark veins and few small dark spots, no more than 22 mm long 8
- 8 *ir* halfway from nodal line to wing tip. CuA1 beyond *mcu* deflected anteriorly, running along margin *Paraprosobole* Whalley
- *ir* nearer to nodal line than to wing tip. CuA1 beyond *mcu* converging to margin ... *Turutanovia* Becker-Migdisova
- 9(6) M forked just before nodal line. M and CuA cross-joined beyond basal cell. Distal CuA2 section diverging from nodal line, separating small apical cell. Nodal line beyond or at midwing. RA continued with long anterior branch; anteriormost apical cell narrow triangular; *ir* reclined. Protabanini **stat.n.** 10
- M forked proximally, no nearer to nodal line than to basal cell. M and CuA connected by short arculus. CuA2 running

- along nodal line up to claval apex. Nodal line before midwing. RA forked distad of *im*, its anterior (and sometimes posterior) branch short; anteriormost apical cell linear; *ir* transverse to inclined (unknown for *Kisylia*) 14
- 10 Costal area wider than intercubital one, finely punctate. Two anterior RA branches. M forked at ~2/3 distance from basal cell to nodal line. Prenodal part coriaceous 11
- Costal area narrower than intercubital one, impunctate. Single anterior RA branch. M forked just before nodal line. Tegmen membranous 12
- 11 CuA stem distally diverging from CuP (intercubital area widest at nodal line). Costal margin rather evenly arched. Prenodal part with dark bands, postnodal part pale
..... **Sunotettigarcta* Hong
- CuA stem converging with CuP (intercubital area widest beyond basal cell). Costal margin more arched proximally. Tegmen entirely suffused, with dark spots along anterior margin *Magrebarcta* **gen.n.**
- 12(10) . Costal margin straight, costal area basally no wider than basal cell. Posterior 2/3 of tegmen dark with pale veins *Tettagalma* Menon
- Costal margin convex, costal area wider. Tegmen pale with dark spots and bands along veins 13
- 13 Subapical cell between M1+2 and M3+4 about twice longer than apical cell between M2 and M3
..... **Liassocicada* Bode (= *Liassotettigarcta* Nel, **syn.n.**)
- Subapical cell between M1+2 and M3+4 slightly longer than apical cell between M2 and M3 *Protabanus* Hong
- 14(9) M forked halfway from basal cell to nodal line; R stem longer than 1/2 M stem. Apical CuA section running along nodal line quite long. Costal area wider than intercubital one. Meunierini **Kisylia* Martynov
- M forked more proximally; R stem shorter. Apical CuA section along nodal line short or undeveloped. Costal area no wider than intercubital one 15
- 15 Costal margin deeply arched near base. RA fork level with M1+2 fork; *ir* transverse. Meunierini *Meuniera* Piton
- Costal margin shallowly, evenly arched. RA fork level with inclined *ir*. *Tettigarctini* **Tettigarcta* White

KEY TO THE GENERA OF TETTIGARCTIDAE FOR WHICH (ONLY) HINDWING IS DESCRIBED

- Incompletely known hindwing of *Architettix* not included, but runs to *Turutanovia*. Incomplete hindwing from Eckfeld runs to *Tettigarcta*.
- 1 Anteriormost apical cell (before RA) no narrower than posteriormost one (CuA fork). Costal area forming triangular projection as high as interradiar area. R forked just below apex of this projection. Cicadoprosobolinae 2
- Anteriormost apical cell narrow, posteriormost one wide. Costal area narrower than interradiar one, at most low triangular. *Tettigarctinae* 3
- 2 CuA forked proximally, nearer to R fork than to M fork; CuA fork as narrow as next apical cells. Both *ir* and *mcu* curved. Cicadoprosobolini? *Shaanxiarcta* **nom.n.**
(= *Involuta* Zhang; tegmen unknown)
- CuA forked nearer to M fork; CuA fork wider than next apical cells. *ir* transverse; *mcu* curved (long and nearly longitudinal in aberrant hindwing provisionally assigned to the genus by Shcherbakov [1986])
..... **Turutanovia* Becker-Migdisova
- 3(1) R forked about halfway to apex of costal projection. Anteriormost apical cell as wide as next one. Subtransverse *ir* nearer to coupling lobe than to wing tip. *mcu* short, inclined. CuA2 subparallel to both distal CuA1 and

- CuP. Pcu apex twice nearer to 1A than to CuP [Whalley, 1983, fig. 1]. Dark band at crossveins. Protabanini?
..... *Eotettigarcta* Zeuner (tegmen unknown)
- R forked nearer to wing base. Anteriormost apical cell narrower than next one. Inclined *ir* nearer to wing tip. *mcu* long, longitudinal. CuA2 diverging from CuA1 and converging with CuP. Pcu apex nearly equidistant from CuA2 and 1A. No dark bands **Tettigarcta* White

Systematic list of fossil Tettigarctidae

Tettigarctidae Distant, 1905

- = Cicadoprosobolidae Evans, 1956;
= Protabanidae Hong, 1982

Cicadoprosobolinae Evans, 1956

Cicadoprosobolini Evans, 1956, **stat.n.**

- (Lower Jurassic – Lower Cretaceous of Eurasia)
Cicadoprosobole sogutensis Becker-Migdisova, 1947, lowermost Jurassic (Dzhil Formation) of Kyrgyzstan (formerly reported as Triassic);
Diphtheropsis incerta Martynov, 1937 (originally described as Homoptera inc. sed.), Lower (?Middle) Jurassic of Kyrgyzstan; transferred to Cicadoprosobolidae by Hamilton [1992];
Diphtheropsis sp., lowermost Jurassic (Dzhil Formation) of Kyrgyzstan (see below);
Elkinda hecatoneura Shcherbakov, 1988, Lower Cretaceous of Transbaikalia;
Hylaeoneura lignei Lameere et Severin, 1897 (as Megaloptera), ?Aptian of Belgium; transferred to Tettigarctidae by Becker-Migdisova [1949];
possibly also:
Shaanxiarcta Shcherbakov, **nom.n.** (= *Involuta* Zhang, 1993, non Cox, 1931, Gastropoda): *Shaanxiarcta perrara* (Zhang, 1993) **comb.n.**, Lower Cretaceous of China (Shaanxi), hindwing;
Liassocicada ignota (Brodie, 1845) (as Diptera), uppermost Triassic (Rhaetian) of England (see below).

Turutanoviini Shcherbakov, **trib.n.**

- (Lower Jurassic – Lower Cretaceous of Eurasia; type genus *Turutanovia* Becker-Migdisova, 1949)
Turutanovia karatavica Becker-Migdisova, 1949, Upper Jurassic of Kazakhstan;
Turutanovia sp., Middle Jurassic of Central Mongolia [Shcherbakov, 1986];
Turutanovia sp., Lower (?Middle) Jurassic of South Siberia [Shcherbakov, 1985];
? *Turutanovia* sp., Lower Cretaceous of West Mongolia [Shcherbakov, 1986]; hindwing;
Paraprosobole rotruda Whalley, 1985, Upper Sinemurian of England;
Shuraboprosobole plachutai Becker-Migdisova, 1949, Lower (?Middle) Jurassic of Tadzhikistan;
Shuraboprosobole sp., Lower (?Middle) Jurassic of South Siberia [Shcherbakov, 1985];
possibly also:
gen. et sp. indet., Upper Sinemurian of England [Whalley, 1985: 141].

Architettigini Shcherbakov, **trib.n.**

- (Lower Cretaceous of Brazil; type genus *Architettix* Hamilton, 1990)
Architettix compacta Hamilton, 1990, Aptian of Brazil (see below).

Tettigarctinae Distant, 1905Protabanini Hong, 1982, **stat.n.**

(Lower Jurassic – Lower Cretaceous and possibly Paleocene of Eurasia and Africa)

Protabanus chaoyangensis Hong, 1982 (as Diptera), Middle Jurassic of China (Liaoning); transferred to Tettigarctidae by Hamilton [1992] and Zhang et al. [1993];

Liassocicada antecedens Bode, 1953 (as Cicadidae), Upper Liassic of Germany; transferred to Tettigarctidae by Hamilton [1992] and Shcherbakov [1996];

Liassocicada mueckeii (Nel, 1996) **comb.n.**, Upper Liassic of Germany (see below);

Tettagalma striata Menon, 2005, Aptian of Brazil;

Magrebarcta africana (Nel, Zarbout, Barale et Philippe, 1998), **comb.n.**, Aptian of Tunisia (see below);

Sunotettigarcta hebeiensis Hong, 1983, Middle Jurassic of China;

S. kudryashevae **sp.n.**, Upper Jurassic of Kazakhstan (see below);

possibly also

Eotettigarcta scotica Zeuner, 1944, Paleocene (Danian) of Isle of Mull, Scotland; hindwing [Whalley 1983: as Eocene].

Meunierini Boulard et Nel, 1990

(Lower Jurassic – Paleocene of Eurasia)

Meuniera haupti Piton, 1936 (as Cicadidae), Paleocene of France; transferred to Tettigarctinae by Cooper [1941: 301]; more thermophilous than *Tettigarcta* (subtropical paleo-oclimatic [Boulard & Nel, 1990]);

Kisylia psylloides Martynov, 1937 (as Homoptera inc. sed.), Lower (?Middle) Jurassic of Kyrgyzstan; transferred to Cicadoprosobolidae by Hamilton [1990].

possibly also

nymphal exuvium in amber, Upper Cretaceous (Turonian, ca. 90 Myr) of New Jersey [Shcherbakov, 2004; Grimaldi & Engel, 2005; Shcherbakov, in prep.].

Tettigarctini Distant, 1905

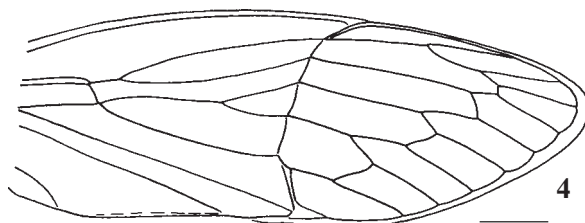
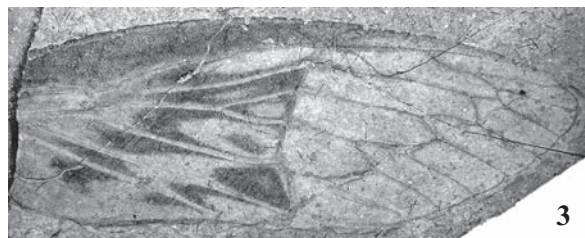
(Eocene – Recent)

gen. et sp. indet., Middle Eocene (Lutetian) of Eckfeld, Germany; incomplete hindwing [Wappler, 2003]. Very similar to *Tettigarcta*.

Remarks and new taxa

Diphtheropsis Martynov, 1937 is a poorly known genus. *D. incerta* Martynov, 1937 is based on anterior prenodal part of large tegmen. Very similar but smaller and apparently not conspecific prenodal part of tegmen from somewhat older deposits (*Diphtheropsis* sp., PIN 371/525, Sogyuty, Kyrgyzstan; Dzhi Formation, lowermost Jurassic) shares enough characters with *Cicadoprosobole* to be included into the same tribe.

'*Liassocicada*' *ignota* (Brodie, 1845) was originally described as *Asilus? ignotus* from the Lillstock Formation, Rhaetian of England. The formation is considered uppermost Triassic, but a Jurassic ammonite was once collected in the underlying Westbury Formation [Donovan et al., 1989]. Whalley [1983] transferred the species to the genus *Liassocicada* Bode (as *L. ignotata*) and assigned this genus to Cicadidae. Carpenter [1992] doubted this family placement, leaving the genus in Homoptera incertae familiae. Shcherbakov [1996] transferred this species to Tettigarctidae. Tegminal venation is mostly invisible, but the large CuA fork, inclined *mcu*, and traces of nodal line [see Whalley, 1983, fig. 7]



Figs 3–4. *Sunotettigarcta kudryashevae* **sp.n.**, holotype PIN 2784/2163, Aulie, Upper Jurassic of Karatau, Kazakhstan: 3 — tegmen; 4 — its venation. Scale bar 5 mm.

Рис. 3–4. *Sunotettigarcta kudryashevae* **sp.n.**, голотип ПИН 2784/2163, Аулие, верхняя юра Каратау, Казахстан: 3 — переднее крыло; 4 — его жилкование. Масштабная линейка 5 мм.

confirm the placement into Tettigarctidae. Hindwing venation as traceable in the holotype [ibid., fig. 2] excludes the species from Tettigarctinae, being even more primitive than in the known hindwings of other Cicadoprosobolinae in the S-shaped Pcu distally diverging from 1A and converging to CuP (anal areas of left and right wings overlap up to CuP). Therefore, '*L. ignota*' does not belong to the genus *Liassocicada* and possibly represents an undescribed genus. One of several '*L. ignota*' specimens was suggested to be a nymph [Whalley, 1983: 145], but is similar in all essential respects to the others, doubtless adults.

Architettix compacta Hamilton, 1990. One of paratypes was supposed to be a nymph [Hamilton, 1990], but its long tarsi and fully developed male genitalia are definitely adult features.

Liassocicada Bode, 1953 (= *Liassotettigarcta* Nel, 1996, **syn.n.**). The type species of these genera, both from the Upper Liassic of Germany, are so similar in the size, venation and colour pattern that may be conspecific.

Magrebarcta Shcherbakov, **gen.n.** Type species *Liassotettigarcta africana* Nel, Zarbout, Barale et Philippe, 1998. The species differs considerably from *Liassocicada* and *Protabanus* and is placed in a separate genus, related to *Sunotettigarcta* (for diagnostic characters see the key above).

Sunotettigarcta hebeiensis Hong, 1983. The species based on incomplete prenodal part of tegmen doubtless belongs to Protabanini and is distinct at generic level. The genus seems to be the most primitive in the tribe; the second species is described below.

Sunotettigarcta kudryashevae Shcherbakov, **sp.n.**

MATERIAL. Holotype right tegmen PIN 2784/2163 (part & counterpart) — Aulie (Mikhailovka), Karatau Range, South Kazakhstan; Karabastau Formation, Upper Jurassic, Oxfordian–Kimmeridgian (ca. 155 Ma).

DESCRIPTION (Figs 3–4). Tegmen ca. 47 mm long, elongate (3:1). Costal margin rather evenly arched, costal area wider than intercubital one. Nodal line beyond midwing. Two anterior RA branches; *ir* short. M forked at ~2/3 distance from basal cell to nodal line. CuA stem distally diverging

from CuP. Prenodal part somewhat coriaceous, with punctate, dark costal area and two oblique dark bands from clavus to nodal line; postnodal part mostly pale.

COMPARISON. Distinct from *S. hebeiensis* Hong, 1983 (reconstructed tegmen length ca. 26 mm) in the larger size and different colour pattern.

ETYMOLOGY. After Irina V. Kudryasheva, an expert in nymphal Cicadidae.

Taxa excluded from Tettigarctidae:

Austroprosbole Evans, 1943 (Permian of Australia), *Austroprosboloides* Riek, 1973 (Permian of S. Africa) and *Prosbolomorpha* Riek, 1974 (Triassic of S. Africa), described in Cicadoprosobolidae, were transferred to Dunstaniidae [Shcherbakov, 1984]. Triassic *Mesodiphthera* Tillyard, 1919 (Australia) and *Shaandongia* Hong, 1985 [in Liu et al., 1985] (China) assigned to Cicadoprosobolidae by Hamilton [1992] belong elsewhere. Triassic *Leptoprosbole* Riek, 1976 (S. Africa), *Quadrisbole* Lin, 1986, *Lacunisbole* Lin, 1986, *Kerjievoprosbole* Lin, 1992, and Jurassic *Luanpingia* Hong, 1983 (all China) described in Tettigarctidae belong elsewhere. Cretaceous *Sinocicadia shandongensis* Hong et Wang, 1990 (China) described in Tettigarctidae belongs to Fulgoroidea.

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