

## SYSTEMATICS AND PHYLOGENY OF PERMIAN CICADOMORPHA (CIMICIDA AND CICADINA)

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**ABSTRACT:** The systematics of Permian cicadomorphs are reviewed at the family level. The rank of four taxa are changed, and six other taxa have been relegated to synonymy. A new family, the *Serpentivenidae*, is described, including a new genus and species, *Serpentivena tigrina*. Diagnoses based on the forewing are presented for all taxa. An outline of the forewing morphology is given. Evolution of the cicadomorphs during the Permian Period is briefly discussed.

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The forewings of cicadids are encountered in the fossil state significantly more often than the hindwings, and provide the investigator with better diagnostic features than the remains of bodies deformed during burial. Previously, in descriptions of extinct cicadids, by no means all the important characters of the forewing have been recorded, so that the systematic position of many forms has been erroneously determined. Study of the forewings of all modern [11], and most extinct families of cicadids, has enabled the author to broaden the scope of the characters used in diagnosis, and to reconsider current views on the systematics of extinct representatives of the suborder.

The suborder Cicadina has been divided into two infraorders, Cicadomorpha and Fulgoromorpha [20]. The latter includes two superfamilies only — the Permian Coleoscytoidea (stat. nov.) and the Fulgoroidea, known from the Late Permian to the present. The author intends to discuss the origin and early evolution of the fulgoromorphs in a subsequent paper. The families Prosbolidae [1], Dysmorphoptilidae (= Eoscartrellidae) [15], Scytinopteridae [3], and Stenoviciidae [4], and the superfamily Palaeontinoidea (Dunstaniidae, Mesogereonidae, and Palaeontinidae) [2, 5], represented in the Permian, have been correctly assigned to the cicadomorphs, and also the Mesozoic families Hylcellidae, Archijassidae [5], Cicadoprosbolidae, Proceropidae [15], and Ipsviciidae [4]. In addition, on the basis of the wing structure, the families Pereboriidae and Mundidae, previously placed in the Fulgoroidea [3, 9], the Prosbolopseidae, close to the Coleorrhyncha [3], the Cicadopsyllidae, described among the Sternorrhyncha [8], the Ignatolidae, considered a transitional group between the Protoblattoidea and the Homoptera [22], and the Paraknightiidae, earlier included in the bugs [14], must be included in the cicadomorphs.

A few genera, described from isolated hindwings, have not been considered in this paper. The genera *Kaltanopibrocha*, *Kondomoprobole* and *Mesoatraxis* are known from forewings, but not hindwings, as was erroneously indicated in the original descriptions [2, 4].

All the material on the genera mentioned in this work, housed in the collections of the Paleontological Institute, AN SSSR, and also the photographs of type species of all the Australian genera, except *Elliptoscarta* and *Triassocixius*, and the South African genus *Ignotala*, kindly presented by Dr. Ya. Kukalova-Pek (Carleton University, Ottawa), have been examined by the author. I thank A.P. Rasnitsyn and A.G. Ponomarenko (PIN), and A.F. Yemel'yanov (Zoological Institute of Academy of Sciences of the USSR (ZIN)), for discussions and help with the work.

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## MORPHOLOGY OF THE FOREWINGS OF THE CICADIDS

The structures of the forewing, being morphologically stable, and consequently, valuable in clarifying the relations between cicadid families, as a rule, perform one of three functions: they fix its base to the thorax at rest, they ensure its coupling with the hindwing during flight, or they determine the nature of the deformation of the wing during the time of vibration (flapping).

The fixation of the wing on the thorax in the cicadomorphs is achieved through the lower carinae of C and Sc, and the posterobasal margin of the clavus. On C, there are up to three carinae [6], of which the lower and upper are more weakly developed, and in impressions are most commonly concealed in the rock, whereas the forewing is deflected upwards and forms a *rant* (Fig. 1a, d, f) between C and the edge of the wing (new terms and symbols are shown in italics). The rant is widest near the base, where C is usually bent backwards and forms the *basal bend* of C. In many cicadomorphs, this bend appears as the angle from which a short lower carina (CP) extends (Fig. 1d-f; 2a). In the ignotalids and palaeontinoids, the costal field is divided along a median ridge (Fig. 2b). In the scytinopteroids, the rant as far as the basal bend of C, is subdivided by an arcuate line (Fig. 1f), beyond the apex of which is a small spindle-like convex portion of the rant. Sc is concave at the base and passes along R + M (Fig. 1a; 2a), and in the scytinopteroids, it is strongly convex anteriorly over some distance, and forms an arc (Fig. 1e-g). Distally, Sc is fused with R, and in the ignotalids and some palaeontinoids, it is secondarily free. The base of the lower carina of C and CP is fixed on the mesopleura, and the short lower carina of Sc on the metapleura, as in modern cercopoids. The posterobasal margin of the clavus in all cicadids is inserted into a groove along the lateral margin of the mesoscutellum. In the paranaitiids, the clavi of the right and left wings are fixed, one above the other, as a result of overlap of convex bands passing along their posterior margins.

The structure of the clavus (the regions of the wing, lying behind CuP) has in many ways been determined by the position and length of the fold that serves for coupling with the hindwing. The coupling fold developed along the posterior margin of the clavus, and this margin was freed from the apices of veins Pcu and A<sub>1</sub> (notation according to [17]) as a result of the confluence of A<sub>1</sub> with Pcu, and Pcu + A<sub>1</sub> into the apex of the clavus or close to it. Among the cicadomorphs, a similar structure of the clavus is clearly seen only in primitive forms (Fig. 1a-c, e, h). In more advanced representatives of the infraorder, the anal field, which abuts the posterior margin of the clavus, is folded back in the distal part and reduced (Fig. 1d; 2), and consequently the *anal carina* (Fig. 1d, g; 2a), developed along the distal part of A<sub>1</sub> and Pcu + A<sub>1</sub>, appears to be part of the posterior margin of the clavus. Such a condition with "free" Pcu and A<sub>1</sub> appears to be primitive, but is in fact secondary. In scytinopteroids, the inclination of the anal field, on the other hand, decreases in association with the shifting of the coupling fold from the posterior margin of the clavus toward Pcu + A<sub>1</sub>, and probably, its shortening.

Deformation of the wing in flight took place mainly along folds. The morphologically most distinct longitudinal fold is the claval, which passes along CuP and bifurcates toward the base. The portion of the wing between the branches of the claval fold, the *cubital triangle* (Fig. 1f), encloses a short common trunk of CuA + CuP; in the fulgoromorphs, it is reduced. Of the transverse folds, the nodal line is usually the most strongly developed (Fig. 1b; 2b), joining the apices of the rant and clavus. It divides the remigium (the region of the wing, lying forward of CuP) into pre- and post-nodal parts. The nodal line is usually morphologically weakly expressed, and its position depends on the variation in thickness and sign of the longitudinal veins, their breaks or bends, the arrangement of the transverse veins in the series, or variation in the nature of the sculpture.

Near the apex of the rant, the free apical segment of Sc passes into the wing margin, extending from R and designated R<sub>a</sub> (according to [7]); Fig. 1a, c, g, h; 2a); R<sub>a</sub> in a number of primitive cicadomorphs retains a subcosta with typical concavity, and is frequently displaced with R<sub>1</sub> into the trunk of R (Fig. 1g), and in cases where the subcosta is secondarily freed, is reunited with it. R<sub>a</sub> may bear additional branches. Of them, the prenodal branches, located more basally than R<sub>a</sub> (Fig. 1c; 2), have a subcostal origin and may extend from R, the first segment of R<sub>1</sub> (from the base up to R<sub>a</sub>), and from R<sub>a</sub> itself (Fig. 2a). The additional post-nodal branches (Fig. 1c; 2a) usually extend from R<sub>1</sub> beyond R<sub>a</sub>, but in a number of cicadomorphs, they are partially displaced onto R<sub>a</sub> and assume a longitudinal direction (Fig. 1h).

In the scytinopteroids, instead of the nodal line from which a groove sometimes remains (Fig. 1g), another transverse fold, the costal effraction, is developed [14] (Fig. 1e-g), joining the apex of the basal cell with the anterior margin of the wing. The basal cell is bordered by the sides of R + M and the first segment of CuA, and is closed at the apex by the first segment of M and either the arculus (the transverse

vein between M and CuA (Fig. 2a) or the anastomosis, formed by the fusion of M and CuA at a single point (Fig. 1e) or over some distance (Fig. 1h).

Sculpture sometimes covers the entire wing, but is usually concentrated in definite regions of the wing [25], primarily on the clavus, and the costal and anterocubital fields. Macrosculpture most commonly comprises the modified bases of hairs: on the wing membrane, indented points, pits, or granules, and on the veins, grains. Macrosculpture, in each element of which a pit and a tubercle, situated near the wing base, are combined, is termed rasp-like. Microsculpture is not associated with hairs and consists of smaller elements, filling the spaces in the macrosculpture. Near the contact between the lower side of the costal field (in sectionally-constructed wings) and the tip of the metafemur, the elements of the microsculpture may be united in the costellae of the stridulating field [16].

The structure of the post-nodal portion of the wing plays a definite aerodynamic role. The vein passing along it is lightly corrugated in some cases, and in others, bears a marginal rim (Fig. 1h; 2).

## SYSTEMATIC REVIEW OF PERMIAN CICADOMORPHS

### INFRAORDER CICADOMORPHA Latreille, 1802

Cicadariae: Latreille, 1802

Cicadomorpha: Evans, 1946, p. 57.

Jassidomorpha: Evans, 1946, p. 57.

Prosbolomorpha: Popov, 1980, p. 58 (syn. nov.).

Diagnosis. The cubital triangle encloses the whole of the short, common trunk of CuA + CuP. The basal cell and the first segment of the CuA are long. Pcu and A<sub>1</sub> fuse usually in the distal third of the clavus, and Pcu + A<sub>1</sub> enter its apex (rarely into CuP and never into the posterior margin of the clavus). The anal field, without strong transverse veins, is frequently bent back in the distal part. Macrosculpture is, as a rule, developed and is almost always dotted. Often (especially in primitive forms), a nodal line or costal effraction is developed, the basal bend C is strong, the rant beyond it is sharply constricted, and the basal cell is closed by anastomosis or by a short arculus.

Composition. In addition to the four superfamilies described below, the infraorder contains the Mesozoic-Cenozoic Cicadoidea, Cercopoidea, and Cicadelloidea, and also not less than two undescribed Mesozoic superfamilies.

### SUPERFAMILY PROSBOLOIDEA Handlirsch, 1906

Prosbolidae: Handlirsch, 1906-1908, p. 390.

Prosboloidea: Yemel'yanov, 1977, p. 38 (pars).

Diagnosis (Figs. 1a-d; 2a). No costal effraction. Rant not subdivided at the base, costal field without median projection. Sc without arc, fusing with R immediately beyond the basal cell, concave (sometimes excluding a small sector in front of the fusion). R<sub>a</sub>, as a rule, without post-nodal branches. A nodal line is normally developed, and less frequently, absent. The transverse m-cu (the only one or the first) without a longitudinal segment, short, and/or does not pass along the nodal line. CuA without displacement along the nodal line. The anal field is, as a rule, strongly constricted distally, and inclined or bent back. The macrosculpture is concentrated in the prenodal part of the wing, or less frequently, covers the wing uniformly.

Composition. Four families.

### FAMILY INGRUIDAE Becker-Migdisova, 1960, stat. nov.

Ingruidae: Bekker-Migdisova, 1946, p. 753 (nom. nud.)

Ingruinae: Bekker-Migdisova, 1960, p. 18.

Diagnosis (Fig. 1a). Rang, beyond the faintly noticeable basal bend of C, scarcely constricted, no CP. Sc, toward the apex of the basal cell, extends from R + M, and is convex in front of the depression in R. Basal cell closed by arculus or punctate anastomosis, scarcely narrowing toward apex. R<sub>a</sub> simple, not longer than first segment of R<sub>1</sub>. M, beyond basal cell, curved toward R or straight; M<sub>3+4</sub>, as rule, simple. Transverse veins two in number (r-m and m-cu), and sometimes a further two are added to them on the nodal line. Anal field distally weakly constricted and inclined. Macrosculpture of weak pits or scarcely noticeable punctae, distributed uniformly along wing. No stridulating field.

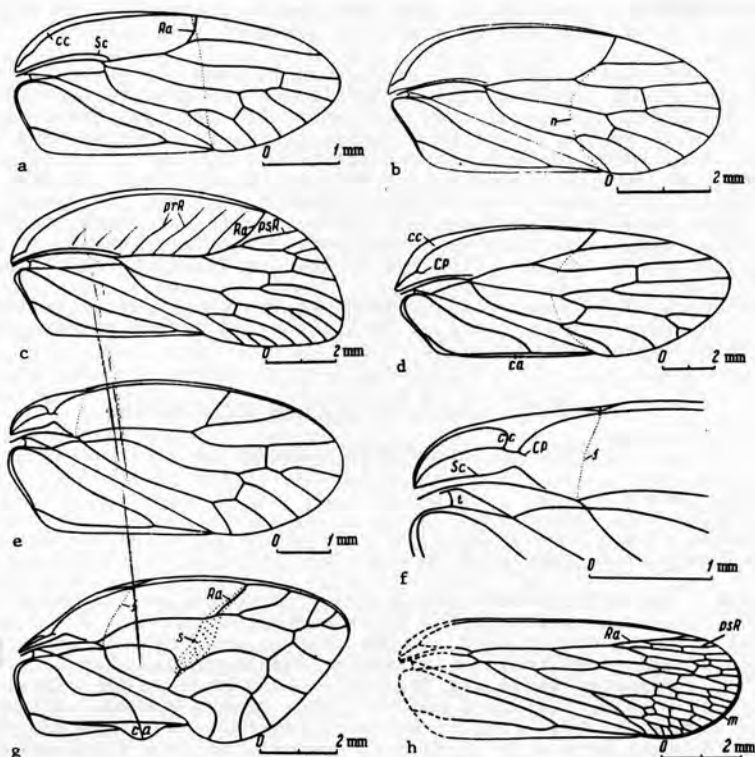


Fig. 1. Forewings of Permian and Triassic cicadomorphs: a) *Scytoneurella major* G. Zalesky; Spec. No. 1700/29; Ural forelands, Sylva River at Chekarda village; Lower Permian, Kungurian Stage; b) *Prosboloneura kondomensis* Becker-Migdisova; holotype No. 679/17; Kuzbass, Kaltan locality; Upper Permian, Kuznetsk Formation; c) *Prosbolopsis ovalis* Martynov; Spec. No. 3353/715; Arkhangel'sk oblast', Soyana River; Upper Permian, lower Kazanian substage; d) *Permocicada integra* Becker-Migdisova; Spec. No. 3353/759; Arkhangel'sk oblast', Soyana River; Upper Permian, lower Kazanian substage; e, f) *Scytinoptera sibirica* Becker-Migdisova; e) Spec. No. 1197/565, f) Spec. No. 600/356, base of wing; Kuzbass, Kaltan locality; Upper Permian, Kuznetsk Group; g) *Serpentivena tigrina* sp. nov.; holotype No. 2785/3635 (anal carina, illustrated from Spec. No. 2240/3424); Southern Fergana, Dzhaylyaucho locality; Middle-Upper Triassic, Madygen Formation; h) *Szytophara extensa* Martynov; holotype No. 100/16; Orenburg oblast', Kargala settlement; Upper Permian, lower Tatarian substage. Abbreviations: ca) anal carina; cc) rant; CP) additional lower carina in costal field; f) costal effraction; m) marginal rim; n) nodal line; prR) prenodal branch of R; psR) post-nodal branch of R; s) nodal groove; t) cubital triangle; other notations are standard.

**Composition.** *Scytoneurella* G. Zal.; Lower Permian of Europe; *Ingruo* B.-M., *Permododa* B.-M., and *Kaltanospes* B.-M.; Upper Permian of Eurasia.

#### FAMILY PROSBOLOPSEIDAE Becker-Migdisova, 1946

Prosbolopsidae: Bekker-Migdisova, 1946, p. 757.

Prosbolopseidae: Bekker-Migdisova, 1960, p. 85.

**Diagnosis** (Fig. 1b, c). Rant, beyond the basal bend of C, is scarcely constricted, and there is no CP. Sc passes close to R + M, and is concave. The basal cell, as a rule, is closed by a punctate anastomosis, and usually narrows at the apex.  $R_a$  is simple and comparatively short or slants more weakly than the post-nodal branches of R. M beyond the basal cell as it were slightly curved toward  $CuA$ ;  $M_{3+4}$  most often simple. Transverse veins two (r-m and m-cu), three (plus ir), or

several. Anal field strongly constricted distally and inclined. Macrosculpture usually made of punctae, concentrated in the costal field and on the clavus. No stridulating field.

Composition. Two subfamilies.

#### SUBFAMILY IVAIINAE Becker-Migdisova, 1960

Ivaiidae: Bekker-Migdisova, 1946, p. 753 (nom. nud.).

Ivaiinae: Bekker-Migdisova, 1960, p. 24.

Mundidae: Bekker-Migdisova, 1960, p. 31 (syn. nov.).

Diagnosis (Fig. 1b). C, up to basal bend, usually diverges strongly from R + M. As a rule, the basal cell does not reach the level of the mid-length of the clavus and the first segment of CuA diverges from the posterior margin of the clavus.  $R_2$  is shorter than half  $R_1$ , simple. As a rule, there are no post-nodal branches of R, no transverse ir, and branches on  $M_{3+4}$  and CuA. The post-cubital field is wide.

Composition. *Ivaia* B.-M., *Anaprosbole* B.-M., *Scytoneura* B.-M., *Permopibrocha* Mart.; Upper Permian of Europe; *Mundus* B.-M., *Sojanopsylla* B.-M., and *Cicadopsis* B.-M.; Upper Permian of Eurasia; *Prosboloneura* B.-M.; Upper Permian of Siberia; in addition, undescribed genera from the Lower Permian of Europe and the Upper Permian of Europe and Siberia.

#### SUBFAMILY PROSOLOPSEINAE Becker-Migdisova, 1946, stat. nov.

Prosolopsidae: Bekker-Migdisova, 1946, p. 757 (pars).

Prosolopseidae: Bekker-Migdisova, 1960, p. 85.

Diagnosis (Fig. 1c). C, up to basal bend, almost parallel to base of R + M. Basal cell reaches the level of the mid-length of the clavus, and the first segment of CuA is almost parallel to the posterior margin of the clavus.  $R_2$  longer than half of  $R_1$ . Post-nodal branches of R (usually the first of them, as it were, extends from  $R_2$ ) and a transverse ir are developed, and  $M_{3+4}$  and/or  $CuA_1$  are branched. Post-cubital field narrow.

Composition. *Prosolopsis* Mart.; Upper Permian of Europe; *Kaltanopibrocha* B.-M.; Upper Permian of Siberia.

#### FAMILY PROSBOLIDAE Handlirsch, 1906

Prosbolidae: Handlirsch, 1906-1908, p. 390.

Cicadopsyllinae: Martynov, 1930, p. 172 (syn. nov.).

Permoglyphidae: Evans, 1943, p. 183 (syn. nov.).

Permocicadopsidae: Bekker-Migdisova, 1946, p. 748.

Sojanoneuridae: Bekker-Migdisova, 1946, p. 750.

Permojassinae: Bekker-Migdisova, 1960, p. 17 (syn. nov.).

Diagnosis (Fig. 1d). Rant is beyond basal bend of C and markedly constricted, even if a very short CP is developed. Sc parallel to R + M, concave, usually weakened distally. Basal cell closed by a punctate anastomosis, less frequently by a short arculus, usually gradually narrowing toward the apex.  $R_2$  simple, not longer than the first segment of  $R_1$ . M beyond basal cell seemingly slightly bent toward CuA;  $M_{3+4}$ , as a rule, branched. Transverse veins two in number (r-m and m-cu), less frequently, many. Anal field distally bent backward. Macrosculpture made up of punctae, concentrated in the costal field and on the clavus. No stridulating field.

Composition. *Permocicada* Mart., *Cicadopsylla* Mart., *Sojanoneura* Mart., and *Permodiphtheroides* Mart.; Upper Permian of Europe; *Prosbol* Handl. and *Permocicadopsis* B.-M.; Upper Permian of Eurasia; *Evanscicada* B.-M., *Dictyoprosbole* Mart., *Tychoscytina* B.-M., *Kaltanopsis* B.-M., and *Kaltanetta* B.-M.; Upper Permian of Siberia; *Beaufortiscus* Riek; Upper Permian of South Africa; *Orthoscytina* Till., *Homaloscytina* Till., *Stenoscytina* Till., *Permojassus* Till., *Elliptoscarta* Till., *Permoglyphis* Till., *Permodiphthera* Till., and *Permobrachus* Ev.; Upper Permian of Australia; in addition, undescribed genera from the Upper Permian of Siberia and South Africa.

Remarks. The Jurassic genus *Mesocicada* B.-M., described in the Prosbolidae, does not belong to the Prosboloidea.

## FAMILY DYSMORPHOPTILIDAE Handlirsch, 1906

Dysmorphoptilidae: Handlirsch, 1906-1908, p. 402.  
Eoscarterellidae: Evans, 1956, p. 220 (syn. nov.).

**Diagnosis** (Fig. 2a). Rant beyond basal bend of C strongly constricted; CP long, with apex close to Sc, which at this point, extends somewhat from R + M, forming a very low-angled "arc"; Sc concave over its whole extent. Basal cell closed by arculus, and less frequently, by an extensive anastomosis, weakly or not narrowing toward the apex.  $R_a$  longer than first segment of  $R_1$ , more strongly inclined than the post-nodal branches, and as a rule, bearing, as it were, weak prenodal branches of R. M beyond basal cell usually curved toward CuA;  $M_{3+4}$  branched. Transverse veins three in number (ir, r-m, and m-cu), rarely many. Anal field distally folded back, Macrosculpture punctate, and as a rule, covering the wing uniformly. Stridulating field almost always noticeable.

**Composition.** *Permocixiella* B.-M.; Upper Permian of Siberia; *Dysmorphoscarterella* Riek; Upper Permian of South Africa; *Belmontocarta* Ev.; Upper Permian of Australia; *Tennentsia* Riek; Upper Triassic of South Africa; *Triassocixius* Till., *Eoscartoides* Ev., *Eoscarterella* Ev. = *Prosbolopsites* B.-M., *Trifidella* Ev., *Alotridus* Ev., and *Dysmorphoptiloides* Ev.; Upper Triassic of Australia; *Dysmorphoptila* Handl.; Lower Jurassic of Europe; *Mesotraais* B.-M.; Lower-Middle Jurassic of Middle Asia; in addition, several undescribed genera from the Upper Permian of Siberia and the Middle-Upper Triassic of Middle Asia, and also possibly, *Magnaciacadia* Hong & Chen from the Middle Triassic of China and an undescribed genus from the Upper Permian of South America (Ingriunae gen. et sp. [21]).

## SUPERFAMILY PEREBORIOIDEA Zalessky, 1930, stat. nov.

Pereboridae: Zalessky, 1930, p. 1026.  
Ignotaloidea: Riek, 1973, p. 522 (syn. nov.).

**Diagnosis** (Fig. 1h). No costal efracation. Rant not subdivided at base; if it is weakly expressed, then the costal field has a median projection. Sc without arc, fusing with  $R_1$  or R, or free over its whole extent, distally convex.  $R_a$  bears post-nodal branches. Nodal line expressed weakly or absent. Transverse m-cu (first) short, not passing along nodal line, without longitudinal segment. CuA without displacement along nodal line. Anal field wide, weakly inclined (the structure of the field in the Ignotalidae is unknown). Macrosculpture, if expressed, is concentrated in the prenodal part of the wing, and in the post-nodal part is only developed in the form of patches, covered by granules.

**Composition.** Two families.

## FAMILY PEREBORIIDAE Zalessky, 1930

Pereboridae: Zalessky, 1930, p. 1026.  
Pereboriidae: Bekker-Migdisova, 1960, p. 94.

**Diagnosis** (Fig. 1h). Anterior margin of wing moderately convex at the base, rant well-defined, CP well-developed, and costal field without median projection. Sc enters  $R_1$  or R. The first segment of CuA is developed (basal cell discrete). Macrosculpture developed.

**Composition.** *Pereboria* M. Zal. and *Scytophara* Mart.; Upper Permian of Europe; *Borisrohdendorfia* B.-M. and *Neuropibrocha* B.-M.; Upper Permian of Siberia; *Gondwanaptera* Pinto & Ornellas; Upper Permian of South America; in addition, an undescribed genus from the Upper Permian of Europe.

## FAMILY IGNOTALIDAE Riek, 1973

Ignotalidae: Riek, 1973, p. 522 (pars).

**Diagnosis.** The anterior margin of the wing is extremely convex at the base, the rant is weakly expressed and not distinct; no CP; costal field with median projection. Sc free over whole extent. First segment of CuA reduced (basal cell not discrete). Macrosculpture not developed.

**Composition.** *Ignotala* Riek and *Megoniella* Riek; Upper Permian of South Africa; in addition, an undescribed genus from the Upper Permian of Siberia.

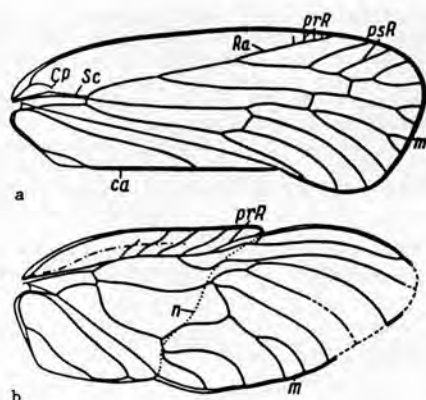


Fig. 2.. Types of venation of forewings of ancient cicadomorphs: a) primitive Permian Dymorphoptilidae; b) Triassic Dunstaniidae. Abbreviations: see Figure 1.

#### SUPERFAMILY PALAEONTINOIDEA Handlirsch, 1906

Palaeontinidae: Handlirsch, 1906-1908, p. 618.

Palaeontinoidea: Bekker-Migdisova, 1949, p. 45.

**Diagnosis** (Fig. 2b). No costal efferaction. Rant not subdivided at the base, and as a rule, weakly developed, with the costal field in this case having a median projection. Sc without arc, fusing with  $R_1$  or with R (in isolated cases, free over whole extent), distally convex.  $R_a$  usually without post-nodal branches. Nodal line well developed. Transverse m-cu (the only one or the first) long, passing in the basal part along the nodal line and/or in the middle part, directly longitudinally. CuA, as a rule, with strong displacement along nodal line. Anal field distally bent backward. Macrosculpture, if expressed, concentrated in prenodal part of wing, and in post-nodal part developed only along veins or along anterior margin.

**Composition.** Three families: besides the Dunstaniidae described below, the Mesogereonidae from the Upper Triassic of South Africa and Australia, and the Palaeontinidae from the Middle-Upper Triassic of Middle Asia and South Africa, the Jurassic of Eurasia, and the Cretaceous of Siberia and Mongolia. In addition, four genera, not assigned to named families: *Beaconiella* Evans and a closely related, undescribed genus from the Middle-Upper Triassic of Middle Asia and Australia, an undescribed genus from the Upper Permian of Kazakhstan, and presumably *Stenoglyphis* Ev. from the Upper Permian of Australia.

#### FAMILY DUNSTANIIDAE Tillyard, 1916

Dunstaniidae: Tillyard, 1916, p. 31.

**Diagnosis** (Fig. 2b). Sc enters R not far from basal cell; the latter is quite narrow, and closed by a short (shorter than the first segment of M) arculus, and rarely by anastomosis. RS simple, bent stepwise at intersection with nodal line.  $M_{1+2}$ , as a rule, strongly bent forward at the base and several times longer than  $M_{3+4}$ . The post-nodal part of the wing is approximately equal in area to the prenodal part.

**Composition.** *Austroprosboloides* Riek; Upper Permian of South Africa; *Austroprosbolus* Ev.; Upper Permian of Australia; *Fletcheriana* Ev.; Middle Triassic of Australia; *Dunstaniodes* B.-M. & Wootton and *Siksteliana* B.-M. & Wootton; Middle-Upper Triassic of Middle Asia; *Prosbolomorpha* Riek; Upper Triassic of South Africa; *Dunstanella* Till. = *Dunstanopsis* Till. = *Paradunstanella* Till.; Upper Triassic of South Africa and Australia; in addition, several undescribed genera from the Middle-Upper Triassic of Middle Asia, and possibly a further one from the Upper Permian of South America ("Prosbolidae — Tettigarctidae" [21]).

**Remarks.** The genus *Permodunstanella* B.-M., described amongst the Dunstaniidae, does not belong to the Cimicida. "*Fletcheriana*" magna Riek from the Upper Triassic of South Africa belongs to the Palaeontinidae.

#### SUPERFAMILY SCYTINOPTEROIDEA Handlirsch, 1906, stat. nov.

Scytinopteridae: Handlirsch, 1906-1908, p. 391.

**Diagnosis** (Figs. 1e-g; 3). Costal effraction is developed, except in some forms that have also lost the claval fold. Rant subdivided at the base, sometimes indistinctly, and costal field lacking median projection. Sc with an arcuate sector fusing with R immediately after the basal cell, concave, and sometimes reduced.  $R_a$  without post-nodal branches. Nodal line replaced by groove or absent. Transvers  $m-cu$  (the only one or the first), if not replaced by anastomosis of M ( $M_2$ ) with  $CuA$ , then short, without a longitudinal segment, and sometimes coinciding with nodal groove.  $CuA$  without displacement at the nodal level. Anal field weakly or moderately constricted distally, inclined in varying degree, not bent backward. Macrosculpture as a rule, covers the wing uniformly.

**Composition.** Besides the four families described below, it includes the Ipsviciidae from the Middle-Upper Triassic and Lower Jurassic of Middle Asia, and the Upper Triassic of Europe and Australia.

#### FAMILY SCYTINOPTERIDAE Handlirsch, 1906

Scytinopteridae: Handlirsch, 1906-1908, p. 391.

**Diagnosis** (Fig. 1e). The arc of Sc almost or completely reaches the apex of R + M. Basal cell short, gradually narrowing beyond the middle part, and is closed by anastomosis (punctate, and less frequently, extensive); first segment of M very short or not expressed.  $R_1$  directed longitudinally;  $R_a$  concave, and, as a rule, extending from the base of  $R_1$ . Transverse r-m single. Nodal groove usually absent, and only in this case, M bends strongly toward  $CuA$  at the nodal level; there is no transverse  $m-cu$  at this level. Anal field with narrow border or without border along posterior margin, strongly inclined, at least in the distal part. The wing is densely covered with simple punctate or slightly rasp-like macrosculpture, and the microsculpture is weak, and there is sometimes a rudimentary stridulating field.

**Composition.** *Anomoscyta* Mart.; Upper Permian of Europe; *Scytinoptera* Handl. = *Scytinopterula* Handl. = *Permocixius* Mart.; Upper Permian of Eurasia; *Surijskovi* B.-M., *Sarbaloptera* B.-M.; *Kondomoprobole* B.-M., and *Tychtoscarta* B.-M.; Upper Permian of Siberia; *Apheloscyta* Till.; Upper Triassic of Australia; in addition, "*Scytinoptera*" *mexicana* Carp. from the Upper Permian of North America, the genus of which is uncertain, and several undescribed genera from the Middle-Upper Triassic of Middle Asia.

**Remarks.** The Triassic "*Scytinoptera*" *distorta* Riek belongs to the Progonocimidae (Peloridiina = Coleorrhyncha).

#### FAMILY SERPENIVENIDAE Shcherbakov, fam. nov.

**Diagnosis** (Figs. 1g; 3). The arc of Sc does not reach the apex of R + M. The basal cell is long, and narrows only in front of the apex, and is closed by a punctate anastomosis; the first segment of M is comparatively long.  $R_1$  is directed longitudinally or is weakly inclined; a concave  $R_a$  extends from its base, and less frequently from R. There are two transverse r-m, but as a rule, they are replaced by an anastomosis of RS +  $M_1$ . Nodal groove well developed; M at this level is strongly bent toward  $CuA$  and joins with it or with the very base of  $CuA_1$  by a transverse vein (sometimes incomplete, that is, not reaching  $CuA$ ). Anal field with narrow border or without border along the posterior margin, and is usually weakly inclined. The wing is covered by a sparse rasp-like sculpture, sometimes very weak, and a well marked microsculpture; no stridulating field.

**Composition.** *Tomioscarta* B.-M.; Upper Permian of Siberia; *Serpentivena* gen. nov.; Middle-Upper Triassic of Middle Asia; in addition, several undescribed genera from the Upper Permian of Kazakhstan and the Middle-Upper Triassic of Middle Asia.

Genus *Serpentivena* Shcherbakov, gen. nov.

**Generic name** from Lat. *serpentinus*, serpentine, and Lat. *vena*, vein.

**Type species.** *S. tigrina* sp. nov.; Middle-Upper Triassic, Southern Fergana.

**Diagnosis** (Figs. 1g; 3). The arc of Sc is located at about the middle of R + M. R is not weakened beyond the basal cell, is bent anteriorly, and farther distally is almost straight.  $R_a$  is strongly concave, and extends from R long before  $R_1$ . RS +  $M_1$  has three branches. The nodal groove between R and M is strong; the transverse  $m-cu$  at this level is rather long, and enters  $CuA$  long before the exit of  $CuA_1$ ;  $CuA$ , beyond the basal cell, is bent backwards.  $Pcu$  at the base and in front of the fusion with  $A_1$  is strongly curved forward, and in the middle part,





Fig. 3. *Serpentivena tigrina* sp. nov.; holotype No. 2785/3635 ( $\times 11$ ); Southern Fergana, Dzhaylyaucho locality; Middle-Upper Triassic, Madygen Formation.

backward. The anal carina in the distal part is wider than the anal field, which is arranged horizontally (except the bands along  $A_1$  and  $Pcu + A_1$ ), and narrows noticeably toward the apex. The punctae and the microsculpture are rather weak, and cover the wing entirely, and the veins are without grains. The margin of the post-nodal part of the wing is most convex at the sites of entry of  $M_1$  and the branches of  $CuA$ , and approaches the line, continuing the posterior margin of the clavus.

Species composition. The type species and one undescribed species from the Middle-Upper Triassic of Southern Fergana.

Comparison. It is distinguished from *Tomioscarta* B.-M. by the exit site of  $R_2$ , the replacement of transverse  $r-m$  by an anastomosis of  $RS + M_1$ , the complete transverse  $m-cu$  at the nodal level, and the uniform distribution of sculpture on the wing.

*Serpentivena tigrina* Shcherbakov, sp. nov.

Specific name from Lat. *tigrinus*, striped.

Holotype. PIN No. 2785/3535(3635), fore- and hindwings together with fragments of body; Kirgiz SSR, Batken region, Dzhaylyaucho locality; Middle-Upper Triassic, Madygen Formation.

Description (Figs. 1g; 3).  $CuA$  with three branches,  $CuA_1$  (before branching) and  $CuA_2$ , curved forwards. Anal carina in vicinity of entry of  $Pcu$  into  $A_1$ , forms a lobe, onto which the prolongation of  $Pcu$  attaches. Wing bears four uneven, dark, transverse cross-bands: at the base of the wing, beyond the basal cell, at the nodal level, and at the apex (second and third are inclined towards the posterior margin of the wing and pass along  $Pcu$  and  $CuA_2$ , respectively), and also individual small dark patches, especially in the costal field. Spaces between cross-bands and all veins light-colored.

Dimensions in mm: length of wing, 7-10 (in holotype, 9); differences in length partly controlled by deformation of enclosing rock; body length of female, together with ovipositor (Spec. No. 2785/3102(3103)), 11.

Distribution. Middle-Upper Triassic of Southern Fergana.

Material. Ten specimens from a single locality, one of them with a complete impression of the body.

FAMILY STENOVICIIDAE Evans, 1956

Stenovicidae: Evans, 1956, p. 206 (pars).

**Diagnosis.** Arc of Sc almost reaches apex of R + M. Basal cell long, narrowing only in front of apex, and closed by extensive anastomosis: first segment of M comparatively long.  $R_1$  weakly inclined, more or less parallel to the weakly-convex  $R_a$  extending from R. Two transverse r-m. No nodal groove, M at nodal level almost straight, joined to  $CuA_1$  by transverse vein or anastomosis. Anal field without border along posterior margin, weakly inclined. Macrosculpture usually weak.

**Composition.** *Stenovicia* Ev., *Stanleyana* Ev., *Permocentrus* Ev., *Permagra* Ev., *Permovicia* Ev., *Palaeovicia* Ev., and *Permoscarta* Ev.; Upper Permian of Australia; in addition, an undescribed genus from the Middle-Upper Triassic of Middle Asia, and a described, but unnamed form from the Upper Permian of Antarctica [23].

**Remarks.** The Triassic genus *Maguviopsis* B.-M., placed in the Stenoviciidae, does not belong in the Scytinopteroidea.

#### FAMILY PARAKNIGHTIIDAE Evans, 1950

Paraknightiidae: Evans, 1950, p. 246.

**Diagnosis.** The arc of Sc is reduced (the structure of Sc in *Tychticola* and a similar undescribed genus, is unknown). Basal cell very long, narrowing only in front of apex, and closed by a short arculus; the first segment of M is long.  $R_1$  is directed longitudinally, very long, with  $R_a$  extending far beyond its base, or weakly inclined and parallel to  $R_a$ , extending from R, and to the branches of RS;  $R_a$  weakly convex. More than one transverse r-m. Nodal groove absent or rudimentary; M at nodal level straight, joined to  $CuA$  or  $CuA_1$  by a transverse vein. Anal field with broad convex band along posterior margin. Wing densely covered with simple punctae, microsculpture not marked, and no stridulating field.

**Composition.** *Tychticola* B.-M.; Upper Permian of Siberia; *Paraknightia* Ev.; Upper Permian of Australia; in addition, undescribed genera from the Upper Permian of Siberia and the Middle-Upper Triassic of Middle Asia.

#### PHYLOGENY OF PERMIAN CICADOMORPHS

The cicadids arose directly from the Archescytinoidea, the ancestral group of the order Hemiptera [10]. Among the cicadomorphs, which had already separated from the fulgoromorphs towards the end of the Early Permian, representatives of the subfamily Ivaiinae were closest in wing structure to the archescytinoids. From this group, which was the ancestor to the remaining cicadomorphs, three main evolutionary lineages of the infraorder diverged.

The first lineage included the two largest families of prosboloids and their descendants. The Prosbolidae, which had separated from the ivaiinids in the Late Permian gave rise to the family Dymorphoptilidae, known since the end of the Late Permian. Probolid genera such as *Permobrachus* and *Orthoscytina* are closest of all to the ancestors of the dymorphoptilids. On the other hand, the prosbolids gave rise to a group of Mesozoic families (Hylcellidae, Chiliocyclidae, etc.), ancestral to all the Mesozoic-Cenozoic superfamilies of cicadomorphs.

The second evolutionary lineage includes the subfamily Prosbolopseinae and the superfamilies Pereborioidea and Palaeontinoidea. The pereborioids inherited from the prosbolopseids the structure of the radial system and the apex of the basal cell. The more primitive family Pereboriidae is characterized by the structure of the rant, similar to that in the prosbolids, but evidently, independently acquired. The probable descendants of the pereboriids, the Ignotalidae, are similar in a number of features of the hindwing (undescribed material) to the prosbolids and palaeontinids (the corresponding characters in the pereboriids are unknown). The ignotalids have been regarded as a group, transitional between the Protoblattoidea and Homoptera [22], but there are much better grounds for the view, according to which the ancestors of the Homoptera are similar to the Permian Psocoptera [10], whereas the ignotalids and pereboriids, with their enriched venation, constitute an extremely advanced superfamily of cicadomorphs.

The palaeontinoids inherited the structure of Sc and apex of the basal cell, and also the nature of the sculpture, from the pereborioids; in some palaeontinoids (*Beaconella*, etc.), a structure of the radial system typical of the pereborioids, is retained. The structure of the anal field, similar to such prosbolids, was acquired independently by the palaeontinoids. In most palaeontinoids, the venation is secondarily oligomerized, but traces of early branching of M and additional branches of R and  $CuA$  are in this instance often retained. The sparse-veined Dunstaniidae appeared already in the Permian, together with primitive multi-veined palaeontinoids (an undescribed genus and possibly, *Stenoglyphis*).

The third evolutionary lineage includes the Ingruidae and Scytinopteroidea. The scytinopteroids inherited the structure of Sc and the anal field from the ingruids, and also later, the branching of M and the uniformly sclerotized wing. During the second half of the Late Permian, the Serpentinaeidae, their probable descendants, the Stenoviciidae, and the Paraknightiidae, similar to both the preceding groups, separated from the Scytinopteridae, the most primitive within the superfamily; and in the Triassic, the Ipsviciidae diverged.

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