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Review of Triassic Orthoptera with Descriptions of New and Little Known Taxa: Part 2

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Abstract—All known Triassic taxa of the suborder Caelifera are listed. New taxa are described in the families Locustavidae (Locustavinae stat. nov.: *Locustavus problematicus* sp. nov., *L. intermedius* sp. nov., *L. deformatus* sp. nov., *L. minutus* sp. nov., *Miolocustavus reductus* gen. et sp. nov., *Brevilocustavus microscopicus* gen. et sp. nov., and *B. distinctus* sp. nov.; and Praelocustopsinae subfam. nov.) and Dzhajloutshellidae (*Dzhajloutshella flexuosa* sp. nov., *Adzhajloutshella plana* sp. nov., and *Triassoxya novozhilovi* gen. et sp. nov.). The latter family and the Lower Jurassic family Regiatidae are united into the superfamily Dzhajloutshelloidea stat. nov. The generic name *Ferganopsis* Sharov, 1968 is synonymized with *Locustavus* Sharov, 1968. Several suprageneric taxa are redescribed based on new data. The placement of the genus *Triassophyllum* in the order Orthoptera is shown to be erroneous.

Key words: Triassic, Orthoptera, Caelifera, new taxa.

INTRODUCTION

In the first part of this paper (Gorochov, 2005), a brief critical review of recent publications containing new taxonomic information on Triassic Orthoptera is given, all known Triassic taxa of the suborder Ensifera are listed, and some new and little-known taxa of this suborder are described. The second part deals with the suborder Caelifera, the largest of the two suborders of the order Orthoptera known since the Lower Triassic, and also with Triassic fossils erroneously assigned to this order.

This paper is based on the study of the collections of the Paleontological Institute of the Russian Academy of Sciences (PIN), where all materials described below are deposited, and on a summary of the literature (Gorochov, 2005). All new materials considered below originate from the Madygen locality (Kyrgyzstan, Osh Region, Batken District, Dzhailoucho area on the northern spurs of the Turkestan Range; Middle or Upper Triassic, Madygen Formation).

LIST OF KNOWN TRIASSIC TAXA OF THE SUBORDER CAELIFERA ANDER, 1936

Since most of the taxa listed originate from the Madygen locality (Middle or Upper Triassic of Kyrgyzstan), distribution and age are only given for those coming from other localities.

Infraorder Acrididea MacLeay, 1821

Superfamily Locustopsoidea Handlirsch, 1906

Locustavidae Sharov, 1968. **Locustavinae** stat. nov.: *Locustavus* Sharov, 1968 [*L. madygenicus* Sharov, 1968; *L. lanceolatus* (Sharov, 1968), comb. nov.; *L. problematicus* sp. nov., *L. intermedius* sp. nov., *L. deformatus* sp. nov.; *L. minutus* sp. nov.]; *Miolocustavus* gen. nov. [*M. reductus* sp. nov.]; *Brevilocustavus* gen. nov. [*B. microscopicus* sp. nov.; *B. distinctus* sp. nov.]. **Praelocustopsinae** subfam. nov.: *Praelocustopsis* Sharov, 1968 [*P. mirabilis* Sharov, 1968 (Lower Triassic of Krasnoyarsk Region)]; *Triassolocusta* Tillyard, 1922 [*T. leptoptera* Tillyard, 1922 (Upper Triassic of Australia)].

Acrididea incertae sedis

"*Locustopsis* (?) sp." (Upper Triassic of Tajikistan; head and prothorax with a long, acute posterior process, presumably belonging to a small nymph that was tentatively assigned to the genus *Locustopsis* Handlirsch, 1906 of the family Locustopsidae Handlirsch, 1906, see Sharov, 1968, text-fig. 34D; however, this species closely resembles living Tetrigoidea Rambur, 1838 in the shape of the pronotum and, conceivably, represents the oldest member of this superfamily, see Gorochov, 2001, text-figs. 21g, 21h for comparison).

Infraorder Tridactylidea Brulle, 1835

Superfamily Dzhajloutshelloidea Gorochov, 1994, stat. nov.

Dzhajloutshellidae Gorochov, 1994: *Dzhajloutshella* Gorochov, 1994 [*D. arcanum* Gorochov, 1994; *D. flexuosa* sp. nov.]; *Adzhajloutshella* Gorochov, 1994 [*A. talis* Gorochov, 1994; *A. plana* sp. nov.]; *Triassoxya* gen. nov. [*T. novozhilovi* sp. nov.].

TRIASSIC FOSSILS ERRONEOUSLY ASSIGNED TO ORTHOPTERA

The genus *Triassophyllum* Papier, Nel, Grauvogel-Stamm, et Gall, 1997 (Middle Triassic of France), described from the forewings, was originally assigned to the family Tettigoniidae (Tettigoniidea, Tettigonioidea) and provisionally placed in the modern subfamily Pseudophyllinae (Papier *et al.*, 1997). However, as

shown earlier (Gorochov, 1988, 1995b), the earliest member of this superfamily is known from the Early Cretaceous and is still very similar to its ancestors from the family Prophalangopsidae (Hagloidea), which appeared in the fossil record only in the Jurassic; thus, a separate family Haglotettigoniidae was created for this genus. True Tettigoniidae presumably appeared no earlier than the Late Cretaceous, and the subfamily Pseudophyllinae, which represents one of the most advanced katydid groups and is characteristic of modern tropical forests in Asia and Africa, appeared even later. According to D.E. Shcherbakov (pers. comm.), the photographs accompanying the original description of *Triassophyllum* show that it belongs to the family Ipsviciidae (Homoptera), which was common in the Triassic.

NEW AND LITTLE-KNOWN TAXA OF THE SUBORDER CAELIFERA

SYSTEMATIC PALEONTOLOGY

Infraorder Acrididea

Superfamily Locustopsoidea Handlirsch, 1906

Family Locustavidae Sharov, 1968

Diagnosis. Locustavidae differ from Locustopsidae in the following characters of forewing venation: "C" straight or slightly curved, but its distal portion not approximated to the Sc stem in such a manner that costal area near the proximal part of "C" is wider than near its distal part; base of CuA1 not remote (or only slightly so) from the forewing base, so that CuA2 not shorter (sometimes possibly only slightly shorter) than CuA stem up to bifurcation into CuA1 and CuA2 (Figs. 1a–1d, 2a–2d).

Composition. Locustavinae stat. nov. and Praelocustopsinae subfam. nov.

Remarks. Previously, only two species that were assigned to two different genera, which are synonymized herein, were placed in this family. In addition, two new genera and several new species are added here, whereas two other genera (*Praelocustopsis, Triassolocusta*), previously treated as belonging to the family Locustopsidae (Sharov, 1968; Vishnyakova, 1980; Zessin, 1983; Gorochov, 1995a, 2001; Gorochov and Rasnitsyn, 2002), are transferred to Locustavidae as members of a new subfamily. The subfamily Locustopsidae now contains only Jurassic and Cretaceous genera, distributed between two subfamilies: Locustopsinae Handlirsch, 1906 and Araripelocustinae Martins-Neto, 1995 (Gorochov and Rasnitsyn, 2002).

Subfamily Locustavinae Sharov, 1968, stat. nov.

Locustavidae: Sharov, 1968, p. 185.

Diagnosis. Forewings with long Sc reaching or entering distal quarter of forewing; base of CuA1 not remote (or only slightly so) from the forewing base, so that CuA2 much longer than CuA stem up to bifurcation into CuA1 and CuA2 (Figs. 1a–1d, 2a–2c).

Composition. *Locustavus, Miolocustavus* gen. nov. and *Brevilocustavus* gen. nov. (all from Middle or Upper Triassic of Kyrgyzstan).

Remarks. Since a long Sc is also characteristic of primitive Triassic tridactylideans (Figs. 2e–2g), it is possible to assume that this feature was inherited by Locustavinae, Locustopsidae, and Tridactylidea from their common ancestor. The fact that CuP and 1A are straight and markedly approximated only in the forewings of Locustavinae and Locustopsidae, and the presence of other more primitive characters in Locustavinae suggest that Locustopsidae may have been derived directly from Locustavinae.

Genus *Locustavus* Sharov, 1968

Ferganopsis Sharov, 1968, p. 186 (syn. nov.).

Type species. *L. madygenicus* Sharov, 1968.

Diagnosis. Forewings medium-sized to large (17.5–32 mm long), with numerous (much more than two) Sc branches in the costal area and three to five branches of MP + CuA1 (not counting supernumerary longitudinal veins, bases of which usually show little or no fusion with MP + CuA1 branches) (Figs. 1a–1d).

Composition. *L. madygenicus, L. lanceolatus* (Sharov, 1968) comb. nov., *L. problematicus* sp. nov., *L. intermedius* sp. nov., *L. deformatus* sp. nov., and *L. minutus* sp. nov.

Remarks. The new species listed above combine the characters that were proposed by Sharov (1968) to distinguish between *Locustavus* and *Ferganopsis*, and some characters of these new species are clearly intermediate between those of *L. madygenicus* and *L. lanceolatus*. Therefore, the structure of the crossveins between Sc and "C" (these crossveins are less than half as long as the proximal Sc branches) remains the only diagnostic feature of *Ferganopsis*, implying the differences of species level only.

Locustavus problematicus Gorochov, sp. nov.

Etymology. Latin *problematicus* (problematic).

Holotype. PIN, no. 2555/1403, nearly complete forewing (part and counterpart); Madygen locality, Madygen Formation.

Description (Fig. 1a). The forewing is large, slightly curved apically; the widened and narrowed parts of the costal area are quite distinctly separated from each other; the crossveins between Sc and the distal part of "C" are only slightly shorter than the proximal Sc branches; RA bears two branches distally; the base of RS is situated slightly distad of the apex of "C"; RS bears five branches; MA bears four branches; the proximal part of MP is clearly developed; the bases of CuA2 and the most proximal branch of MP + CuA1 and those of CuA2 and CuP are approximately equally spaced; MP + CuA1 bears three branches.

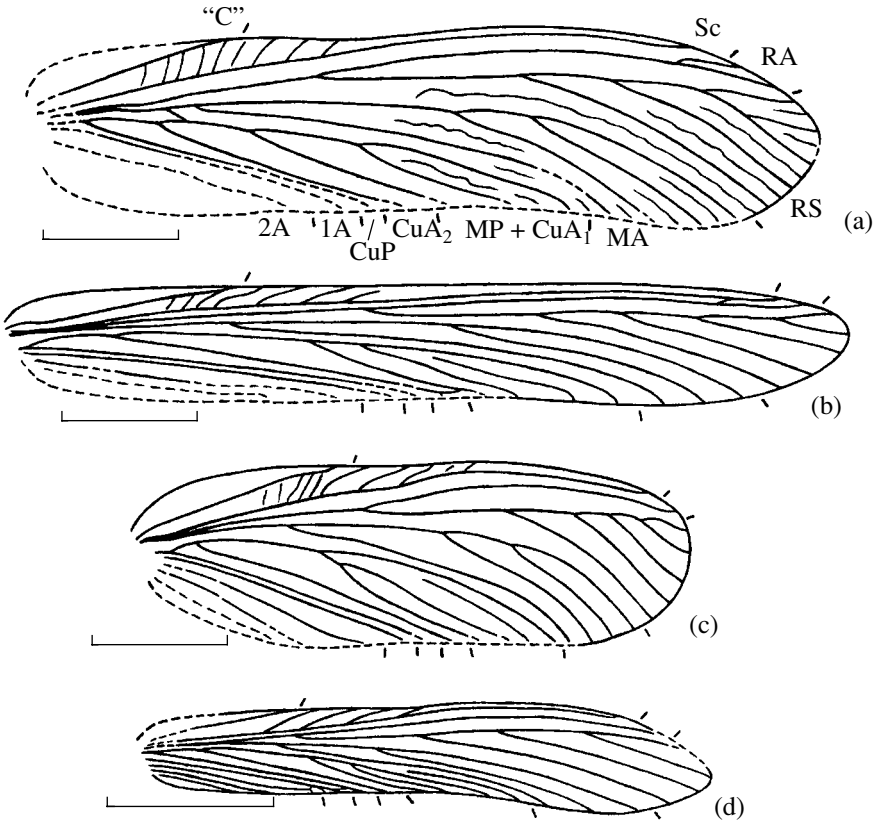

Fig. 1. Forewings of the genus *Locustavus* (Locustopsoidea); (a) *L. problematicus* sp. nov., holotype PIN, no. 2555/1403; (b) *L. intermedius* sp. nov., holotype PIN, no. 2785/2347; (c) *L. deformatus* sp. nov., holotype PIN, no. 2555/1396; and (d) *L. minutus* sp. nov., holotype PIN, no. 2785/2349(2353). Scale bar 5 mm in all figures.

Measurements (mm): forewing length as preserved, 28; estimated full forewing length, 32.

Comparison. This species differs from *L. madygenicus* in the presence of only two branches of RA, the costal area more sharply narrowing in the distal half, the location of the RS base only slightly distad of the apex of "C," the close proximity of the proximal part of MP to the base of CuA2, the base of CuA2 much closer to that of the most proximal branch of MP + CuA1, MP + CuA1 with only three branches, and the only slight curvature of the apical part of the forewing, and from *L. lanceolatus* in the only slight difference in length between the distal crossveins in the "C"–Sc area and the proximal Sc branches, the presence of two branches of RA, the location of the RS base slightly distad of the apex of "C," the fewer RS branches, the presence of a well-developed proximal part of MP, and in the slight curvature of the apical part of the forewing.

Material. Holotype and paratype PIN, no. 2785/2339, incomplete forewing (part and counterpart) from the same locality (the paratype differs from the holotype in the presence of only three branches in MA).

***Locustavus intermedius* Gorochov, sp. nov.**

Etymology. Latin *intermedius* (intermediate).

Holotype. PIN, no. 2785/2347, nearly complete forewing (part and counterpart); Madygen locality, Madygen Formation.

Description (Fig. 1b). The forewing is large, not curved apically; the costal area is evenly tapered towards the apex; the crossveins between Sc and the distal part of "C" are nearly as in *L. problematicus*; RA bears two branches distally, with the anterior branch being partly fused with the apical part of the Sc stem; the base of RS is situated slightly distad of the apex of "C"; RS bears five branches; MA bears three branches; the proximal part of MP is inconspicuous; the distance between the base of CuA2 and that of the most proximal branch of MP + CuA1 is nearly twice the distance between the bases of CuA2 and CuP; and MP + CuA1 with three branches.

Measurements (mm): forewing length as preserved, 32; due to rock deformation the impression is somewhat distorted lengthwise, so that the forewing length during life may have been about 28.

Comparison. This species differs from *L. madygenicus* in the presence of only two RA branches, the

RS base situated only slightly distad of the apex of "C," the reduced proximal part of MP, the greater distance between the base of CuA2 and that of the most proximal branch of MP + CuA1, and the presence of only three MA branches and three MP + CuA1 branches; from *L. lanceolatus* in the above-mentioned features of the shape and venation of the costal area, the RS base located slightly distad of the apex of "C," fewer RS branches, and in the much more widely separated bases of CuA2 and the most proximal branch of MP + CuA1; and from *L. problematicus* sp. nov. in the gradually tapered costal area, the presence of only three MA branches, the much more widely separated bases of CuA2 and the most proximal branch of MP + CuA1, and in the forewing that is not curved apically.

Material. Holotype and paratype PIN, no. 2555/1393, incomplete forewing (part and counterpart) from same locality (the paratype differs from the holotype in that the anterior branch of RA is only slightly fused with the apical part of the Sc stem).

Locustavus deformatus Gorochov, sp. nov.

Etymology. Latin *deformatus* (deformed).

Holotype. PIN, no. 2555/1396, nearly complete forewing (part and counterpart); Madygen locality, Madygen Formation.

Description (Fig. 1c). The forewing is medium-sized, almost not curved apically; the costal area is almost evenly tapered towards the apex; the crossveins between Sc and the distal part of "C" are about 0.67 as long as the proximal branches of Sc; RA is unbranched; the base of RS is situated only slightly distad of the apex of "C"; RS bears five branches; MA bears four branches; the proximal part of MP is inconspicuous; the distance between the bases of CuA2 and the proximal branch of MP + CuA1 is more than three times the distance between the bases of CuA2 and CuP; and MP + CuA1 bears three branches.

Measurements (mm): forewing length, 21 (rock deformation resulted in an considerably increased width of the specimen; thus, the forewing may have been 0.5–0.67 times as wide as shown in the Fig. 1c).

Comparison. This species differs from the other species of the genus in its smaller size and in the very closely spaced bases of CuA2 and CuP; in addition to these characters, it differs from *L. madygenicus, L. problematicus* sp. nov., and *L. intermedius* sp. nov.in the close proximity of the base of RS to the apex of "C"; from *L. lanceolatus* and *L. problematicus* sp. nov., in the much more widely spaced bases of CuA2 and the proximal branch of MP + CuA1; from *L. madygenicus* and *L. problematicus* sp. nov., in the unbranched RA and in the reduced proximal part of MP; from *L. lanceolatus*, in the longer crossveins between Sc and the distal part of "C"; and from *L. intermedius* sp. nov., in the distinctly greater relative length of "C."

Material. Holotype.

Locustavus minutus Gorochov, sp. nov.

Etymology. Latin *minutus* (minute).

Holotype. PIN, no. 2785/2349(2353), nearly complete forewing (part and counterpart); Madygen locality, Madygen Formation.

Description (Fig. 1d). The forewing is smaller than in the other species of this genus and slightly curved apically; the costal area is almost evenly tapered towards the apex; RA is unbranched; the base of RS is situated near the apex of "C"; RS bears four branches; MA bears three branches; the proximal part of MP is inconspicuous; the distance between the bases of CuA2 and the proximal branch of MP + CuA1 is nearly twice the distance between the bases of CuA2 and CuP; and MP + CuA1 bears three branches.

Measurements (mm): forewing length, 17.5.

Comparison. This species differs from the other species of the genus in its smaller size; in addition to this character, it differs from *L. deformatus* sp. nov. in the distinctly longer relative distance between the bases of CuA2 and CuP, from *L. madygenicus, L. problematicus* sp. nov., and *L. intermedius* sp. nov., in the close proximity of the base of RS to the apex of "C," and from *L. lanceolatus*, in the considerably greater distance between the bases of CuA2 and the proximal branch of MP + CuA1.

Material. Holotype and paratypes PIN, nos. 2555/1399, 1406, and 1417, incomplete forewings from same locality (in the paratypes, RS may bear five or even six branches).

Genus *Miolocustavus* Gorochov, gen. nov.

Etymology. From the genus *Locustavus*.

Type species. *M. reductus* sp. nov.

Diagnosis. Forewings medium-sized (about 19 mm long), with only two Sc branches in the costal area (other transverse veins of this area reduced) and two branches of MP + CuA1 (not counting supernumerary longitudinal veins, the bases of which usually show little or no fusion with the branches of MP + CuA1) (Fig. 2a).

Composition. *M. reductus* sp. nov.

Comparison. This genus differs from *Locustavus* in the partial reduction of the transverse veins and in the smaller number of branches on Sc and MP + CuA1.

Remarks. The partial reduction of venation in the costal area is probably due to the overall membranization of the forewing, which usually occurs in Orthoptera when the flight function of forewings becomes more important (the forewings become almost as membranous as in Elcanidea).

Miolocustavus reductus Gorochov, sp. nov.

Etymology. Latin *reductus* (reduced).

Holotype. PIN, no. 2785/1949, nearly complete forewing (positive impression); Madygen locality, Madygen Formation.

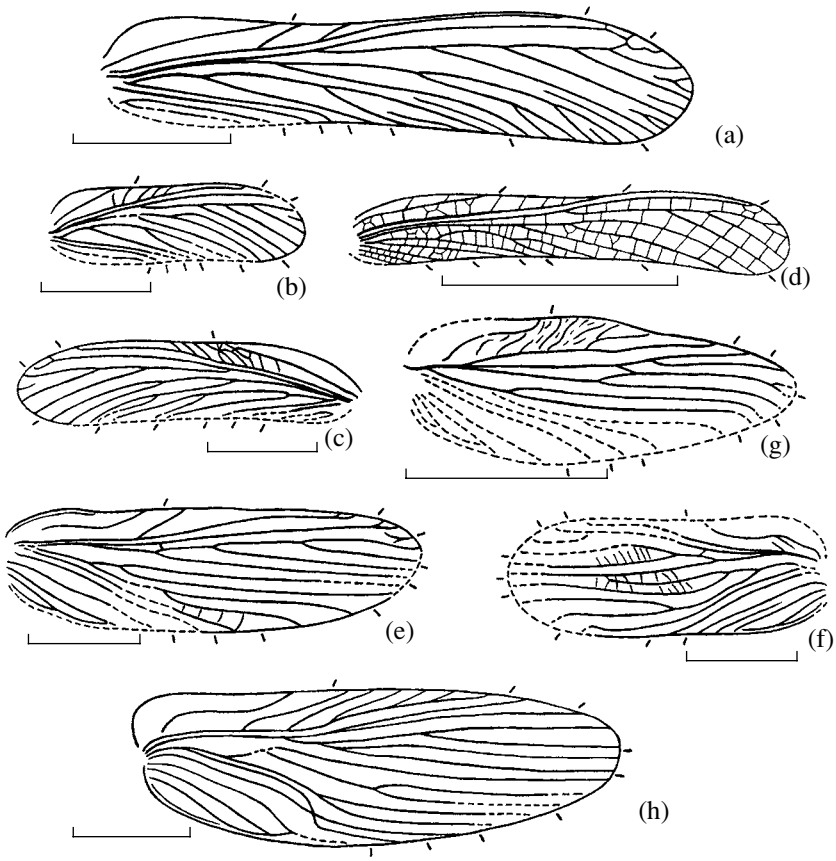

Fig. 2. Forewings of Locustopsoidea (a–d) and Dzhajloutshelloidea (e–h); (a) *Miolocustavus reductus* sp. nov., holotype PIN, no.2785/1949; (b) *Brevilocustavus microscopicus* sp. nov., holotype PIN, no. 2069/2329; (c) *B. distinctus* sp. nov., holotype PIN, no. 2785/1986; (d) *Praelocustopsis mirabilis* Sharov, holotype PIN, no. 2010/2 (after Sharov, 1968); (e) *Adzhajloutshella plana* sp. nov., holotype PIN, no. 2555/1440; (f) *Dzhajloutshella flexuosa* sp. nov., holotype PIN, no. 2240/1980; (g) *Triassoxya novozhilovi* sp. nov., holotype PIN, no. 1548/113(114); and (h) *Regiata scutra* Whalley, holotype, Natural History Museum (London), In. 64027.

D e s c r i p t i o n (Fig. 2a). A forewing with a costal margin that has a fairly deep (but gently sloping) concavity in the proximal two-thirds and a relatively strong (arcuate) convexity in the distal third, not curved apically; the costal area bears no transverse venation and is markedly narrowed in the distal half; Sc is weakly shortened; RA is unbranched; The base of RS is situated only slightly distad of the apex of "C"; RS bears five branches; MA bears three branches, the two distal of which are forked apically; the bases of CuA2 and MP + CuA1 are separated by a greater distance than the bases of CuA2 and CuP.

M e a s u r e m e n t s (mm): forewing length, 19.

M a t e r i a l. Holotype.

Genus *Brevilocustavus* Gorochov, gen. nov.

E t y m o l o g y. From the Latin *brevis* (short) and the genus *Locustavus.*

T y p e s p e c i e s. *B. microscopicus* sp. nov.

D i a g n o s i s. Forewings small (12–15.5 mm long), with numerous (much more than two) Sc branches in the costal area and two branches of MP + CuA1 (not counting supernumerary longitudinal veins, bases of which are normally not, or only very slightly, joined MP + CuA1 branches) (Figs. 2b, 2c).

C o m p o s i t i o n. *B. microscopicus* sp. nov. and *B. distinctus* sp. nov.

C o m p a r i s o n. This genus differs from *Locustavus* and *Miolocustavus* in the smaller size of the forewings, in addition to this character, it differs from *Locustavus* in the smaller number of branches on MP + CuA1 and from *Miolocustavus* in the more abundant venation in the costal area.

R e m a r k s. One of these two new species differs from the other in the presence of nearly parallel longitudinal veins, thus casting doubt on their placement in the same genus. Additional material is needed to resolve this problem.

***Brevilocustavus microscopicus* Gorochov, sp. nov.**

Etymology. Latin *microscopicus* (microscopic).

Holotype. PIN, no. 2069/2329, nearly complete forewing (part and counterpart); Madygen locality, Madygen Formation.

Description (Fig. 2b). The forewing is very small, rounded and only slightly curved apically; longitudinal veins are not parallel; "C" is short, not quite reaching the base of RS; the branches of Sc in the costal area are more or less simple (not forming irregular venation near the apex of "C"); RA is unbranched; RS bears four complete branches; MA bears three branches; the areas between MP + CuA1 and CuA2 and between CuA2 and CuP are quite broad; the distance between the bases of CuA2 and the proximal branch of MP + CuA1 is nearly 1.5 times the distance between the bases of CuA2 and CuP.

Measurements (mm): forewing length, 12.

Material. Holotype.

***Brevilocustavus distinctus* Gorochov, sp. nov.**

Etymology. Latin *distinctus* (distinct).

Holotype. PIN, no. 2785/1986, incomplete forewing (negative impression); Madygen locality, Madygen Formation.

Description (Fig. 2c). The forewing is somewhat larger than in the previous species, oval and almost not curved apically; longitudinal veins are somewhat parallel in the proximal half of the forewing; "C" is rather long, reaching the base of RS; the branches of Sc in the costal area form irregular venation near the apex of "C"; RA bears two short branches apically; RS bears three complete branches; MA bears four branches; the areas between MP + CuA1 and CuA2 and between CuA2 and CuP are narrow; the distance between the bases of CuA2 and the proximal branch of MP + CuA1 is nearly twice the distance between the bases of CuA2 and CuP.

Measurements (mm): forewing length, 15.5.

Comparison. This species differs from *B. microscopicus* sp. nov. in the larger size, partially parallel longitudinal veins, relatively longer "C", irregular venation in the costal area, different number of branches on RS and MA, and also in the different shape of the areas between MP + CuA1 and CuA2 and between CuA2 and CuP.

Material. Holotype.

Subfamily Praelocustopsinae Gorochov, subfam. nov.

Diagnosis. Forewings with short Sc far not reaching distal quarter of forewing; base of CuA1 slightly separated from that of the forewing; thus, CuA2 slightly longer or slightly shorter than the stem of CuA up to the bifurcation into CuA1 and CuA2 (Fig. 2d).

Composition. *Praelocustopsis* (Lower Triassic of Krasnoyarsk Region) and, possibly, *Triassolocusta* (Upper Triassic of Australia).

Remarks. The holotype of the only species of *Triassolocusta* needs reexamination. In the forewings of *Praelocustopsis*, CuP and 1A are not yet so markedly approximated as in Locustavinae and Locustopsidae, implying that Praelocustopsinae originated from some more primitive Locustavidae than Locustavinae. A certain similarity to Locustopsidae was probably independently acquired by Praelocustopsinae, possibly because the flight function of the forewing developed in this subfamily in parallel with that of *Miolocustavus* and Locustopsidae. However, in the latter this increase was combined with the retention of the covering function of the forewings, i.e., with the retention of relatively rich cross-venation; this may be considered as a favorable improvement of the forewings, and may be one of the reasons for post-Triassic expansion of Locustopsidae.

Infraorder Tridactylidea

Superfamily Dzhajloutshelloidea Gorochov, 1994, stat. nov.

Dzhajloutshellidae: Gorochov, 1994, p. 53.

Diagnosis. Forewings with R forked near the forewing midlength or more proximal; MP + CuA1 and CuA2 developed; CuA clearly bifurcating into CuA1 and CuA2; CuP, 1A and branches of 2A normal, not forming a closed oval area in proximal part of forewing and dense, longitudinal parallel venation distal and anal to this area (Figs. 2e–2h).

Composition. Triassic Dzhajloutshellidae and Lower Jurassic Regiatidae Gorochov, 1995 (the latter family comprises *Protochaeta* Handlirsch, 1939, *Regiata* Whalley, 1985 and possibly *Micromacula* Whalley, 1985).

Remarks. Suggestions of a possible superfamilial rank for one or both of these families were made earlier (Gorochov, 1994, 1995a, 2001; Gorochov and Rasnitsyn, 2002). However, the study of numerous new Dzhajloutshellidae specimens and the reexamination of the type material of *Regiata scutra* Whalley, 1985 (Fig. 2h) have now clarified the forewing structure and systematic position of these families. It turns out that in forewing venation they are much more similar to each other than to Tridactyloidea (it is difficult to homologize many longitudinal veins in the forewings of even the most primitive members of the superfamily Mongoloxyinae to those of Dzhajloutshellidae and Regiatidae).

Family Dzhajloutshellidae Gorochov, 1994

Diagnosis. Forewings with distinct traces of fusion of anterior MA branch with RS stem for a short distance; proximal part of RS developed; branches of MP + CuA1 running nearly along same line as the proximal part of CuA1 (i.e., they are almost straight and

their proximal parts are not at a significant angle to the mentioned part of CuA1); CuP and 1A not fused or touching each other (Figs. 2e–2g).

Composition. *Dzhajloutshella, Adzhajloutshella* and *Triassoxya* gen. nov. (Middle or Upper Triassic of Kyrgyzstan).

Remarks. New material of this family would allow the original forewing reconstructions (Gorochov, 1994, text-figs. 1, 2), which were based on material in which the anal parts of the forewings were missing, to be corrected. In fact these forewings were much broader (Figs. 2e, 2g).

Genus *Adzhajloutshella* Gorochov, 1994

Type species. *A. talis* Gorochov, 1994 (Middle or Upper Triassic of Kyrgyzstan).

Diagnosis. Forewings relatively large; costal margin not sinuate; "precostal" area nearly as wide as proximal part of costal area; area Sc-R not widened or weakly so; RA unbranched, i.e., RS branches not shifted onto it; bases of RS and its anterior branch widely spaced; posterior branch of RS fused with anterior branch of MA for relatively short distance; interradial area not wider (or scarcely so) than subcostal one; bifurcation of MA in proximal half of forewing; branches of MP + CuA1 reach (or nearly so) the forewing margin; CuP joining forewing margin in its middle part.

Composition. *A. talis* and *A. plana* sp. nov.

Comparison. This genus differs from *Dzhajloutshella* in the considerably larger forewing (18.5–19.5 mm long), with the "precostal" area nearly as wide as the proximal portion of the costal area, all branches of RS not shifted onto RA, narrow interradial area (not wider or slightly wider than subcostal one), all branches of MP + CuA1 normal, and the CuP apex situated in the central portion of the forewing (Fig. 2e).

Adzhajloutshella plana Gorochov, sp. nov.

Etymology. Latin *planus* (flat).

Holotype. PIN, no. 2555/1440, nearly complete forewing (positive impression); Madygen locality, Madygen Formation.

Description (Fig. 2e). Sc is clearly not reaching the forewing apex; RA is nearly straight; the area between the R and MA branches only slightly narrows apically; the posterior branch of MA is developed along its entire length; MP + CuA1 and CuA2 bears two branches each.

Measurements (mm): forewing length, 18.5.

Comparison. This species differs from *A. talis* in the shorter Sc, straighter branches of R and MA, and the presence of a fully developed posterior branch of MA and only two branches on MP + CuA1.

Material. Holotype and paratype PIN, no. 2240/1957(4252), nearly complete, slightly deformed forewing (part and counterpart) from the same locality.

Genus *Dzhajloutshella* Gorochov, 1994

Type species. *D. arcanum* Gorochov, 1994 (Middle or Upper Triassic of Kyrgyzstan).

Diagnosis (Fig. 2f). Forewings small; costal margin without concavity; "precostal" area wider than proximal portion of costal area; area Sc-R not widened or weakly so; RA not simple, i.e., the base of anterior RS branch shifted onto it; bases of RS and its anterior branch widely spaced; posterior branch of RS fused with anterior branch of MA for a short distance; interradial area distinctly wider than subcostal one; bifurcation of MA located in proximal half of forewing; anterior branch of MP + CuA1 partly reduced, not nearly reaching the forewing margin; CuP joining forewing margin clearly distal to midwing.

Comparison. This genus differs from *Adzhajloutshella* in the smaller forewings (13–15.5 mm long), the "precostal" area wider than the proximal portion of the costal area, the base of the anterior RS branch shifted onto RA, the interradial area distinctly wider than the subcostal area, the retention of only the proximal part of the anterior branch of MP + CuA1, and CuP joining the forewing margin clearly distad of the midwing (Fig. 2f).

Composition. *D. arcanum* and *D. flexuosa* sp. nov.

Dzhajloutshella flexuosa Gorochov, sp. nov.

Etymology. Latin *flexuosa* (curved).

Holotype. PIN, no. 2240/1980, forewing lacking apical part (positive impression); Madygen locality, Madygen Formation.

Description (Fig. 2f). The area between M and CuA (up to the anastomosis with MP) is not widened; the area between the same part of CuA and CuP is not narrowed; MP + CuA1 bears two branches (the vestige of the anterior branch is fairly long, and the posterior branch is slightly arched proximally); CuA2 is also arched proximally, with the distal branches running more or less longitudinally, subparallel to the distal parts of MA and MP + CuA1; CuP is weakly arched distally; and 1A and the branches of 2A are more or less similar in structure to those of *A. plana* sp. nov.

Measurements (mm): length of forewing as preserved, 13.5; estimated full length, 15.5.

Comparison. This species differs from *D. arcanum* in the narrower proximal part of the M–CuA area, the greater width of the same part of the CuA–CuP area, and MP+CuA1 with a lesser number of branches and longer rudiment of the anterior branch.

Material. Holotype.

Genus *Triassoxya* Gorochov, gen. nov.

Etymology. From Triassic and the genus *Xya*.

Type species. *T. novozhilovi* sp. nov.

D i a g n o s i s. Forewings small; costal margin shallowly sinuate about the apex of Sc stem; "precostal" area about as wide as proximal portion of costal area (at least in distal half); Sc–R area distinctly wider in its middle part; the base of anterior RS branch shifted onto RA; bases of RS and its anterior branch in close proximity; posterior branch of RS fused with anterior branch of MA for a long distance; interradial area not wider than subcostal one; bifurcation of MA in distal half of forewing; and MP + CuA1 with two branches reaching the forewing margin.

C o m p a r i s o n. This genus differs from the other genera of this family in the shallow but distinct concavity on the costal margin about the apex of Sc stem, the clearly widened middle part of the area between Sc and R, the bifurcation of MA in the distal half of the forewing, and the considerable length of the fusion of the posterior branch of RS and the anterior branch of MA; it differs from *Dzhajloutshella*, in addition to the above character, in the narrow interradial area, the more closely spaced bases of RS and its anterior branch and from *Adzhajloutshella* in the smaller size and in the base of the anterior branch of RS shifted onto RA (see Figs. 2e–2g for comparison).

C o m p o s i t i o n. *T. novozhilovi* sp. nov.

Triassoxya novozhilovi Gorochov, sp. nov.

E t y m o l o g y. In memory of the collector and paleontologist N.I. Novozhilov.

H o l o t y p e. PIN, no. 1548/113(114), incomplete forewing (part and counterpart); Madygen locality, Madygen Formation.

D e s c r i p t i o n (Fig. 2g). The forewing is very small; the costal area bears rather irregular venation; the areas between longitudinal veins are slightly sclerotized or have dense and finely reticulate (but poorly defined) cross-venation; the base of RS is about halfway between the bifurcation of MP + CuA1 and the apex of RA.

M e a s u r e m e n t s (mm): forewing length, 9.

M a t e r i a l. Holotype.

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