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New and Little Known Mesotitanidae and Paratitanidae (Titanoptera) from the Triassic of Kyrgyzstan

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Abstract—New material on the families Mesotitanidae and Paratitanidae is discussed. A new subfamily Prototitaninae subfam. nov., a new genus *Microtitan* gen. nov., and new species *Prototitan sharovi* sp. nov., *Microtitan zherichini* sp. nov., *Paratitan longispeculum* sp. nov., *P. reductus* sp. nov., *P. venosus* sp. nov., *P. intermedius* sp. nov., *P. latispeculum* sp. nov., *P. bispeculum* sp. nov., and *P. modestus* sp. nov. are described. The subfamily Mesotitaninae stat. nov. and species *Mesotitanodes similis* (Shar.) comb. nov. are characterized.

INTRODUCTION

Until recently, the order Titanoptera has been mainly known through Sharov's paper (1968), in which it was designated to include three families of giant predacious insects possessing a stridulatory apparatus in their elytra. In the same paper, Sharov described two of these families, Paratitanidae and Gigatitanidae, and the vast majority of their Triassic representatives (7 genera and 12 species). All studied impressions came from the locality of Madygen in Kyrgyzstan (Middle or Upper Triassic). Only the family Mesotitanidae, together with its constituent members, one genus and two species, was described earlier from the Middle Triassic of Australia (Tillyard, 1916, 1925); however, the type genus of this family was originally placed in the order Protorthoptera (subsequently in Protohemiptera).

Sharov united Titanoptera, Orthoptera, and Phasmatoptera into a superorder, Orthopteroidea, considering Titanoptera and Phasmatoptera to be descendants of Orthoptera. He named all these three orders "orthopteroid insects"; however, this name in quotation marks is currently used for the entire infraclass Polyneoptera. Subsequently, Titanoptera were included into Orthoptera as a suborder, Mesotitanina (Vishnyakova, 1980), but later, this order was reinstated and proposed as an ancestor of orthopterans and stick-insects (Gorochov, 1987, 2001). In the latter paper, I proposed to include the Carboniferous family Geraridae into the order Titanoptera and to subdivide the order into suborders, Gerarina and Mesotitanina. Geraridae were smaller and lacked strong raptorial legs and stridulatory apparatus. Forms close to this family might be ancestral to Mesotitanina, Orthoptera, and Phasmatoptera.

Since the above book by Sharov was published, there has been no reliable information on new finds of Mesotitanina. Mention made by Vishnyakova (1980) of the presence of this suborder in the Triassic of Ukraine was based on vague fragments, which most probably do not belong to Titanoptera. In contrast, the locality of Madygen again yields abundant fresh material on this group.

A large proportion of species represented in this locality by a single impression might bring us to the conclusion that there were few species but with marked individual variability; however, the same feature is observed in other Madygen insects, Orthoptera (Gorochov, 1986) and Phasmatoptera (Gorochov, 1994). Furthermore, the study of intraspecific variability of the stridulatory apparatus in the elytra extremely diverse Recent Ensifera and stick-insects of the genus *Heteropteryx* demonstrates the remarkable stability of this apparatus within a species, except for cases of brachipterization in one and the same polymorphic species. However, no brachipterization has been recorded in Titanoptera of Madygen. Consequently, one may entertain another hypothesis that the locality of Madygen formed for long under more or less stable conditions, thus allowing repeated changes of close faunas.

MATERIAL

This paper is based on the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN), which contains all the specimens, including the types, both those described by Sharov and those described in this paper. The latter came from the locality of Madygen (Kyrgyzstan, Osh Region, Batken District, Dzhailaucho Valley in the northern spurs of the Turkistan Range; Middle or Upper Triassic, Madygen Formation) and was collected by paleoentomological expeditions of PIN in 1963–1967. It should be noted that many impressions are distorted, i.e., stretched out or constricted; therefore, the main attention in the descriptions is paid to characters that cannot be affected by such distortions.

SYSTEMATIC PALEONTOLOGY

Suborder Mesotitanina Tillyard, 1925

Mesotitanidae: Tillyard, 1925, p. 375.

Mesotitanina: Vishnyakova, 1980, p. 170.

Family Mesotitanidae Tillyard, 1925

Diagnosis. Large and very large insects (elytron length 40–160 mm). Elytron with RS base situated in proximal part of wing, near or proximad MA bifurcation; stridulatory apparatus consisting of three broadened areas (RS–MA_1, MA_1–MA_2, MA_2–MP) crossed by isolated and straight transverse veins more or less parallel to and equally separated from each other (Figs. 1a, 1b).

Composition. Subfamilies Prototitaninae subfam. nov. and Mesotitaninae.

Subfamily Prototitaninae Gorochov, subfam. nov.

Diagnosis. Elytra with parallel longitudinal venation and weakly developed stridulatory apparatus; fields RS–MA_1, MA_1–MA_2, and MA_2–MP relatively narrow (not broader or slightly broader than costal and subcostal areas); RS base situated near MA bifurcation and distad of anastomosis of MP with CuA_1 (Fig. 1a).

Composition. Genus *Prototitan* with *P. primitivus* Sharov, 1968 and *P. sharovi* sp. nov.; locality of Madygen; Middle or Upper Triassic.

Remarks. This subfamily includes probably the most primitive known representatives of Mesotitanina, in which their stridulatory apparatus was still weakly developed.

Genus *Prototitan* Sharov, 1968

Prototitan sharovi Gorochov, sp. nov.

Etymology. In memory of the famous paleoentomologist A.G. Sharov.

Holotype. PIN, no. 2785/2042, part and counterpart of incomplete elytra partially overlapping each other; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 1a). The elytron is long and narrow. RA has five more branches, the branching of RA starts much proximad of the Sc tip; branching of RS

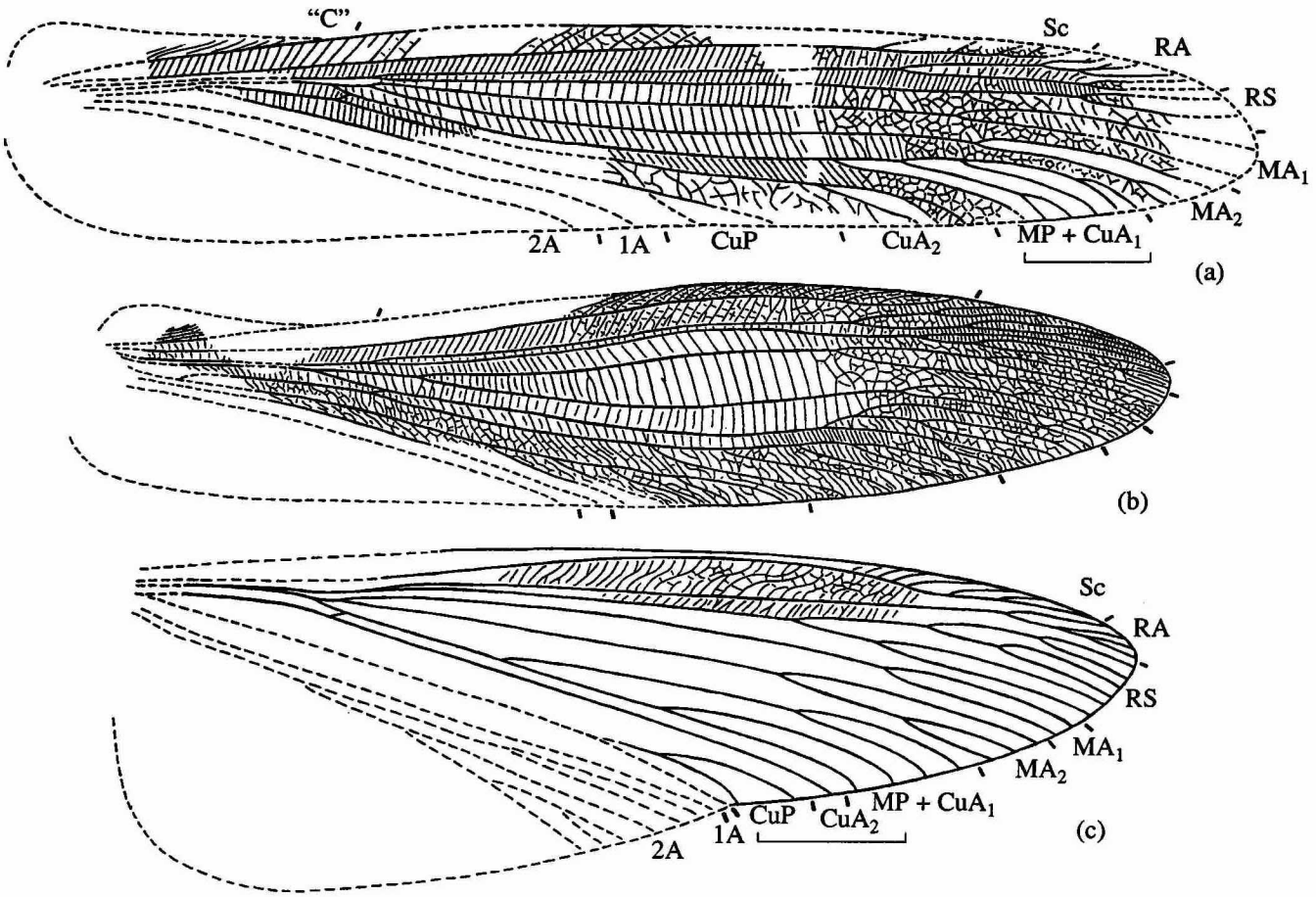

Fig. 1. Wings in the family Mesotitanidae: (a) *Prototitan sharovi* sp. nov., holotype PIN, no. 2785/2042, elytron; (b, c) *Mesotitanodes similis* (Shar.), specimen PIN, no. 2785/2029: (b) elytron, (c) hindwing. Scale bar 10 mm in Figs. 1–3.

starts much distad of the point of the RA branching; branching of MA_1 starts much proximad of the point of the RS branching but distad of the RA branching; branching of MA_2 starts slightly distad of the MA_1 branching; the comb of MP + CuA_1 branches is short; the area between MP + CuA_1 and the anal margin of the elytron near CuA_2 tip is broad and roughly equal to the area between RS and MP + CuA_1 in the same place; the CuA_2 tip is situated clearly distinctly of the elytron midlength.

Measurements, mm: length of the best preserved elytron, 82; estimated length of elytron, ~100.

Comparison. This species markedly differs from *P. primitivus* in the RA branches being more numerous, the comb of MP + CuA_1 branches being considerably shorter an obviously wider area between MP + CuA_1 and the anal margin of the elytron, a more distal tip of CuA_2, and in some other features.

Material. Holotype.

Subfamily Mesotitaninae Tillyard, 1925, stat. nov.

Mesotitanidae: Tillyard, 1925, p. 375.

Clathrotitanidae: Riek, 1954, p. 165.

Diagnosis. Elytra with non-parallel longitudinal venation and well-developed stridulatory apparatus, fields RS–MA_1, MA_1–MA_2, and MA_2–MP or only field MA_1–MA_2 considerably widened (clearly wider than costal and subcostal areas); RS base situated distad of MA bifurcation and near or proximad of MP and CuA_1 anastomosis (Fig. 1b).

Composition. Three genera, *Mesotitan* Tillyard, 1916 (= *Clathrotitan* McKeown, 1937) with *M. giganteus* Tillyard, 1916 and *M. scullyi* Tillyard, 1925 (= *M. tillyardi* McKeown, 1937 = *C. andersoni* McKeown, 1937) from the Middle Triassic of Australia; *Mesotitanodes* with *M. tillyardi* Sharov, 1968 and *P. similis*; and *Ultratitan* Sharov, 1968 with *U. superior* Sharov, 1968 from the Middle or Upper Triassic of the locality of Madygen.

Remark. This subfamily is probably a somewhat specialized descendant of Prototitaninae.

Genus *Mesotitanodes* Sharov, 1968

***Mesotitanodes similis* (Sharov, 1968), comb. nov.**

Prototitan similis Sharov, 1968, p. 197, text-fig. 48B.

Holotype. PIN, no. 2555/1481, part and counterpart of proximal halves of forewings and hindwings and fragments of fore and hind legs; locality of Madygen; Middle or Upper Triassic.

Description (Figs. 1b, 1c). The elytron is very similar to but considerably narrower than *M. tillyardi*, with the MA_2–MP field being not wider than the subcostal field and with small differences in the number of the main longitudinal veins in the apical field of the elytron. The hindwing is less similar to that assigned to *M. tillyardi* (Sharov, 1968, text-fig. 48D), the costal field has oblique and reticulate transverse venation, RS has six branches, which occupy a large area of the apical part of the wing, MA_1 has two branches, branching of MA_2 starts slightly proximad of the RS branching, MP + CuA_1 has four branches, and they bifurcate clearly closer to MA bifurcation rather than to the point of MA_2 bifurcation.

Measurements, mm: length of the best preserved elytron (Fig. 1b), 71; estimated length of elytron, ~75.

Remarks. The description resulted from the study of types and better preserved new material. This species may turn out to be a synonym of *M. tillyardi*, the holotype of which is much similar to the above elytron; however, this holotype might be greatly extended due to the deformation of rocks. One of the *M. tillyardi* paratypes (PIN, no. 2555/1455, hindwing impression) differs essentially from the hindwing of the new species. It cannot be excluded that this paratype belongs to a separate, yet undescribed species of the genus *Mesotitanodes*.

Material. Holotype and paratype PIN, no. 2555/1521 (impression of the proximal half of the hindwing), and new material, specimen PIN, no. 2785/2029, impressions of incomplete forewings and hindwings.

Family Paratitanidae Sharov, 1968

Diagnosis. Medium-sized and large insects (elytron length, 30–70 mm). Elytra with RS base in their distal part (near speculum apex); stridulatory apparatus consisting of same three broadened fields as in Mesotitanidae, but the MA_1–MA_2 field always wider than other fields of elytra (widened part of this field called speculum); transverse venation pattern of these broadened fields as in Mesotitanidae (Figs. 2a–2e, 3a–3c).

Composition. The genera *Paratitan* Sharov, 1968 with *P. ovalis* Sharov, 1968, *P. libelluloides* Sharov, 1968, *P. longispeculum* sp. nov., *P. reductus* sp. nov., *P. venosus* sp. nov., *P. intermedius* sp. nov., *P. latispeculum* sp. nov., *P. bispeculum* sp. nov., *P. modestus* sp. nov. and *Microtitan* gen. nov. with *M. zherichini* sp. nov.; locality of Madygen, Middle or Upper Triassic.

Genus *Microtitan* Gorochov, gen. nov.

Etymology. From the genus *Mesotitan*.

Type species. *M. zherichini* sp. nov.

Diagnosis. Elytra small for this order (elytron length, 32–35 mm); comblike part of CuA_2 (from base of most proximal branch to apex of most distal branch) clearly longer than half length of elytron; distal (situated in distal half of elytron) part of area between CuA_2 and anal margin of elytron very narrow (noticeably narrower than areas between MA_2 and MP + CuA_1 in same part of elytron); branches of CuA_2 short (Fig. 2a).

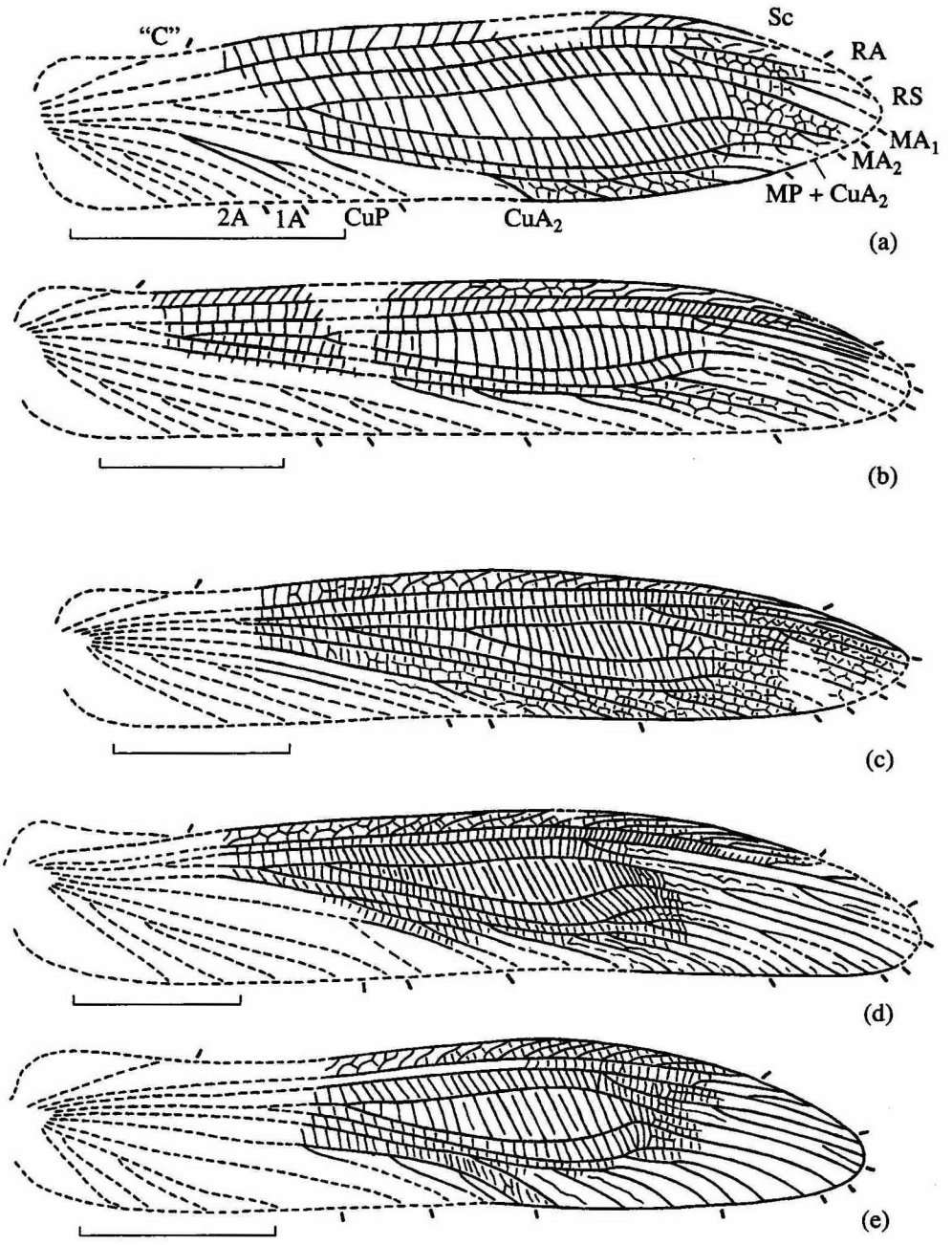

Fig. 2. Elytra in the family Paratitanidae: (a) *Microtitan zherichini* sp. nov., holotype PIN, no. 2240/589; (b) *Paratitan longispeculum* sp. nov., holotype PIN, no. 2240/4543; (c) *P. reductus* sp. nov., holotype PIN, no. 2785/2021; (d) *P. venosus* sp. nov., holotype PIN, no. 2555/1456; (e) *P. intermedius* sp. nov., holotype PIN, no. 2555/1520.

Species composition. Type species.

Comparison. This new genus differs from the genus *Paratitan* in its elytra being smaller, much longer comb of CuA_2, and in a considerably narrower field between CuA_2 and the anal margin of the elytron.

***Microtitan zherichini* Gorochov, sp. nov.**

Etymology. In memory of the great paleoentomologist V.V. Zherikhin.

Holotype. PIN, no. 2240/589, part and counterpart of an incomplete elytron; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 2a). The costal field is narrow, not wider than the field between Sc and R; RS appears to have two (or more) branches and its base is situated near the distal part of the speculum (widened area between MA_1 and MA_2); the speculum is long and situated in the middle of the elytron (along the midline);

MP + CuA_1 has two branches in its distal portion; CuA_2 has six or more branches; CuP probably has three branches.

Measurements, mm: impression length, 25; estimated length of elytron, 32–35.

Material. Holotype.

Genus *Paratitan* Sharov, 1968

Paratitan longispeculum Gorochov, sp. nov.

Etymology. From Latin *longus* (long) and *speculum* (speculum).

Holotype. PIN, no. 2240/4543, part and counterpart of an incomplete elytron; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 2b). The elytron is of medium size and of a structure typical of this genus, but clearly differs from previously known species in the following features: from *P. libelluloides*, in an unbrached RS, considerably longer speculum (distance between the speculum base and the RS base is 2.7 times as long as the distance between the MP base and the speculum base, whereas this ratio is 1.2 in *P. libelluloides*) and in CuA_1 having four branches; from *P. ovalis*, in a narrower costal field, which is nearly equal to the field between Sc and R, an unbranched RS, whose base is situated considerably distad of the widest part of the speculum, and in MA_2 being clearly curved near the speculum apex.

Measurements, mm: impression length, 41; estimated length of elytron, 48–50.

Comparison. Differences from previously described species are given above.

Material. Holotype.

Paratitan reductus Gorochov, sp. nov.

Etymology. From Latin *reductus* (reduced).

Holotype. PIN, no. 2785/2021, part and counterpart of incomplete elytron; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 2c). The elytron generally resembles those in described species of this genus, differing in the following features: from *P. libelluloides*, in the unbranched MP+ CuA_1 and long CuP and CuA_2 (CuP reaches nearly to the center of the speculum, the CuA_2 apex extends much distad of the speculum apex and of the RS base); from *P. ovalis*, in a narrower costal field, which is clearly narrower at the RS base than the Sc–R field, and in a narrower field between R (proximad of the RS base) and MA_1, as well as in less numerous branches of RA and RS; from *P. longispeculum*, in the short speculum, unbranched MP + CuA_1, nearly straight MA_2 and CuA_2 having three branches.

Measurements, mm: impression length, 39; estimated length of elytron, 48–50.

Comparison. Differences from previously described species are given above.

Material. Holotype.

Paratitan venosus Gorochov, sp. nov.

Etymology. From Latin *venosus* (veined).

Holotype. PIN, no. 2555/1456, part and counterpart of an incomplete elytron; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 2d). The elytron resembles those described in species of this genus, differing in the following features: from *P. libelluloides*, in a somewhat broader costal field, which is noticeably wider at the RS base than the field between Sc and R, well-distinct long and gently sloping branches of Sc, MA_1 having two branches, clearly shorter MA between the MP and speculum bases, and in MP + CuA_1 and CuA_2 having some more branches; from *P. ovalis*, in the fewer number of RA and RS branches, a narrower field between R (proximad of RS) and MA_1, MA_1 having two branches, and MA_2 being distinctly curved near the speculum apex; from *P. longispeculum*, in a wider costal field, branched RA, RS and MA_1, shorter speculum, smaller distance between the MP and speculum bases, and in a distinctly wider field between MA_2 and MP + CuA_1 near the speculum apex; from *P. reductus*, in a wider costal field, longer speculum and RS, a noticeably smaller distance between the MP and speculum bases, MA_1 having two branches, clearly curved MA_2, branched MP + CuA_1, and in the multibranched CuA_2.

Measurements, mm: impression length, 41; estimated length of elytron, ~55.

Comparison. Differences from previously described species are given above.

Material. Holotype.

Paratitan intermedius Gorochov, sp. nov.

Etymology. From Latin *intermedius* (intermediate).

Holotype. PIN, no. 2555/1520, part and counterpart of incomplete elytron; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 2e). The elytron resembles those in described species of this genus, differing in the following features: from *P. libelluloides*, in a wider costal field, which is clearly wider than the field between Sc and R near the RS base, in the RS having 2 branches, a narrow field between R (proximad of RS) and MA_1, wider speculum, longer CuA_2, which extends clearly distad of the speculum apex and RS base, in the base of the CuA_2 proximal branch situated far distad of the speculum base, and in the four-branched CuP; from *P. ovalis*, in less numerous branches of RA and RS, whose bases are situated much more distad of the widest part of the speculum, a narrower field between R (proximad of RS) and MA_1, the nearly angular bent of MA_2, and in the four-branched CuP; from *P. longispeculum*, in a wider costal field, branched RA and RS,

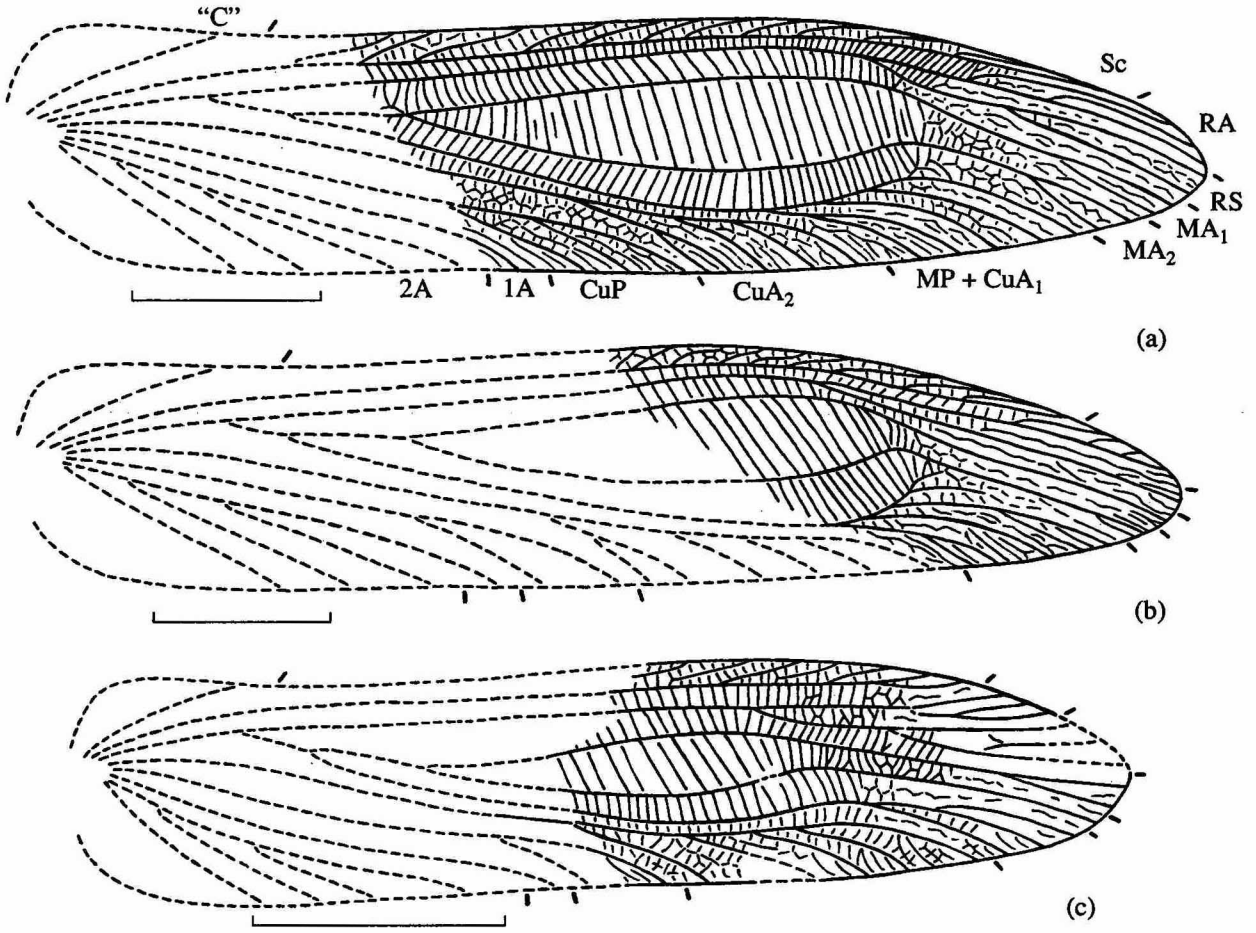

Fig. 3. Elytra in the genus *Paratitan*: (a) *P. latispeculum* sp. nov., holotype PIN, no. 2555/1478; (b) *P. bispeculum* sp. nov., holotype PIN, no. 2240/4588; (c) *P. modestus* sp. nov., holotype PIN, no. 2255/1479.

and in a shorter and wider speculum; from *P. reductus*, in a wider costal field near the RS base, longer and wider speculum, MA_2 being almost angular near the speculum apex, branched $MP + CuA_1$, and in CuA_2 and CuP having more branches; from *P. venosus*, in a shorter distal part of the elytron (the speculum is not shorter than RS and noticeably longer than the MA_2 section distad of the speculum), wider speculum, unbranched MA_1, somewhat less branched CuA_2 and $MP + CuA_1$, and in the four-branched CuP.

Measurements, mm: impression length, 29; estimated length of elytron, ~45.

Comparison. Differences from previously described species are given above.

Material. Holotype.

***Paratitan latispeculum* Gorochov, sp. nov.**

Etymology. From Latin *latus* (broad) and *speculum* (speculum).

Holotype. PIN, no. 2555/1478, part and counterpart of an incomplete elytron; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 3a). It differs from described species in the following characters: from *P. libelluloides*, in the field between Sc and R (proximad of RS) being clearly narrower than the costal field and the field between R and MA_1, the presence of noticeable gently sloping branches of Sc and RA, a clearly larger speculum, a wider field between MA_2 and $MP + CuA_1$, and more numerous branches of MA_2, $MP + CuA_1$, CuA_2 and CuP; from *P. ovalis*, in narrower fields Sc–R and R–MA_1, a different position of RS, MA_2 shape, different number of RS and MA_2 branches, larger speculum, and in a shorter distal part of the elytron; from *P. longispeculum*, in a wider costal field, speculum and fields R–MA_1 and between MA_2 and $MP + CuA_1$, the presence of noticeable gently sloping branches Sc and RA, branched RS and MA_2, and five-branched $MP + CuA_1$; from *P. reductus*, in a wider distal part of the costal field and a wider Sc–R field, a distinctly larger speculum, curved MA_2, and in a greater number of MA_2, MP +

CuA_1, CuA_2 and CuP branches; from *P. venosus*, in a larger speculum, shorter distal part of the elytron, unbranched MA_1, somewhat more numerous MA_2 and MP + CuA_1 branches, and in the smaller number of CuA_2 branches; from *P. intermedius*, in a larger speculum, a somewhat shorter distal part of the elytron, more numerous branches of MA_2 and MP + CuA_1, a longer CuA_2, which clearly does not reaching the speculum apex, and in less numerous branches of CuP.

Measurements, mm: impression length, 47; estimated length of elytron, ~65.

Comparison. Differences from previously described species are given above.

Material. Holotype.

***Paratitan bispeculum* Gorochov, sp. nov.**

Etymology. From Latin *bis* (double) and *speculum* (speculum).

Holotype. PIN, no. 2240/4588, part and counterpart of the distal part of elytron; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 3b). The elytron resembles that of *P. latispeculum* in the size of the stridulatory apparatus, but easily differs from the latter in distinctly narrower Sc–R (distad of RS base) and R–MA (near RS base) fields, a considerably wider field MA–MP near MP + CuA_1 branches, and in the loss of contact between apices of the most distal branches of the latter vein and the elytron margin.

Measurements, mm: impression length, 34; estimated length of elytron, 60–65.

Comparison. From other described species of this genus, the new species differs in the same characters as from *P. latispeculum*.

Material. Holotype.

***Paratitan modestus* Gorochov, sp. nov.**

Etymology. From Latin *modestus* (modest).

Holotype. PIN, no. 2255/1479; part and counterpart of distal half of elytron; locality of Madygen; Middle or Upper Triassic.

Description (Fig. 3c). The elytron differs from that of *P. ovalis* in the shorter branches of RA and more distal position of the RS base. From other species, it differs in a nearly straight distal part of Sc having weakly gently sloping, medium length branches, as well as in the three-branched RS; additionally, from *P. libelluloides*, in a longer comb of CuA_2 branches, from *P. longispeculum*, in the presence of RA branches, from *P. reductus*, in the branched MP + CuA_1, from *P. venosus*, in shorter and less numerous branches of MP + CuA_1, from *P. intermedius*, *P. latispeculum* and *P. bispeculum*, in clearly narrower speculum (relating to the width of the elytron).

Measurements, mm: impression length, 2; estimated length of elytron, ~42.

Comparison. Differences from previously described species are given above.

Material. Holotype.

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