

# The First Representative of the Suborder Mesotitanina from the Paleozoic and Notes on the System and Evolution of the Order Titanoptera (Insecta: Polyneoptera)

A. V. Gorochov

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034 Russia

e-mail: orthopt@zin.ru

Received February 7, 2007

**Abstract**—A new subfamily, genus, and species (Deinotitaninae subfam. nov., *Deinotitan orenburgensis* gen. et sp. nov.) of the family Mesotitanidae (Titanoptera) are described from the Severodvinian (Upper Permian) of the Orenburg Region. This family belongs to the suborder Mesotitanina; both are recorded in the Paleozoic for the first time. The present finding and unpublished data suggest that the Mesozoic stage of the evolution of the superorder Orthopteroidea might start in the Late Permian. Taxonomy and early evolution of the order Titanoptera are discussed. *Minititan* nom. nov. is proposed for *Microtitan* Gorochov, 2003 (nec *Microtitan* Granger et Gregory, 1943).

**DOI:** 10.1134/S0031030107060056

**Key words:** Mesotitanina, new taxa, Upper Permian, evolution, classification, Orenburg Region, Russia.

## INTRODUCTION

Recently, interest in the small extinct order Titanoptera has increased considerably. This was connected with publications on the taxonomy and morphology of the Carboniferous family Geraridae (Burnham, 1983; Kukalová-Peck and Brauckmann, 1992) implying or supposing that this family belongs not to Polyneoptera but to some other infraclass of Pterygota. Moreover, assumptions were expressed on the possible origin of the orders Orthoptera and Phasmatoptera from some primitive Carboniferous Titanoptera, then known only from their Triassic representatives (Gorochov, 1994), and on advisability of assigning Carboniferous Geraridae to this order as a separate suborder Gerarina (Gorochov, 2001a). In the latter paper some data of Burnham, Kukalová-Peck, and Brauckmann were refuted, and the opinion of Sharov (1968) on the possible close relationship of Geraridae (= Sthenaropodidae) to ancestors of the order Orthoptera was supported.

Proximity of Geraridae to ancestors of Orthoptera or at least their belonging to Polyneoptera were also supported by some other authors (Bethoux and Nel, 2002; Rasnitsyn, 2002). Descriptions of the new and redescriptions of some other taxa of Carboniferous Geraridae and Triassic Mesotitanina have appeared (Brauckmann et al., 2001; Bethoux and Nel, 2003; Gorochov, 2003, 2004). The last of these papers is a general one, proposing scenarios of the origin and early morpho-ecological evolution of Titanoptera, describing the only problematic Permian member of the order (incertae subordinis) and suggesting the higher classification of the order. Besides that, it contains additional

arguments for an earlier tentative supposition (Gorochov, 2001b) that the recently described extant “order” Mantophasmatodea possibly belongs in Titanoptera.

Another discussion concerning this order has arisen due to different views on the role of flight in evolution of Geraridae. The hypothesis explaining characteristic wing structure of Geraridae by improvement of their flight (Gorochov, 2001a) raised an objection from some colleagues (Bethoux and Nel, 2003), believing that the flight of Geraridae was still imperfect and they were (nearly) passive flyers in the sense of Brodsky (1988). On the one hand, this objection is more of a misunderstanding: Gorochov did not term the flight of Geraridae perfect, just assuming that the flight of their hypothetical cockroach-like ancestors was less perfect, because their forewings were transformed into protective elytra (though probably less elytrized than in most cockroaches) and almost did not participate in flight, and their hind wings were less costalized and possessed an enlarged anal lobe of about the same size as in Geraridae. On the other hand, to rank Geraridae among passive flyers is clearly a mistake, because Brodsky termed flight passive if wings are not moving to create lift: gliding, hovering, parachuting. The first two types are flight elements in some best flyers among modern insects: dragonflies and some butterflies. Hovering with partial parachuting is probably peculiar to only very small feather-winged forms, while parachuting with elements of gliding might be characteristic of the as yet unknown earliest Pterygota. As for Geraridae, judging from their wing structure they were clearly active fly-

ers, although obviously not as strong as contemporaneous Meganisoptera, Palaeodictyoptera, etc.

Another assumption expressed in the same paper of Gorochov on perfection of flight in Geraridae owing to shift of their ancestors to phytophylly was reconsidered, and now better substantiated seems to be a hypothesis on retention of geophylly in this group with development of adaptations to more or less free life on the ground (Gorochov, 2004). With the shift to phytophylly is now associated the origin of the suborder Mesotitanina, formerly known only from the Triassic.

The representative of the order Titanoptera described below from the Severodvinian of the Upper Permian belongs to or is close to one of the Triassic families of Mesotitanina and presents the most reliable evidence on existence of the order in the Paleozoic, because placement of Geraridae in Titanoptera is not yet sufficiently reliable. Moreover, this find is the first clear indication that the Mesozoic evolutionary stage of the superorder Orthopteroidea possibly started not in the Early Triassic (Gorochov, 1995; Gorochov and Rasnitsyn, 2002), but rather in the Late Permian. The latter assumption is further supported by finds in the Urzhumian (upper Middle Permian) of Udmurtia of the subfamily Meselcaninae (Orthoptera, Permelcanidae) (unpublished); formerly this subfamily was recorded only from the Triassic.

## MATERIAL

This paper is based on the study of material kept in the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN), including the holotype of the species described herein.

## SYSTEMATIC PALEONTOLOGY

### PROPOSED CLASSIFICATION OF THE ORDER TITANOPTERA

Suborder Gerarina Handlirsch, 1906

The family Geraridae Handlirsch, 1906 includes *Gerarus* Scudder, 1885 (= *Genopteryx* Scudder, 1885) and *Nacekomia* Richardson, 1956 from the Middle Carboniferous; *Sthenaropoda* Brongniart, 1885 (= *Archaeacridites* Meunier, 1909), *Osnogerarus* Kukalová-Peck et Brauckmann, 1992, *Cantabrala* Kukalová-Peck et Brauckmann, 1992 and *Brachygerarus* Gorochov, 2004 from the Upper Carboniferous; and possibly also insufficiently preserved *Rossites* Richardson, 1956 from the Middle Carboniferous and *Permotitan* Gorochov, 2004 from the mid-Permian.

Suborder Mesotitanina Tillyard, 1925

The family Mesotitanidae Tillyard, 1925 includes Deinotitaninae subfam. nov. [*Deinotitan* gen. nov. from the Upper Permian]; Mesotitaninae Tillyard, 1925 (= Clatrotitanidae Riek, 1954) [Mesotitan Tillyard, 1916 (= Clatrotitan McKeown, 1937) from the Middle Triassic; *Mesotitanodes* Sharov, 1968 and *Ultratitan*

Sharov, 1968 from the Middle or Upper Triassic]; Prototitaninae Gorochov, 2003 [*Prototitan* Sharov, 1968 from the Middle or Upper Triassic].

The family Paratitanidae Sharov, 1968 includes *Paratitan* Sharov, 1968 and *Minititan* Gorochov, nom. nov. (= *Microtitan* Gorochov, 2003; nec *Microtitan* Granger et Gregory, 1943—Mammalia: Brontotheoriidae) from the Middle or Upper Triassic.

The family Gigatitanidae Sharov, 1968 includes *Gigatitan* Sharov, 1968, *Ootitan* Sharov, 1968 and *Nanotitan* Sharov, 1968 from the Middle or Upper Triassic.

### ?Suborder Mantophasmatina Klass, Zompro, Kristensen et Adis, 2002

The family Mantophasmatidae Klass, Zompro, Kristensen et Adis, 2002 includes several subfamilies and/or tribes, described as families and represented by a few apterous genera in Eocene Baltic amber and the modern fauna of Africa (Zompro, 2001; Zompro et al., 2002; Klass et al., 2002, 2003).

## Family Mesotitanidae Tillyard, 1925

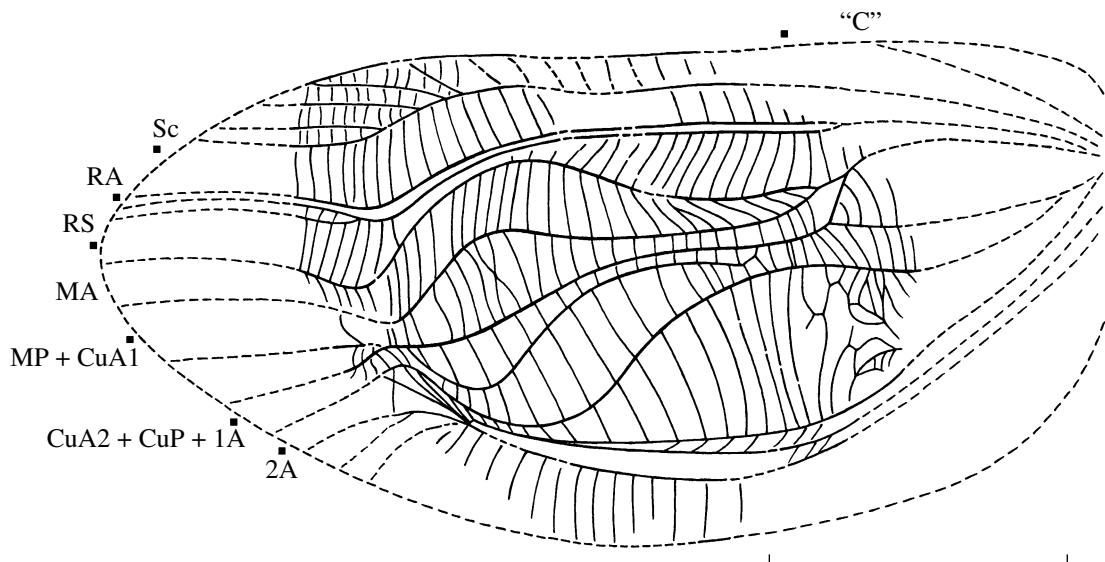
### Subfamily Deinotitaninae Gorochov, subfam. nov.

**D i a g n o s i s.** Elytra with nonparallelized longitudinal venation and well developed stridulatory apparatus; Sc-RA area and all areas between RS and CuP conspicuously widened in either proximal or distal wing half (CuA2-CuP area most widened); Sc, RA, RS, CuA2, branches of MA and MP+CuA1 markedly S-shaped; proximal section of CuA1 probably quite long; CuP, 1A and stem of 2A arched, almost fused or contiguous distally (Fig. 1).

**C o m p o s i t i o n.** *Deinotitan* gen. nov.

**C o m p a r i s o n.** The new subfamily differs from Mesotitaninae in such characters of elytra as higher number of widened areas in the stridulatory apparatus, conspicuous S-shaped curvature of main branches of all longitudinal veins between subcostal and intercubital areas, characteristic structure of CuP, 1A and 2A, and possibly also in longer proximal section of CuA1. Distinct from Prototitaninae, in addition to the above-mentioned characters, in nonparallelized elytral venation with well developed stridulatory apparatus, bearing much wider sound-emitting areas.

**R e m a r k s.** The two earliest members of the suborder (Upper Permian *Deinotitan* and Middle Triassic *Mesotitan*) possess at least one common character distinguishing them from all presumably younger taxa. In their elytra the proximal section of CuA1 is much longer than the proximal section of MP, whereas in Prototitaninae, Paratitanidae, Gigatitanidae, and the remaining Mesotitaninae, either these sections are of equal length or the former one is shorter. If the presence of long proximal section of CuA1 is a symplesiomorphy, one may assume that Mesotitaninae might be ancestral not only to Paratitanidae, but to Gigatitanidae and Prototitaninae as well. The somewhat simplified venation of the latter subfamily, that caused Sharov



**Fig. 1.** *Deinotitan orenburgensis* sp. nov., holotype PIN, no. 3700/167, left elytron; Novo-Aleksandrovka locality; Upper Permian. Scale bar, 10 mm.



**Fig. 2.** Imprint of a left elytron of *Deinotitan orenburgensis* sp. nov.

(1968) and Gorochov (2003) to treat this venation as primitive, may be explained by reduction of the stridulatory apparatus. On the contrary, if the above character was

independently acquired by *Deinotitan* and *Mesotitan*, then Prototitaninae might be indeed primitive group, expected to be found at least in the Upper Permian.

### Genus *Deinotitan* Gorochov, gen. nov.

**E t y m o l o g y.** From the Greek *deinos* (terrible) and the generic name *Mesotitan*.

**T y p e s p e c i e s.** *D. orenburgensis* sp. nov.

**D i a g n o s i s.** Elytron with costal area slightly widened distally; Sc with distinct branches only near apex (more proximal branches, if developed, indistinguishable from crossveins); subcostal area somewhat widened about origin of distal Sc branch; R forked in proximal part of elytron; RA and RS simple and closely approximating each other about sound-emitting areas of stridulatory apparatus; radial area widened between proximal sections of RS and MA1, markedly narrowed more distally and widened again in apical part; area between M (before forking into MA and MP) and CuA1 widened; intermedial area gradually widened in proximal half and narrowed distally; areas between MA2 and CuA2 relatively narrow proximally, widened distally, and narrowed again at the apex of stridulatory apparatus; area CuA2–CuP markedly widened in proximal and markedly narrowed in distal part of stridulatory apparatus; areas CuP–1A and 1A–2A rather narrow; area between 2A and anal margin of elytron widened and filled almost exclusively with crossveins (or branches of 2A likened to crossveins); CuP fused with 1A about narrowed part of cubital area, and with stem of 2A somewhat more distally (latter fusion indistinct, possibly, the veins only touch each other there, and later some of them merge with CuA2) (Fig. 1).

**C o m p o s i t i o n.** Type species.

#### *Deinotitan orenburgensis* Gorochov, sp. nov.

**E t y m o l o g y.** From the Orenburg Region.

**H o l o t y p e.** PIN, no 3700/167, elytron (positive impression, base and apex missing); Orenburg Region, Tyulgan District, 6 km north of the village of Troitskoe, Novo-Aleksandrovka locality; Upper Permian, Severodvinian Stage (Severodvinian Horizon of the Upper Tatarian Substage in the former stratigraphic scale).

**D e s c r i p t i o n** (Figs. 1, 2). Most crossveins oriented almost perpendicular to longitudinal axis of elytron, but in proximal half of stridulatory apparatus these crossveins in the area RS–MA and between branches of MA inclined in opposite directions relative to each other (especially strongly inclined between the latter branches); cross-venation at base of widened part of area CuA2–CuP irregular, forming a meshwork of cells; certain irregularity of cross-venation observed also about narrowing of areas between MA and 2A in distal part of elytron.

**M e a s u r e m e n t s** (mm): length of preserved elytron part, 21; reconstructed length of elytron, 32–36.

**M a t e r i a l.** Holotype.

### ACKNOWLEDGMENTS

I am grateful to all the members of Arthropoda Lab (PIN) for their assistance and to D.E. Shcherbakov for the photograph of the imprint.

The study was supported by the Presidium of the Russian Academy of Sciences, Program “Biosphere Origin and Evolution” and the Russian Foundation for Basic Research (project no. 04-04-48189).

### REFERENCES

1. O. Bethoux and A. Nel, “Venational Pattern and Revision of Orthoptera sensu nov.,” *Zootaxa* **96**, 1–88 (2002).
2. O. Bethoux and A. Nel, “Wing Venation Morphology and Variability of *Gerarus fischeri* (Brongniart, 1885) *sensu* Burnham (Panorthoptera; Upper Carboniferous, Commentry, France), with Inferences on Flight Performance,” *Org. Divers. Evol.* **3**, 173–183 (2003).
3. C. Brauckmann, A. Arillo, and V. M. Ortúñ, “A New Geraridae (Insecta, Hemipteroid Stem Assemblage) from the Upper Carboniferous of La Magdalena (León, Northern Spain),” *Boll. Geol. Minero* **112** (2), 57–62 (2001).
4. A. K. Brodsky, *Flight Mechanics in Insects and Evolution of Their Wings* (Leningr. Gos. Univ., Leningrad, 1988) [in Russian].
5. L. Burnham, “Studies on Upper Carboniferous Insects: 1. The Geraridae (Order Protorthoptera),” *Psyche* **90** (1–2), 1–57 (1983).
6. A. V. Gorochov, “On Permian and Triassic Stick Insects (Phasmoptera) from Eurasia,” *Paleontol. Zh.*, No. 4, 64–75 (1994).
7. A. V. Gorochov, “The System and Evolution of Orthopterans of the Suborder Ensifera (Orthoptera). Parts 1 and 2,” *Tr. Zool. Inst. Ross. Akad. Nauk* **260**, 1–224 (1995).
8. A. V. Gorochov, “On the Higher Classification of the Polyneoptera (Short Course),” *Acta Geol. Leopold.* **24** (52/53), 11–56 (2001a).
9. A. V. Gorochov, “The Most Interesting Finds of Orthopteroid Insects at the End of the 20th Century and a New Recent Genus and Species,” *J. Orthopt. Res.* **10** (2), 353–367 (2001b).
10. A. V. Gorochov, “New and Little Known Mesotitanidae and Paratitanidae (Titanoptera) from the Triassic of Kyrgyzstan,” *Paleontol. Zh.*, No. 4, 62–69 (2003) [Paleontol. J. **37** (4), 400–406 (2003)].
11. A. V. Gorochov, “Primitive Titanoptera and Early Evolution of Polyneoptera,” *Chteniya Pamyati N.A. Kholodkovskogo* **57** (1), 1–54 (2004).
12. A. V. Gorochov and A. P. Rasnitsyn, “2.2.2.3. Superorder Gryllidea Laicharting, 1781 (= Orthopteroidea Handlirsch, 1903),” in *History of Insects*, Ed. by A. P. Rasnitsyn and D. L. J. Quicke (Kluwer Academic, Dordrecht, 2002), pp. 293–303.
13. K.-D. Klass, O. Zompro, N. P. Kristensen, and J. Adis, “Mantophasmatodea: A New Insect Order with Extant

- Members in the Afrotropics," *Science* **296** (5572), 1456–1459 (2002).
14. K.-D. Klass, M. D. Picker, J. Damgaard, et al., "The Taxonomy, Genitalic Morphology, and Phylogenetic Relationships of Southern African Mantophasmatodea," *Entomol. Abh.* **61** (1), 3–67 (2003).
  15. J. Kukalová-Peck and C. Brauckmann, "Most Paleozoic Protorthoptera Are Ancestral Hemipteroids: Major Wing Braces As Clues to a New Phylogeny of Neoptera (Insecta)," *Can. J. Zool.* **70**, 2452–2473 (1992).
  16. A. P. Rasnitsyn, "2.2.2.0.1. Order Eoblattida Handlirsch, 1903 (= Cacurgida Handlirsch, 1906, = Protoblattodea Handlirsch, 1906)," in *History of Insects*, Ed. by A. P. Rasnitsyn and D. L. J. Quicke (Kluwer Academic, Dordrecht, 2002), pp. 256–260.
  17. A. G. Sharov, "Phylogeny of Orthopteroid Insects," *Tr. Paleontol. Inst. Akad. Nauk SSSR* **118**, 1–217 (1968).
  18. O. Zompro, "The Phasmatodea and Raptophasma n. gen., Orthoptera incertae sedis, in Baltic Amber (Insecta: Orthoptera)," *Mitt. Geol.-Palaeontol. Inst. Univ. Hamburg* **85**, 229–261 (2001).
  19. O. Zompro, J. Adis, and W. Weitschat, "A Review of the Order Mantophasmatodea (Insecta)," *Zool. Anz.* **241**, 269–279 (2002).