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# Madygen, Triassic Lagerstätte number one, before and after Sharov

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**ABSTRACT**

The insect fauna of the world's richest Triassic fossil locality, Madygen (Ladinian–Carnian of Kyrgyzstan) is reviewed; other groups of animals and plants recorded from the locality are also listed. The research history, fossil preservation and paleoenvironment of the Madygen Formation are briefly discussed. The site was discovered in 1933, and the better part of fossils was collected from the outcrop richest in insects, Dzhayloucho, during five expeditions headed by Alexander Sharov, who discovered there and described two peculiar gliding reptiles that made Madygen worldwide known. The entomofauna includes 20 orders (including the earliest Hymenoptera and early Diptera) and nearly 100 families. The insect assemblage is numerically dominated by Coleoptera, Blattodea, and Auchenorrhyncha. In Dzhayloucho, subdominants are Mecoptera, Orthoptera, and Protorthoptera. The largest insects belong to Titanoptera, the order established by Sharov and the most diverse in Madygen. Amphibiotic insects are rare and represented almost exclusively by adults. In some outcrops phyllopod Kazacharthra are common. The paleoenvironment may be reconstructed as an intermontane river valley in seasonally arid climate, with mineralized oxbow lakes and ephemeral ponds on the floodplain.

**KEY WORDS**: Middle–Late Triassic. Insects. Composition of entomofauna. Paleoenvironment.

## INTRODUCTION

The world renown fossil site near the village of Madygen, in foothills of the Turkestan Range (south of Fergana Valley), Kyrgyzstan has yielded more than twenty thousand insect specimens, as well as abundant plants, bivalves, crustaceans, fishes and unusual tetrapods. Some of these diverse insects and vertebrates are preserved in remarkable detail.

The fossil site was discovered in 1933 by Evgeny A. Kochnev, who named the rock sequence comprising fossiliferous shales, sandstones and (in some places) thin coal seams as the Madygen Formation (Kochnev 1934). This formation, cropping out in five adjacent areas (southwestern, northern, eastern *etc.*) and covering about 10 km$^2$ near Madygen (Fig. 1), unconformably overlies Carboniferous marine limestones and is transgressively covered by Jurassic continental deposits.

The plants collected by Kochnev (from the eastern area) were dated as Early Triassic (Brick 1936), and some thirty insect specimens found by him were provisionally identified by Andrei V. Martynov, but not treated taxonomically before Martynov's untimely death in 1938. Several hemipteran insects from this collection were described by Elena E. Becker-Migdisova (1953) who dated them as not earlier than Early Triassic.

With the beginning of geological mapping in 1945, further Madygen plants were collected and partly assigned to the Late Permian taxa by Tatiana A. Sixtel (1949, 1962, 1966; cited after Dobruskina 1995). According to her ideas the Madygen Formation contains both Permian and Triassic strata (cropping out in different areas), and the Permian Madygen flora was rich in Mesozoic elements.

This view was disproved by Inna A. Dobruskina who performed large-scale geological mapping of the Madygen Formation in 1967, re-interpreted 'Permian' Madygen plants as Triassic taxa and dated the formation Ladinian–Carnian (Dobruskina 1970, 1995).

Insect collecting from several outcrops of the Madygen Formation was initiated by Sixtel and continued by numerous field parties of the Paleontological Institute, USSR (now Russian) Academy of Sciences, Moscow (headed by Nestor I. Novozhilov, Becker-Migdisova and others) in 1957–1971.

Novojilov (1970: 36) considered the upper part of Madygen Formation and all other localities containing phyllopod crustaceans of the order Kazacharthra to be Early Liassic in age, because one of these localities, Ketmen was then dated Jurassic based on megaflora. Now Ketmen and all other occurrences of Kazacharthra are regarded as Triassic (Dobruskina 1995).

The richest of Madygen outcrops in respect to insects, Dzhailoucho (in the northern outcrop area) was discovered by Sixtel and then successfully exploited by five expeditions headed by Alexander G. Sharov between 1962 and 1967. These five field seasons resulted in ca. 15500 insect specimens (twice more than ca. 7000 specimens collected

Figure 1. View to the village of Madygen and southwestern outcrop area of Madygen Formation from Tokhto-Buz Mountain

from this and other Madygen outcrops by all other field parties).

Alexander G. Sharov (1922–1973) graduated from the Moscow University (Fig. 9) as an entomologist whose advisors were Evgeny S. Smirnov and Alexey A. Zakhvatkin, gained a PhD from the Institute of Animal Morphology, Moscow for his monograph on silverfish ontogeny, and joined the Paleontological Institute in 1955. During his splendid (and unfortunately short) scientific career he studied the evolution of insects, first orthopteroids and later other groups (*e.g.* palaeodictyopteroids) and arthropods in general. Sharov's (1966) monograph on the evolution of Arthropoda and origin of insects was severely criticized by Sidnie Manton. In this book Sharov *inter alia* advocated the crustacean origin of Atelocerata, an idea then unpopular but now confirmed by molecular data. He established two insect orders, Monura and Titanoptera, the latter based primarily on Dzhailoucho material.

An excellent fossil hunter, Sharov collected important materials from several classical Paleozoic and Mesozoic localities. In search of rarely found complete specimens of orthopteroids and other large insects he organized intensive excavations, and pursuing various rarities was lucky enough to discover hairy pterosaurs in the Jurassic of Karatau, Kazakhstan and two very peculiar gliding reptiles at Dzhailoucho. These gliders described by Sharov as *Longisquama* and *Podopteryx* (now *Sharovipteryx*), have made Madygen worldwide known and generated unflagging interest to this Lagerstätte among researchers. Thousands of fossils collected by Sharov's expeditions are still insuperable and form the basis for our studies of the Madygen fauna.

In the 1970s and 1980s not much fossil collecting was done at Madygen, but taxonomic papers on Madygen insects continued to appear. In 1987, a field excursion was organized by Dobruskina and M.G. Minich to coordinate research on the Madygen Formation. It was concluded that the data on all insect groups and vertebrates did not contradict the Ladinian–Carnian age estimate, and that the same insect species occur in the different outcrop areas confirming the beds are more or less synchronous. This and many other results of studies on the Madygen Formation were summarized by Dobruskina (1995).

Research on the ecosystem of Madygen Formation has been resumed by S. Voigt (Freiberg) and colleagues (Voigt *et al.* 2006) and by the author.

## FLORA AND NON-INSECT FAUNA

The Madygen megaflora, reviewed by Dobruskina (1995), is rich in pteridosperms: *Lepidopteris, Pelta-spermun, Scytophyllum, Vittaephyllum, Madygenopteris, Madygenia, Uralophyllum, Edyndella, Glossophyllum* (Fig. 2A)*, Leuthardtia, Ptilozamites, Rhaphidopteris, Ctenopteris*. It also contains conifers (*Podozamites, Cycadocarpidium, Voltzia, Borystenia, Swedenborgia*), ginkgophytes (*Ginkgoites, Baiera, Sphenobaiera*), ferns (*Danaeopsis, Cladophlebis, Chiropteris*), horsetails (*Neocalamites* common at Dzhailoucho – Fig. 2B), lycopsids (*Ferganodendron, Tomiostrobus*), thallophytes (leaflike thalli of *Thallites*), and *Mesenteriophyllum* (*incertae sedis*). A few plants apparently remain undescribed, *e.g.* dichotomous floating hepatics abundant on some bedding planes at Dzhailoucho and resembling modern crystalwort *Riccia fluitans*. Stoneworts (Charales) were reported from the Madygen Formation by Sixtel (1960). Several attempts to extract spores and pollen from the Madygen Formation have been unsuccessful (Voigt *et al.* 2006).

Four genera of freshwater bivalves were mentioned from the Madygen Formation (dated Early Triassic) by Kolesnikov (1980; cited after Dobruskina 1995). Several tiny floating statoblasts of freshwater bryozoans (Plumatellidae, Phylactolaemata) were recently found (pers. obs.); similar flotoblasts described as *Plumatella* spp. occur regularly in Jurassic insect localities (Vinogradov 1985).

The only common aquatic gill-breathing macroarthropods in the Madygen Formation are tadpole shrimps of the extinct order of phyllopod crustaceans, Kazacharthra established by Novojilov (1957). They are only found in several outcrops of the southwestern area (often in abundance) and are assigned to the species *Almatium gusevi* (Chernyshev) (Novojilov 1970: 36) and *Jeanrogerium sornayi* Novojilov (N.I. Novojilov, letter to I.A. Dobruskina of 09.01.1970), both first described from Ketmen Mountains, Kazakhstan. Madygen kazacharthrans presumably lived in shallow ponds on a wet floodplain (Voigt 2007). Other crustacean groups occurring in the Madygen Formation are the Ostracoda (undescribed; see Dobruskina 1995) and Decapoda (undetermined; Voigt *et al.* 2006).

The Conchostraca described from Madygen and dated Norian (or less probably Rhaetian–Early Liasssic) in age by Novojilov & Kapel'ka (1960) were in fact collected from Jurassic beds overlying the Madygen Formation in its eastern area (Dobruskina 1995); these beds also yielded some insects and invertebrate traces (see below).

Fishes of the Madygen Formation have been revieved by Sytchevskaya (1999). They belong to Dipnoi (Asiatoceratodontidae, 1 genus and 1 species described) and Actinopterygii: Evenkiidae (1/1), Palaeoniscidae (2/2; Fig. 3), Perleididae (2/2), and Saurichthyidae (1/1). Among several new finds are elasmobranch egg capsules most likely produced by hybodont sharks (Fischer *et al.* 2007).


Figure 2. Pteridosperm *Glossophyllum ? ereminae* (Sixtel) Dobruskina (A) and horsetail *Neocalamites hoerensis* (Schimper) Halle (B)

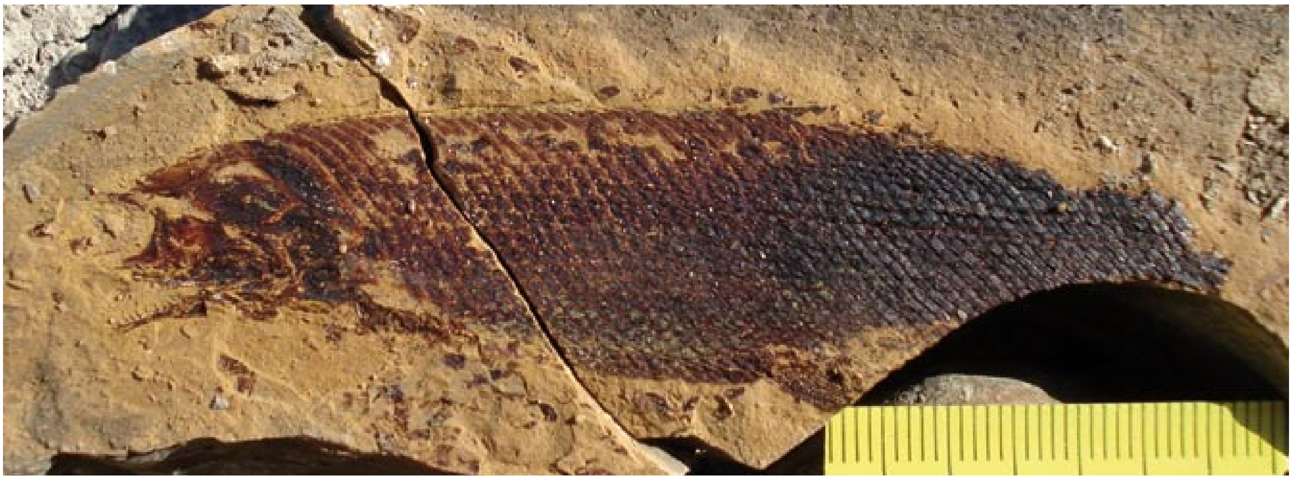

Figure 3. Palaeoniscid *Ferganiscus* Sytchevskaya 1999

Tetrapods of Madygen Formation are represented by: *Triassurus* interpreted as a stem-caudate or temnospondyl larva (Milner 2000), the primitive cynodont *Madysaurus* (Tatarinov 2005), and two gliding reptiles. The prolacertiform *Sharovipteryx* with a flying membrane stretched between its hind legs may be related to pterosaurs, and peculiar construction of this early glider has raised discussion on its aerodynamics (Dyke *et al.* 2006). Variously placed *Longisquama,* with a row of duplicate feathers along its back, was presumably able to parachute, and lies at the heart of debate over dinosaur *versus* archosauromorph origin of birds (Feduccia *et al.* 2005).

## INSECTS

Twenty insect orders (almost all known in the Triassic, except for Thysanoptera and Megaloptera) and nearly one hundred families have been recorded, and more than half thousand species described from the Madygen Formation (Tab. 1). This is by far the richest Triassic insect fauna, the only Permian fauna of similar (but lower) familial diversity being known from the Kungurian of Chekarda in the Urals. Of 106 insect families known to exist in Madygen times, only ten are not yet found from this site (but are recorded in both older and younger faunas; Shcherbakov, 2008).

The insect assemblages found in the different outcrop areas are essentially similar in taxonomic composition, including presence of many shared species. This is in accordance with the opinion that the beds cropping out in different areas are roughly synchronous and not separated by significant time span. The described species known from more than one outcrop area of the Madygen Formation are: *Xamenophlebia ornata* Pritykina 1981, *Thuringoblatta sogdianensis* Vishniakova 1998, *Megakhosarodes paulivenosus* Storozhenko 1993, *Permonka triassica* Rasnitsyn 1977, *Notocupoides triassicus* Ponomarenko 1966, *Prochoristella longa* Novokshonov 1997, *Mesageta rieki* Novokshonov 1997, *Choristopanorpa ridibunda* Novokshonov 2001, *Thaumatomerope sogdiana* Rasnitsyn 1974.

The Madygen Formation was dated as Ladinian–Carnian based on megaflora (Dobruskina 1995), and sometimes as Carnian based on insects (Ponomarenko 2002a). However, several groups (Blattodea, Orthoptera, Homoptera) contain the Madygen taxa more primitive than their relatives from the Carnian of South Africa and Australia. It makes the Ladinian age estimate more probable for Madygen (Shcherbakov 2008).

The Madygen insect assemblage is numerically dominated by insects with sclerotized forewings: Coleoptera, Blattodea, and Homoptera Auchenorrhyncha. In most outcrops, few other insects are present. In Dzhailoucho, subdominants are Mecoptera, Protorthoptera *s.l.*, and Orthoptera, with other common groups including Miomoptera, Phasmatodea and Neuroptera. Nearly all insects are flying adults; immatures are very rare and fragmentarily preserved. Aquatic (more exactly, amphibiotic) insects are less numerous than terrestrial, but exact proportion is difficult to establish, because there are quite common water beetles (abundant Schizophoroidea and rare Triaplidae), and should be some groups of Neuroptera, Mecoptera, Diptera and Protorthoptera with aquatic immatures (like in the extant Sisyridae, Nannochoristidae, Limoniidae, Tanyderidae, and presumably in the Permian Lemmatophoridae – Beckemeyer & Hall 2007). The entirely amphibiotic orders (Ephemeroptera, Odonata, Plecoptera, Trichoptera) are uncommon, and their immatures are exceptionally rare and surely allochthonous. In these latter orders immatures are always hydropneustic, obtaining oxygen from the water using tracheal gills, whereas water beetles and nearly all water bugs are aeropneustic (breathe with atmospheric air), and larvae of aquatic Coleoptera and Diptera use either of the two modes.

Beetles, mostly preserved as isolated elytra, dominate the insect assemblage, constituting one quarter of total insects collected from the Madygen Formation, and certainly more than half of the insects in Dzhailoucho (where only the best beetle specimens were collected). The 11 families and 73 species already described (Ponomarenko 1969, 1977, 2002a) constitutes only a fraction of their real diversity. About 90% of specimens belong to the suborder Archostemata, with five families represented. The oldest extant family of beetles, the xylomycetophagous Cupedidae, is very abundant (20–40% of total beetles) and diverse, with three subfamilies (two of them extant), Triadocupedinae (7 genera/16 species), Ommatinae (4/12), and Cupedinae (1/2), and 30 species described altogether – more species than are now living in the world. This was heyday of cupedids – never again were they so flourishing. Another archostematan family, the Schizophoridae appears to be less diversified (10/17), but as it is not as easily identified by isolated elytra, this family may in fact be even more diverse and abundant than Cupedidae. The Schizophoridae and Catiniidae (4/5) belonging to the Schizophoroidea were mostly detrito- or algophagous; they possess an elytro-thoracic interlocking device ('schiza') and were therefore amphibiotic (but not actively swimming). Some schizophorids were quite large (up to 35 mm) and some others were apparently specialized mollusc-eaters, like certain carabids. Other archostematan groups in the Madygen fauna are the xylophilous Tricoleidae (2/3) and hydrophilid-like Ademosynidae (3/7). The suborder Adephaga is represented by aquatic haliploids, possibly algophagous Triaplidae (1/2), and primitive ground beetles, the predatory Trachypacheidae (1/1). The assemblage contains the tiny rhynchophorous Obrieniidae (3/5), described as the earliest known weevils and presumed to develop in gymnosperm strobiles (Zherikhin & Gratshev 1993), but their assignment to Curculionoidea has been doubted (Kuschel 2003). Other Polyphaga mostly remain undescribed, and include at least algophagous Hydrophilidae, xylodetritophagous Elateridae and presumed Artematopoidea.

Cockroaches are subdominant in the insect assemblage, constituting more than one quarter of specimens collected (at Dzhailoucho only complete and/or well-preserved cockroach specimens were taken). (Paraphyletic Blattodea, Homoptera, Protorthoptera *etc.* are accepted, so far as paraphyletic taxa are no less natural and legitimate than holophyletic: Rasnitsyn 1996.) A short account of the cockroach fauna was given by Vishnyakova (1998) who stated that Madygen cockroaches look more primitive than those of Late Triassic entomofaunas, estimated their diversity as no less than 11 genera with 27 species, and decribed four species of two genera in the Mesoblattinidae. Triassic genera assigned to the latter family are now placed in Phyloblattidae (Fig. 4) and Caloblattinidae (Vršanský *et al.* 2002), two commonest families in the Madygen fauna, that contains also Subioblattidae (1/1; Papier & Nel, 2001), Spiloblattinidae, Poroblattinidae, Blattulidae and possibly Archimylacridae. All these families still retained an external ovipositor.

The Homoptera are third in abundance (one quarter of total insects collected), and with their 17 recorded families the most diverse, but mostly undsecribed yet (Shcherbakov & Popov 2002). The most abundant are various Cicadomorpha with tegminized forewings, especially the medium-sized Dysmorphoptilidae (Permian–Jurassic) and the diverse Mesozoic Hylicellidae, and usually small to minute Chiliocyclidae, Scytinopteroidea (Ipsviciidae, Scytinopteridae, Serpentivenidae, Stenoviciidae, Para-knightiidae), and Coleorrhyncha (Progonocimicidae). Large cicadas (Dunstaniidae, plus Triassic Mesogereonidae and Curvicubitidae) are rarer, while Fulgoroidea (Permo-Triassic Surijokocixiidae) are small and underrepresented in the collections. Rare Sternorrhyncha comprise the Protopsyllidiidae

Figure 4. Cockroach (Phyloblattidae, Blattodea)

(Permian–Cretaceous) which are ancestral to whiteflies and jumping plantlice, the latest Pincombeidae (ancestral to aphids and coccids), and the earliest aphids (Creaphididae) and precoccids (Naibiidae; Shcherbakov 2007; Fig. 5).

The Mecoptera are also quite common (about 1600 specimens) and diverse (43 species described: Novokshonov 1997a–c, 2001). The Permochoristidae (7/17) known from the Permian to Jurassic and the Permo-Triassic Parachoristidae (5/14) dominate; other families recorded are the Triassic Thaumatomeropidae (2/6) plus the Mesozoic Mesopsychidae (1/5) and Pseudopolycentropodidae (1/1). The genus *Panorpaenigma* Novokshonov 2001, tentatively assigned to Parachoristidae, may in fact represent the earliest find of the family Orthophlebiidae (Jurassic–Paleogene).

The Protorthoptera *s.l.* (including Grylloblattodea) are roughly equal in abundance (about 1500 specimens) and diversity (47 species described; Storozhenko 1998) to the scorpionflies. The most diversified are the Blattogryllidae (9/14), a family known from the terminal Permian to Early Cretaceous and considered directly ancestral to the extant wingless Grylloblattidae. The Ideliidae (4/7) and Megakhosaridae (2/3) are Permian relicts; one more Permo-Triassic family is the Tunguskapteridae (1/1). The Gorochoviidae (3/8), Mesorthopteridae (3/7) and Madygenophlebiidae (2/4) are Triassic endemics, while the Geinitziidae (1/3) survived into the Jurassic. Judging by high abundance of several protorthopteran groups (at least in Permian assemblages), their nymphs lived in or near the water.

The fossil assemblage is biased against large insects, but they were preferentially collected. The Orthoptera (about 1400 specimens; Sharov 1968; Gorochov 2005a, b) are unusually diverse (11 families and more than hundred species). Nearly all families belong to Ensifera, and most of them are Triassic endemics: Proparagryllacrididae (4 subfamilies, 10/16), Xenopteridae (3 subfamilies, 11/15), Mesoedischiidae (1/3), Hagloedischiidae (1/1), and Gryll–avidae (3/3). Other ensiferan families are either Permian relicts such as the Permelcanidae (1/2), or survived into the Jurassic such as the Haglidae (4 subfamilies, 35/46), Bintoniellidae (3 subfamilies, 7/10) and Tuphellidae (2/4). Rare Caelifera are represented by two Triassic families: Locustavidae (early members of infraorder Acrididea; 3/9) and Dzhajloutshellidae (earliest find of infraorder Tridactylidea; 3/5).

Figure 5. Forewing of *Coccavus* Shcherbakov 2007 (Naibiidae, Homoptera)

The Titanoptera are known almost exclusively from the Madygen Formation (about 200 specimens, 21 species; Gorochov 2003), with the exception of two species from the Middle Triassic of Australia and a unique Permian find (Gorochov 2007); however, this order also possibly includes the Carboniferous Geraridae and living relict Mantophasmatodea (Gorochov 2004). Three families are recorded from Madygen: Mesotitanidae (3/5), Paratitanidae (2/10), and Gigatitanidae (3/6).

The stick insects known since the Late Permian (Gorochov & Rasnitsyn 2002) are not rare (more than 350 specimens) but less diverse (12 species described; Gorochov 1994) in the assemblage. Two or three families in the Madygen fauna belong to the Phasmatodea, all endemic of the Triassic: Prochresmodidae (2/8), Aeroplanidae (1/2), and possibly also Xiphopteridae (1/2) that alternatively may represent an aberrant orthopteran group.

The Miomoptera are represented only by the family Permosialidae (2/3), recorded from the Permian to Jurassic. Most of about 500 specimens collected belong to the very common, small-sized species *Permonka triassica*, with this genus surviving into the Jurassic (Rasnitsyn 2002b).

The Neuroptera are not abundant (more than 200 specimens) but are diverse (undescribed). The extremely multiveined Osmylopsychopidae are common (Fig. 6), and some fossils possibly belong to the extant families Osmylidae and Polystoechotidae. Triassic neuropterans were nearly as diverse in their wing structure as living ones (except for long-winged forms) (Ponomarenko 2002b).

The Glosselytrodea are rare and should be regarded as Permian relicts at Madygen. They are represented by two families, the Jurinidae and Polycytellidae, both known since the Permian (Rasnitsyn 2002c).

There are some groups known from very rare finds, such as the Dermaptera, represented by the Mesozoic Protodiplateidae (Shcherbakov 2002), and the Psocoptera, belonging to the otherwise Permian family Psocidiidae; Rasnitsyn 2002a).

Among the rarest groups are sawflies and true flies, with almost all finds confined to Dzhailoucho. Sawflies at least were specially looked for and they are often preserved as more or less complete insects. True flies (isolated wings only) seem to be found more regularly, especially tiny midge wings which are easily overlooked. The sawflies found there (about 60 specimens; Rasnitsyn 1969) are the earliest known members of the order Hymenoptera and are represented by only one family, the extant Xyelidae (two subfamilies, 12/25). Modern xyelid larvae develop inside male gymnosperm strobiles or on leaves of trees.

The Madygen Diptera were first discussed by Kovalev (1983) and treated taxonomically by Shcherbakov *et al.* (1995). This is the next earliest of known Triassic dipterofaunas after the Anisian Grès à Voltzia of the Vosges, France. Five families (with 11 species) are described, all in the Nematocera, most of them (sub)endemic to the Triassic except for the extant Limoniidae and Mesozoic Protorhyphidae. Two families belong to the Tipulomorpha *s.l.* – Vladipteridae (2/3) and Limoniidae (2/3) – and two

Figure 6. Forewing of Osmylopsychopidae (Neuroptera)

more to the Psychodomorpha *s.l.* – Nadipteridae (1/1) and Hennigmatidae (2/2); their larvae possibly developed in the water or moist soil. The Protorhyphidae (1/2) belong to Bibionomorpha *s.l.*, and their larvae presumably lived in decaying plant matter. No Culicomorpha are yet known.

True bugs are exceptionally rare. Only three adults are collected, all from the southwestern area (beds with Kazacharthra crustaceans), and belong to an extinct group of primitive Nepomorpha, two of them allied to *Heterochterus* Evans 1971 described from the Late Triassic (Carnian) of Mt. Crosby, Australia. They were presumably shore dwelling or amphibiotic, like their relatives, living Ochteroidea, the most primitive extant nepomorphans, more littoral at the adult stage and more aquatic at nymphal stages. All pre-Rhaetian Heteroptera belong to Nepomorpha, and no land bugs had yet evolved in Madygen times (Shcherbakov & Popov 2002).

Turning to the entirely amphibiotic orders, we find the Odonata the most abundant (about 100 specimens, all adults), and nearly as diverse in Madygen (10 families with 30 species) as in the Jurassic of Karatau or Solnhofen. This rich fauna is dominated by stalk-winged forms analogous to modern damselflies, and appears more archaic than those of Ipswich or Molteno (Pritykina 1981). Most groups are Triassic endemics: Triadophlebiidae (1/3), Paurophlebiidae (5/11), Zygophlebiidae (4/4), Mitophlebiidae (1/1), Xamenophlebiidae (1/1), Batkeniidae (1/1). Other families either are Permian relicts as the Triadotypidae *s.l.* (1/1) and Kennedyidae (1/2), or survived into the Jurassic as the Protomyrmeleontidae (2/4) and Triassolestidae (2/2).

The Trichoptera (some 25 specimens; Sukatsheva 1973) are represented by three families: the Permo-Triassic Cladochoristidae (1/1) of the ancestral suborder Permotrichoptera, plus the Mesozoic Necrotauliidae (1/1) and Triassic Prorhyacophilidae (1/1) (*incertae subordinis*). The find of a fourth family, the extant Philopotamidae (1/1), is now considered doubtful (Ivanov & Sukatsheva 2002).

Adult stoneflies (about 80 specimens) all belong to Perlariopseidae (5/13) and the only known nymphal specimen to the species *Siberioperla ovalis* Sinitshenkova 1987 (Siberioperlidae), also known from the Late Triassic of Kendyrlik, Kazakhstan. These are the earliest finds of these families, which are widespread in the Jurassic (Sinitshenkova 1987).

The only known mayfly nymph fragment resembles the Jurassic genus *Mesobaetis* Brauer, Redtenbacher & Ganglbauer 1889 (Siphlonuridae; Sinitshenkova 2000).

In sandstones of the southwestern outcrop area, interpreted as near-shore lake sediments, thin layers full of similarly oriented, arched subcylindrical structures (ca. 5 x 0.5–1 mm) were found and attributed to endobenthic holometabolan larvae (Trichoptera or Diptera; Voigt *et al.* 2006). In our opinion, a non-insect origin for these traces is more probable.

At Dzhailoucho, traces of arthropod feeding on the fern and gymnosperm leaves are quite common, often represented by sizeable holes (pers. obs.), presumably produced by orthopteroids. A probable mine from Dzhailoucho was mentioned by Zherikhin (2002b: fig.476).

**Insects erroneously listed from the Madygen Formation**

The following four taxa of aquatic insects should be excluded from the Madygen Formation insect list and considered rather Jurassic in age, as they were found in the aforementioned beds with Conchostraca overlying the Madygen Formation in the eastern area (Fig. 7) and dated Norian (or Rhaetian–Early Liassic) by Novojilov & Kapel'ka (1960) and Jurassic by Dobruskina (1995):

• *Mesoleuctra brachypoda* Sinitshenkova 1987 (Mesoleuctridae, Plecoptera; 10 nymphs, 9 of them on single slab), genus widespread in the Jurassic;

• cf. Protereismatidae, Misthodotidae or Litophlebiidae (Ephemeroptera; 1 nymphal fragment; Sinitshenkova 2000);

• Naucoridae (Heteroptera; 1 nymphal and 1 adult abdomen; Zherikhin 2002: fig. 28);

• ?*Shurabella lepyroniopsis* Becker-Migdisova 1949 (Shurabellidae, Corixoidea, Heteroptera; 2 adults, det. Yu.A. Popov), the species very abundant in Sai-Sagul (Shurab III), Sogul Formation, Lower–Middle Jurassic of Kyrgyzstan (Sukacheva & Rasnitsyn 2004).

In the same Jurassic beds N.I. Novojilov (unpublished) discovered the bedding surfaces with abundant invertebrate trackways, some of them left by small freshwater horseshoe crabs and attributable to the ichnogenus *Kouphichnium* Nopcsa 1923. Some of these surfaces bear a fine network of raised lines, maybe traces of silt-dwelling microdrile Oligochaeta or other wormlike creatures (pers. obs.). These beds apparently contain the sub-assemblage of aquatic insects and other invertebrates more diverse than in the Madygen Formation, among others the Mesoleuctridae and Shurabellidae that confirm its Jurassic age.

## PRESERVATION AND PALEOENVIRONMENT

Dzhailoucho is probably the richest fossil insect site in the world in terms of diversity and especially of abundance, and the problem is not to find more insects but rather to choose which finds are worth collecting (so all collections are more or less biased due to selecting better specimens). Isolated elytra and wings are much more numerous than the more or less complete insects. The clayey matrix is poorly lithified and dissolves after heavy rains;

Figure 7. Part of the eastern outcrop area of Madygen Formation and overlying Jurassic deposits

it is impregnated with gypsum. Nevertheless, some layers yield the insect fossils preserved in minute detail, including the wing microsculpture and dark pattern (same is true of the southwestern area). The rock is distorted linearly, so that complete specimens buried with appendages spread often show one forewing much extended lengthwise and another (lying at the right angle to the former) crosswise. Such deformations may be corrected photographically or graphically (Ponomarenko 1969: 5-8).

The composition of insect remains changes from layer to layer. Several bedding planes are literally tiled with tiny, often hard-to-see wings, which were seldom noticed and are much underrepresented in the collections. In some other layers either beetle or cockroach parts are preferentially buried, sorted according to their size and nature and sometimes even aligned in the same direction (Fig. 8), apparently by the action of very slow water currents. Sometimes one can even see several parts of a disarticulated specimen laying one by one in a row. This is in accordance with Sixtel's view that the Dzhailoucho beds were left by a shrinking, mineralized oxbow lake of the Madygen River flowing northwest. She reconstructed the paleoclimate as seasonal and arid, and the landscape as intermontane river valley (Sixtel 1960).

Figure 8. Elytra of schizophorid beetles aligned at burial

The virtual absence of gill-breathing aquatic animals other than Ostracoda and fishes in most outcrops of the Madygen Formation contrasts sharply with the abundance of gill-breathing Kazacharthra phyllopods in several outcrops of the southwestern area (where littoral bugs are also found). Modern relatives of Kazacharthra, tadpole shrimps (Notostraca) live in temporary pools, so siltstones with Kazacharthra were presumably formed in seasonal ponds on a floodplain.

One of the Jurassic–Cretaceous lake types, characterized by extremely numerous water bugs (often Shurabellidae or Corixidae) and few if any immatures of other aquatic insects, is reconstructed as low in dissolved oxygen and sometimes saline (*e.g.* Jurassic Karatau Lake; Sinitshenkova 2002: 399, 414). Jurassic assemblages of this type are attributed either to lacustrine (probably oxbow-lake) lenses within a coal-bearing fluvial sequence (with the impoverishment of water fauna explainable by low dissolved oxygen in warm paleoclimate, *e.g.* localities in Central Asia) or to coastal plain environments (probably sediments of brackish pools and lagoons with high algal production, *e.g.* localities in Transbaikalia and North America). The Dzhailoucho Lake was presumably similar to the above in many respects, but none of truly aquatic bug families had evolved yet in Madygen times. Likewise, the Dzhailoucho Lake pertains to the coal-bearing fluvial sequence, and its water was highly mineralized and low in oxygen (dipnoan fishes were common there). Along the shore tall horsetails grew as helophytes (emergent semi-aquatic plants). Crystalwort-like hepatics formed thick floating mats on or under the water surface, creating a microhabitat that was somewhat richer in oxygen and densely populated by diverse insects and other invertebrates. This habitat was very important in insect evolution, and the origin of adephagan beetles, true flies, and true bugs in the Early Triassic may be associated with their expansion into continental waters (Kalugina 1980; Shcherbakov & Popov 2002), subsequent to the appearance of floating macrophytes (Ponomarenko 1996).

EPHEMEROPTERA
?Siphlonuridae

ODONATA
Triadotypidae
Triadophlebiidae
Paurophlebiidae
Mitophlebiidae
Zygophlebiidae
Xamenophlebiidae
Kennedyidae
Protomyrmeleontidae
Batkeniidae
Triassolestidae

BLATTODEA
Poroblattinidae
Phyloblattidae
Caloblattinidae
Subioblattidae
Spiloblattinidae
Blattulidae
?Archimylacridae

TITANOPTERA
Mesotitanidae
Paratitanidae
Gigatitanidae

ORTHOPTERA
Permelcanidae
Bintoniellidae
Proparagryllacrididae
Mesoedischiidae
Xenopteridae
Hagloedischiidae
Tuphellidae
Haglidae
Gryllavidae
Locustavidae
Dzhajloutshellidae

PHASMATODEA
Xiphopteridae
Prochresmodidae
Aeroplanidae

PROTORTHOPTERA
Ideliidae
Tunguskapteridae
Geinitziidae
Mesorthopteridae
Madygenophlebiidae
Gorochoviidae
Megakhosaridae
Blattogryllidae

MIOMOPTERA
Permosialidae

PLECOPTERA
Perlariopseidae
Siberioperlidae

DERMAPTERA
Protodiplateidae

PSOCOPTERA
Psocidiidae

HOMOPTERA
Pincombeidae

| | | | |
|---|---|---|---|
| Creaphididae | HETEROPTERA | Catiniidae | Pseudopolycentropodidae |
| Naibiidae | ?Ochteroidea | Triaplidae | |
| Protopsyllidiidae | | Trachypacheidae | TRICHOPTERA |
| Surijokocixiidae | NEUROPTERA | Hydrophilidae | Cladochoristidae |
| Dysmorphoptilidae | ?Osmylidae | ?Artematopoidea | Prorhyacophilidae |
| Curvicubitidae | ?Polystoechotidae | Elateridae | Necrotauliidae |
| Dunstaniidae | Osmylopsychopidae | Obrieniidae | ?Philopotamidae |
| Mesogereonidae | | | |
| Hylicellidae | GLOSSELYTRODEA | HYMENOPTERA | DIPTERA |
| Chiliocyclidae | Jurinidae | Xyelidae | Vladipteridae |
| Paraknightiidae | Polycytellidae | | Limoniidae |
| Scytinopteridae | | MECOPTERA | Nadipteridae |
| Stenoviciidae | COLEOPTERA | Permochoristidae | Hennigmatidae |
| Ipsviciidae | Cupedidae | Parachoristidae | Protorhyphidae |
| Serpentivenidae | Ademosynidae | ?Orthophlebiidae | |
| Progonocimicidae | Tricoleidae | Mesopsychidae | |
| | Schizophoridae | Thaumatomeropidae | |

Table 1. Insect families recorded from Madygen Formation

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Figure 9. Alexander G. Sharov

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