Upper Jurassic Lagerstätte Shar Teg, Southwestern Mongolia

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Abstract—One of the most interesting Mesozoic Lagerstätten, Shar Teg in southwestern Mongolia, is reviewed. The geological structure and oryctocoenoses of Shar Teg are described. Shar Teg is one of the most diverse Jurassic Lagerstätten in terms of fossils represented. Fossils from Shar Teg include aquatic and terrestrial plants, mollusks, crustaceans, insects, fishes, amphibians, reptiles, and mammals. Insects are the most diverse group. To date, a total of 297 species of 161 families and 22 orders have been described or recorded in Shar Teg, making it possible to reconstruct comprehensively the Jurassic biota of the locality. The orycto-coenosis composition is peculiar; it includes only six species described from other localities. The orycto-coenosis appears to link the faunas of eastern Asia, Central Asia, and Europe. A total of 31 new species are described.

Keywords: plants, animals, new taxa, oryctocoenosis, Lagerstätte, Upper Jurassic, southwestern Mongolia **DOI:** 10.1134/S0031030114140160

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PREFACE

The evolution of ecosystems, especially continental, remains the least studied and most vague aspect of our notion about historical transformations of the organic world. The greatest obstacle on this way is the fact that organic diversity that has been examined and described is insufficient. In this respect, Lagerstätten occupy a special place among localities of fossil remains. Exceptionally high diversity of fossil plants and animals is found in some of them. Studying these plants and animals, we can produce somewhat more realistic estimations of diversity of early biotas and use such estimations as a basis for hypotheses about trophic and informational organization of ecosystems and association of biota with abiotic components of ecosystems. Such a Lagerstätte is the Jurassic Shar Teg locality in extreme southwestern Mongolia. This locality has yielded one of the most diverse assemblages of fossil remains. To date, a total of 297 species of 161 families and 22 orders have been described or recorded from Shar Teg. These include aquatic and terrestrial plants, mollusks, crustaceans, insects, fishes, amphibians, reptiles, and mammals. The latest finds of the Mongolian-Japanese Expedition have shown that the diversity of the Shar Teg oryctocoenosis is far from exhausted, giving us hope that eventually the biota of that time will be known comprehensively. Unfortunately, Shar Teg has not attracted as much attention as it deserves and remains are insufficiently studied, partly because of the difficulty of accessing this locality. Shar Teg is also interesting as a link in the chain connecting fossil localities of Central Asia, Siberia, and China, provide a better paleobiogeographic picture of these regions, and establish stratigraphic relations of the major fossil localities with greater precision.

The locality is situated in a large fenster near the southeastern extremity of the Aj Bogd Range, southwestern Gobi–Altai Province, Mongolia. The section includes the Shar Teg and Ulan Malgait sequences, separated by caliche (calcareous weathering crust). The lower Shar Teg sequence is formed mostly by gray, green, and yellow sandstone and siltstone. Caliche armors all exposures of the Shar Teg sequence. The Ulan Malgait sequence consists of red and variegated sandstone and siltstone. Thus, the locality is formed by deposits of two lakes that sequentially occupied the same depression; the second of these lakes was much larger, but less deep.

Shar Teg deposits are characterized by abundant fossil remains of plants, ostracodes, "conchostracans," gastropods, bivalves, fishes, turtles, and labyrinthodonts, all represented by a few species. Insects are more diverse, represented by both terrestrial and aquatic forms. Among plants, horsetails are dominant; remains of liverworts, lycopods, ferns, ginkgophytes, and conifers are rare.

As noted above, the Shar Teg oryctocoenosis has been described incompletely and unevenly. Only some taxa, mainly rather scarce, have been thoroughly examined. The oryctocoenosis is briefly described below. Sections written by specialists in particular taxa are provided with titles that contain names of orders; the names of the authors of these sections are indicated in Contents. The limited size of this monograph and the unevenly studied taxa made it impossible to treat all insects at the same level. Only the most general information, selected by the editors who compiled the monograph, is provided for the sake of coherence for taxa that have been comprehensively studied and, on the contrary, taxa that have not been studied. Many taxa are illustrated and some illustrations show interesting material that remains undescribed. The illustrations include photographs, SEM images, and explanatory drawings. The general description section is followed by the systematic section, rather small because of the limited size of this monograph.

MATERIAL AND METHODS

The material available from Shar Teg includes several thousands of fossil specimens collected by the Joint Soviet-Mongolian Paleontological Expedition in 1987 and 1989. The expedition party was headed by Yu.M. Gubin and included specialists in fossil vertebrates and insects of the Paleontological Institute, Academy of Sciences of the Soviet Union (currently Borissiak Paleontological Institute, Russian Academy of Sciences), S.M. Sinitsa of Chita Institute of Natural Resources, Siberian Branch, Academy of Sciences of the Soviet Union (currently Institute of Natural Resources, Ecology and Cryology, Siberian Branch, Russian Academy of Sciences), and the paleobotanist Zh. Sodov of the Institute of Geology, Mongolian Academy of Sciences (currently Institute of Geology and Mineral Resources, Mongolian Academy of Sciences). Most of the material collected is stored in the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia (PIN). The botanical material was stored in the Institute of Geology, Mongolian Academy of Sciences (Ulan Bator, Mongolia) but could not be found after the untimely death of Zh. Sodov. The material of ostracodes and "conchostracans" is stored in the Institute of Natural Resources, Ecology and Cryology, Siberian Branch, Russian Academy of Sciences (Chita, Russia).

The material was examined and photographed using a Leica M165c light stereomicroscope with digital camera and a TESCAH (NESCAN)/Vega XMU scanning electron microscope at PIN.

Scale bars are 1 mm in all Figs., unless stated otherwise.

1. GEOLOGICAL DESCRIPTION OF THE SHAR TEG LOCALITY

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The Shar Teg locality of fossil remains is situated in a large fenster near the southeastern extremity of the Aj Bogd Range, southwestern Gobi–Altai Province, Mongolia (Figs. 1, 2). The Shar Teg and Ulan Malgait sequences, separated by caliche (calcareous weathering crust) are recognized in the section of this locality. The lower Shar Teg sequence is formed mostly by gray, green, and yellow sandstone and siltstone, with marking beds of violet and multicolored siltstone, which form table elevations on the bottom of the fenster. The



Fig. 1. Map of the working area.

deposits form gentle folds with angles up to 20° on wings. South of Mount Ulan Malgait, the Shar Teg sequence overthrusts the Ulan Malgait one. Caliche armors all exposures of the Shar Teg strata, usually lying as an uneven hilly sole on green sandstone or, less often, on purple siltstone. The Ulan Malgait sequence consists of red and multicolored, subhorizontal or inclined at an angle up to $5^{\circ}-7^{\circ}$ sandstone and siltstone and sparse psephites, broken by small cracks with a maximum amplitude of 2-3 m. The deposits of the sequence form rocky ledges around the fenster.

In the descriptions of particular beds provided below, only fossil remains of aquatic organisms are listed in full; terrestrial organisms are mostly identified to larger groups.

Shar Teg Sequence

Exposures of the Shar Teg sequence stretch as an interrupted band almost latitudinally, from the area of Mount Ulan Malgait to Mount Shar Teg, crossed by three broad dry channels or gullies, named here Western, Central, and Eastern, according to their relative positions (Figs. 3, 4). The most complete and well-exposed sections of the sequence have been examined between the Western and Central gullies in the area of Mount Ulan Malgait.

The deposits underlying the Shar Teg sequence and basal horizons of the sequence itself are not exposed anywhere. The earliest part of the visible section of this sequence emerges in the nucleus of the central anticline north of Mount Ulan Malgait (Fig. 5). On the wings of the anticline and along its eastern limit, all beds are clearly traceable, up to caliche at the boundary between this sequence and the overlying Ulan Malgait sequence.

The Shar Teg sequence is cyclic in structure, with sandstone at the base and siltstone or mudstone at the top of cyclites. Some cyclites have clear marking features, such as multicolored or purple coloration of



Fig. 2. Geologicial position of the Shar Teg locality.

rocks, presence of authigenic marcasite, coarse tree remains, and others, making it possible to detect the presence of these cyclites even in isolated outcrops. A total of nine cyclites have been recognized in the visible part of the sequence (Figs. 5, 11). These cyclites are described below sequentially from base to top, beginning from the nucleus of the central anticline.

Cyclite I. A member of alternating sandstone and siltstone (>20 m), forming regularly connected pairs of beds, known as ajaxes (outcrops 423, 441, and 442, Figs. 5-7), lies at the base of the visible part of the cyclite. The sandstone (0.2-1.0 m thick) is brown at the base of beds and yellow-brown at the top, finegrained, quartz, massive or with coarse lenticular lavered structure accentuated by plant detritus; nodules and "block pavement" texture are typically present on the bed surface. Siltstone at the top of ajaxes (1.0-2.5 m)thick) is yellow-brown, sandy, massive, often with signs of pressure. The top of the cyclite in the southern wing of the central anticline (outcrops 423 and 441; 7-8 m thick) is formed by green siltstone, with interbeds of gravish and greenish brown siltstone and mudstone at most 1-2 cm thick. In the northern wing of the anticline (outcrops 442, Bed 1; Fig. 10), the top of the cyclites includes some massive green siltstone with white (1.5 m) carbonate nodules and thin-layer green siltstone (1 m thick) with scattered fossil remains of the conchostracan Pseudestheria sp., ostracodes Darwinula sarytirmensis Sharapova, D. oblonga (Roemer), and *D. nimia* Sinitsa (samples 423/1, 423/2, 441/2, 442/1), caddisfly cases of Terrindusia cf. minuta Vialov et Sukatsheva, Folindusia digna Sukatsheva, and F. adumbrata Sukatsheva, and fish scales. The cyclite is 10–26 m of visible thickness.

Cyclite II. At the base of this cyclite (0.5-2.0 m) thick), there are light yellow and gray fine-grain massive sandstones (outcrops 423, 441, 442, and others, Figs. 6–10); at the top (at most 4–5 m thick), there is siltstone. The southern wing of the central anticline (outcrops 423 and 441; Figs. 6, 7) is formed by gray,



Fig. 3. Geological scheme of the central and northwestern sites of the working area.



Fig. 4. Geological scheme of the east-southeastern and eastern sites of the working area.

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Fig. 5. Geological sections of the Shar Teg and Ulan Malgait sequences of the central part.



Fig. 6. Geological section of outcrop 423.

Cyclite III. The base (2–6 m thick) is formed of yellow–gray and yellow–brown fine-grained, well-sorted, massive sandstone; the top (25 m thick) is formed of multicolored finely horizontally layered silt-

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stone and sandy and marlaceous siltstone and mudstone.

In the southern wing of the central anticline (outcrop 423, Beds 5–6; outcrop 441, Bed 4, Figs. 6, 7), siltstone and mudstone (at most 25 m thick) alternate in the shape of yellow–gray, yellow–green, gray, white, or bluish 1-10-cm-thick layers.

In the northern wing (outcrop 442, Bed 3; Fig. 10), the top of the cyclite decreases in thickness to 10 m and is formed of gray and greenish gray horizontally layered siltstone. Near the eastern limit of the fold, only the top of the cyclite outcrops, very similar in structure.

The following fossils come from the top of the siltstones (samples 423/6, 441/4, 443/1, and 443/3, Figs. 6–10), mostly from marlaceous siltstone: valves



Fig. 7. Geological section of outcrop 441.



Fig. 8. Geological section of outcrops 433 and 425.



Fig. 9. Geological section of outcrops 433 and 443.



Fig. 10. Geological section of outcrops 442, 435, and 434.



Fig. 11. Geological section of outcrop 422.



Fig. 12. Geological section of outcrop 424.

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Fig. 13. Structural details of Bed 4, outcrop 424, and stratigraphic column of outcrop 424.

and shells (often as shell pavements) of the conchostracan Pseudestheria sp.; ostracodes Darwinula sarytirmensis Sharapova, D. nimia Sinitsa, and Lycopterocypris sp.; remains of aquatic insects Leptophlebiidae: Clavineta contabilis Sinitshenkova; Siphlonuridae; Corixidae: Coryphocorixa zhangi Popov; Gyrinidae: Mesogyrus elongates Ponomarenko; Coptoclavidae: Coptoclavella jurassica Ponomarenko and Timarchopsis longus Ponomarenko; Liadytidae: Liadytes aspidytoides Prokin et al.; Memptus sp.; Spercheidae: Prospercheus cristatus Prokin; Helophoridae: Helophorus (Mesosperchus) inceptivus Fikáček et al. and H. (M.) costalis Ponomarenko sp. nov.; propria Hydrophiloidea: Polysitum sharategense Ponomarenko, Hydrobiites mongolicus Ponomarenko, and *H. minor* Ponomarenko; Sialidae: Sharasialis fusiformis Ponomarenko: most Diptera (see Chapter 2.2, Table 1); Protomyrmeleontidae: Protomyrmeleon; Heterophlebiidae; Oreopteridae; Euthemistidae; Siberioperlidae: Sharaperla obliqua Sinitshenkova; Platyperlidae: Platyperla mendosa Sinitshenkova; Perlomorpha inc. sed.: Triangulaperla optanda Sinitshenkova and Bestioperlisca inulta Sinitshenkova; Mesoleuctridae: Mesoleuctroides derelictus Sinitshenkova; Perlariopseidae: Dicronemoura attenuata Sinitshenkova, Karanemoura perpropingua Sinitshenkova, and Mongolonemoura inversa Sinitshenkova; caddisfly cases Ostracindusia callida Sukatsheva, Folindusia digna Sukatsheva, F. adumbrata Sukatsheva, F. pilarius Sukatsheva, F. megasporae Sukatsheva, and Terrindusia minuta Sukatsheva; remains of terrestrial insects; fish scales; liverwort thalli Ricciopsis sp.; megaspores of aquatic lycopod Limnoniobe in caddisfly cases; fern pinnae Sphenopteris sp.; horsetail stems and diaphragms Equisetites sp.; conifer leaves and winged **Cyclite IV.** In the southern wing of the central anticline (outcrop 423, Bed 7; Fig. 6; outcrop 441, Bed 5; Fig. 7), an interbed of brown fine-grained, calcareous, massive sandstone lies at the base of the cyclite (0.2-0.3 m thick), overlain by a member (8-30 m thick) of white or white-yellow to yellow-brown massive, fine-grained to silty sandstone, containing interbeds of yellow siltstone with large horsetail stems. In the northern wing (outcrop 442, Beds 4 and 5; Fig. 10), white sandstone lies directly at the base of the cyclite and contains interbeds of brown fine-grained calcareous sandstone at most 0.2 m thick and sandy siltstone at most 2–4 m thick and lenses of gray and purple siltstones at most 1 m thick.

The top of the cyclite is formed of massive gray sandy siltstone (3 m thick), with interbeds of coalbearing siltstone and powder of carbonized plant detritus and pieces of wood at most 10 cm thick. Fossils recorded in siltstone at the top of the cyclite include accumulations of brown thin-walled bivalve shells (sample 433/2; Fig. 8), "conchostracan" shells of *Palaeolynceus* sp., insect remains, fish scales, horsetail stems of *Neocalamites* ex gr. *pinitoides* (Chachl.) Chachlov, fern pinnae and frond fragments, conifer leaves and winged seeds, and the anemochore *Baisia* ex gr. *hirsuta* Krassil.....

......The cyclite is 12-35 m thick.

Cyclite V. Sandstone at the base of the cyclite (outcrops 423, 441, and 442, Figs. 6, 7, 10) is gray, yellow gray, pale yellow, fine-grained, well-sorted, massive, and in places passing into sandy siltstone (outcrop



Fig. 14. Geological section of outcrops 424-II and 424-III.

423; Fig. 6) with caddisfly cases of F. megasporae Sukatsheva, built of megaspores of the aquatic lycopod *Limnoniobe*. In the southern wing of the central anticline (outcrop 441; Fig. 7), sandstone contains carbonate nodules and marcasite nodules.

The top of the cyclite (2-7 m thick) is formed of gray, purple-brown and purple-gravish brown, cloddy or layered massive siltstone. In the southern wing of the central anticline, it is overlain by greenish yellow siltstone (1-7 m thick) with a fine horizontal layered structure. Fossils recorded in the interbed of brown siltstone (5-6 cm thick) include gastropod shells, the ostracodes Darwinula sarytirmensis Sharapova and D. nimia Sinitsa (samples 423/8 and 433/3), caddisfly cases of *Ostracindusia* sp., fish scales, liverwort thalli of *Rhicciopsis* sp., fern pinnae, and conifer leaves and winged seeds.....

Cyclite VI. Sandstone at the base of the cyclite (outcrop 423, Beds 9 and 10; Fig. 6; outcrop 441, Beds 9 and 10; 7–12 m thick; Fig. 7) is gray, yellowwhite, and white, fine-grained, well-sorted, massive in the northern wing, or with a lenticular, diagonal, horizontal texture in the southern wing, and passing in places into silty sandstone. The layered structure is accentuated by coal-bearing detritus, decreasing in amount from the base to top. In outcrop 423, the base of the sandstone contains an interbed (10 cm thick) of siltstone of complex convolute texture.

The top of the cyclite in the northern wing (outcrop 434, Bed 1; Fig. 10) is represented by brown-grayish brown siltstone (1 m thick), gradually replaced from base to top by layered green siltstone (0.2 m thick). In the southern wing (outcrop 423, Beds 9 and 10; Fig. 6), siltstone is multicolored at the base (7 m thick) and purple at the top (3-6 m thick).

Southwest of Mount Ulan Malgait (outcrops 424 and 426; Figs. 12–14, 16), sandstone at the base of the cyclite (5 m thick) is fine- and coarse-grained and contains a scattered or vaguely lenticular gravel

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admixture; the top of the cyclite is formed by siltstone, multicolored at the base (2.5 m thick) and at the top (3 m thick) and purple in the middle (5 m thick).

East of Mount Ulan Malgait (outcrop 425; Fig. 8), sandstone (8 m thick) is vellow-gravish brown, finegrained, massive; siltstone at the top of the cyclite (6 m thick) is purple with lenticular beds of sandstone (at most 1 m thick), yellow-grayish brown, with grains of various size and coarse material.....The cyclite is 13–20 m thick.

Cyclite VII. In the section of the central anticline, sandstone at the base of the cyclite (outcrop 423, Bed 11; Fig. 6; outcrop 441, Bed 11; 4–7 m thick; Fig. 7) is gray, yellow-grayish brown, fine-grained, well-sorted, massive. The top of the cyclite in the northern wing of the anticline (outcrop 434, Bed 2; Fig. 10) is formed of greenish yellow and pale yellow siltstone (3–4 m thick), massive or horizontally layered, with sporadic "conchostracan" valves and insect remains at the top. In the southern wing (outcrop 423, Bed 11; Fig. 6; outcrop 441, Bed 11; Fig. 7), the top of the cyclite (6.5 m thick) is formed of interbedding green sandy siltstone, pure siltstone, and mudstone. The siltstone has massive or cloddy texture and sparse vertically fossilized stems of large horsetails. The fossils include sporadic "conchostracan" valves, remains of the aquatic insects Corixidae and Coptoclavidae, Tanyderidae ?Nannotanyderus incertus Lukashevich, Protanyderus nebulosus Lukashevich et Krzeminski, Chironomidae Oryctochlus brundini Lukashevich (434/2), caddisfly cases of *Secrindusia expressa* Sukatsheva (423/11) and Conchindusia longaeva Sukatsheva (434/2), fish bones, turtle bones, and, in a small interbed of grayish brown siltstone (5 cm thick), sparse shells of gastropods and the ostracodes Darwinula sarytirmensis Sharapova and D. nimia Sinitsa (sample 423/11).

Southwest of Mount Ulan Malgait (outcrops 424 and 426; Figs. 5, 12-14, 16), sandstone at the base of the cyclite (1.0-1.5 m thick) is whitish yellow, fine-



Fig. 15. Pattern of contact between the Shar Teg and Ulan Malgait sequences, outcrop 437.



Fig. 16. Tectonic contact: overthrust of the Shar Teg sequence on the red beds of the Ulan Malgait sequence.

grained, wedging out in places. The top of the cyclite is represented by the following rocks, from base to top:

(1) greenish gray siltstone	with chaotically depos-
	0.7 m thick;
(2) purple siltstone form interbed.	ning complexly curving

(3) green cloddy siltstone with chaotically deposited horsetail stems and bones of fish, labyrinthodonts, and turtles.....0.7 m thick;

(4) green massive siltstone with chaotically deposited sparse charophyte oogonia and shells of gastropods and ostracodes *Darwinula oblonga* (Roemer) and *D. nimia* Sinitsa...... at most 1 m thick; (5) green massive or vaguely horizontally layered sandy siltstone.....at most 1.5 m thick;

(6) green siltstone with chaotically deposited shells of gastropods and ostracodes *D. nimia* Sinitsa......at most 0.4 m thick:

(7) yellow-green sandy siltstone, with deep narrow cracks filled with bluish mudstone; fossils include sparse insect remains and stems and leaves of slender horsetails *Equisetum* sp. deposited in cracks (sample 424/4; Fig. 13)......at most 5 m thick;

(8) purple siltstone.....at most 4 m thick;

(9) green sandy siltstone.....at most 4 m thick;

East of Mount Ulan Malgait (outcrops 422 and 425; Figs. 8, 11) the following rocks lie at the top of the cyclite:

(1) cloddy greenish gray siltstone with chaotically deposited charophyte oogonia, stems of large horsetails, small gastropods, the ostracodes *Darwinula sarytirmensis* Sharapova and *D. nimia* Sinitsa, caddisfly cases of *Conchindusia longaeva* Sukatsheva, *Folindusia digna* Sukatsheva, and Folindusia megasporae Sukatsheva, fish scales, turtle shell fragments, and megaspores of the aquatic lycopod Limnoniobe in caddisfly cases (sample 422/4).....0.8 m thick;

(2) coal-bearing siltstone with powdered soot material.....0.02 m thick;

(4) brown-gray siltstone with fine horizontal layered texture, containing shell pavements of "conchostracan" valves of *Pseudestheria* sp., the ostracodes *Darwinula sarytirmensis* Sharapova and *D. nimia* Sinitsa, sparse caddisfly cases of *Folindusia adumbrata* Sukatsheva, *F. pilarius* Sukatsheva, and *Terrindusia minuta* Sukatsheva, remains of the insect *Memptus* sp., charophyte oogonia *Jurella abshirica* Kyansep-Romashkina and *J. ovalis* Kyansep-Romashkina, and abundant fish scales (sample 425/4)......0.8 m thick.

In addition to the area of Mount Ulan Malgait. fragmentary exposures of deposits of the top layers of cyclite VII are found along the right bank of the Western gully (outcrop 473; Fig. 4) and at the base of the section of the Shar Teg sequence in the area of Mount Shar Teg (outcrops 428, 452; Figs. 4, 18). They typically contain fossil remains of the thin-stem horsetail Equisetum sp. in cracks in green horizontally layered siltstone filled with blue mudstone. An exposure of yellow and yellow-grayish brown siltstone about 2 m thick is found 100 m southeast of Mount Shar Teg, separated from the main outcrops by a matted area. Fossils recorded here include gastropod shells, the ostracodes Darwinula nimia Sinitsa, D. aff. leguminella (Forbes), and Lycopterocypris sp., scarce remains of aquatic insects, including the Limoniidae Tipunia jorgi Lukashevich, caddisfly cases of Ostracindusia callida Sukatsheva, and fish scales.....

Cyclite VIII. At the base of the section of this cyclite of the central anticline, there is gray or yellow– gray fine-grained sandstone (5–12 m thick), gradually replaced by massive or vaguely layered silty sandstone, with abundant carbonate marcasite nodules in the shape of cakes, tubes, etc. (outcrop 423, Beds 13 and 14; Fig. 6; outcrop 441, Beds 13 and 14; Fig. 7). Siltstone at the top of the cyclite in the southern wing (outcrops 423, 441; 10 m thick) is purple or purple–grayish brown, vaguely layered; in the northern wing (outcrop 434, Bed 3; Fig. 10), it is purple only at the base (2.5 m thick), becoming green upwards (13 m thick), with an interbed of marlaceous siltstone (0.3 m thick) with uneven hilly surfaces.

Southwest of Mount Ulan Malgait (outcrops 424 and 426; Figs. 5, 12, 14, 16), sandstone at the base of cyclite VIII (2.5 m thick) is yellow—white and white. East of Mount Ulan Malgait (outcrops 422 and 425; Figs. 8, 11), sandstone (15 m thick) is gray, fine-grained to silty, massive, medially with an interbed (1 m) of purple siltstone. Siltstone at the top of the cyclite (5 m thick) is gray, with an interbed of marlaceous siltstone. Scattered fossils of horsetails, the con-chostracan Pseudestheria sp., insects, caddisfly cases of *Terrindusia minuta* Sukatsheva, and fish scales (sample 425/7) have been found deposited 3–5 cm from the top.

Gray and yellow-gray beds of cyclite VIII are also exposed west of Mount Ulan Malgait along the right bank of the Western gully, where they are 8 m thick, including 7-m-thick lower sandstone (outcrop 439; Figs. 4, 19). On Mount Shar Teg, they are only 2.5 m thick, including 0.5-m-thick sandstone (outcrop 452; Fig. 4). In a ledge of the right bank of the gully 65 km southeast of Mount Ulan Malgait (outcrop 465; Fig. 18), gray beds are found in the lower part of the cyclite: sandstone (5 m thick) with marcasite nodules and overlying sandy (1 m thick) and marlaceous (0.2 m thick) siltstone. Higher beds are formed by green horizontally layered sandy siltstone (0.7 m thick), containing impressions of horsetail stems, conifer seeds and leaves, and insects. The upper 5 m of this siltstone is multicolored. At the left head of the Central gully (outcrop 445; Fig. 4), there is green horizontally layered siltstone at most 1 m thick, containing scattered "conchostracan" fossils at the top of cyclite VIII......

Southwest of Mount Ulan Malgait (outcrops 424 and 426; Figs. 4, 12, 16), the thickness of sandstone with marcasite nodules at the base of the cyclite decreases to 2.5-3 m; purple and gray siltstone at the top of the cyclite also decreases in thickness to 2.5-3 m. East of Mount Ulan Malgait (outcrops 422 and 425; Figs. 8, 11), sandstone is 13 m thick and contains, in addition to carbonate and marcasite nodules, veins of barite and pale blue celestine at most 5-10 cm thick.



Fig. 17. Geological sections of outcrops 456 and 454.

Siltstone (12 m thick) is purple at the base, multicolored in the middle, and green at the top, with hilly carbonate interbeds and lenses at most 10 cm thick. The deposits of this cyclite retain all their principal features in exposures of the Shar Teg sequence on the right bank of the Western gully (outcrop 473; Fig. 4) and in the left head of the Central gully (outcrop 445; Fig. 4), although here they do not contain carbonate or marcasite nodules.

Cyclite IX. The most complete section of the cyclite has been found in outcrop 423. The multicolored silt-stone of cyclite VIII is overlain by the following rocks (from base to top):

(1) greenish fine- to medium-grained sandstone (1.5 m thick) with hilly strata of white-pink limestone (5-10 cm thick);

(2) calcareous breccia (1 m thick) consisting of white limestone fragments (at most 1 cm thick) in calcareous cement;

(3) white, dense massive limestone (2 m thick), with "con in con" at the base;

(4) white scaly marl (1.5 m thick) with hilly interbeds and lenses of white dense limestone (5-10 cm thick).

The studied deposits of the Shar Teg sequence are at most about 200 m thick in the southern wing of the central anticline. In the northern wing, the thickness of the same layers is over 100 m, decreasing more or less evenly both in sandstone at the base of cyclites and in siltstone at the top. The study of the upper beds of the Shar Teg sequence shows that the thickness of deposits invariably decreases with distance from the southern wing of the central anticline.

The description of the Shar Teg sequence provided here contains data on the position of all points where fossils have been collected, except for two, the precise position of which remains unclear because fossils were collected there in isolated outcrops. One of the two points (outcrop 451; Fig. 4) is situated in the upper part of the Central gully; fossils collected here in yellow and greenish gray siltstone about 4 m thick include the anemochore Baisia ex gr. hirsuta Krassil., "conchostracan" shells, sparse insect remains, including the Limoniidae Architipula krzeminskii Lukashevich, and caddisfly cases of Conchindusia longaeva Sukatsheva at the top (sample 451/3) and fern pinnae, conifer seeds and leaves, and sparse ostracode valves of Darwinula nimia Sinitsa in a coal-bearing siltstone interbed (0.1 m thick) in the middle of the member (sample 451/2). The second point is situated on the left bank of the gully 6.5 km southwest of Mount Ulan Malgait (outcrop 466: Fig. 3): fossils collected here at the boundary between purple and green (at the top) siltstone include the anemochore Baisia ex gr. hirsuta Krassil., conifer leaves, and insect remains (sample 466/1; Fig. 4).

The area of Mount Shar Teg (outcrops 428 and 454; Figs. 4, 17, 18) contains fragmentary sections of the Shar Teg sequence with incomplete cyclites VI–IX. Fossils found in siltstone of cyclite VII include abundant ostracodes *Darwinula nimia* Sinitsa, *D.* aff. *leguminella* (Forbes), and *Lycopterocypris* sp., gastropod shells, and fish scales (sample 454/2). The rocks identified here include marking beds of green siltstone with cracks a few millimeters thick filled with bluish mudstone and horsetail stems (cyclite VII), purple siltstone with lenses of gray carbonate (cyclite VIII), and green



Fig. 18. Geological sections of outcrops 465 and 428.



Fig. 19. Geological sections of outcrops 473, 438, and 439.

sandstone with interbeds and lenses of white nodular carbonate (Bed IX).

A small field of deposits of cyclites VII–IX of the Shar Teg sequence has been found 6.5 km southeast of Mount Ulan Malgait (outcrops 465 and 466; Fig. 3). Fossils recorded in siltstone in outcrops 465 and 466 include insect remains, horsetail stems of *Equisetites* sp., conifer leaves and seeds, fern pinnae. The marking beds consist of purple siltstone (cyclite VIII) and overlying green sandstone with lenses and interbeds of pink–gray limestone (Bed IX). Green limestone of

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Mount Shar Teg and the southern area are overlain by calcareous weathering crust, caliche (Figs. 18, 20).

Sandstone (thin sections 436/5, 423/1, and 428/1) and mudstone (thin section 423/6) of the sequence have been studied microscopically. Sandstone of cyclite I (thin section 423/1) is fine- to mediumgrained, carbonate, consisting of colorless carbonate grains, scarce quartz grains (0.3–0.5 mm thick), and irregularly shaped microcline (0.3–0.5 mm thick). Cement is carbonate, grayish brown. Sandstone of cyclite VIII (thin section 428/1) is fine-grained, silty,



Fig. 20. Sketches of the structure of caliche limestones of the Shar Teg locality.

micaceous, consisting of acute-angled and rounded fragments of minerals and rocks distributed irregularly (0.08-0.3 mm thick). Quartz in the fragments is colorless and cracked. Plagioclase is weakly rounded, tabular with polysynthetic doubles (andesine), usually fresh, less often, strongly saussiritized. Potassium feldspar grains are moderately or weakly rounded, pelitized with microperthites. Biotite is brown-grayish brown sheetlike, substituted by calcite. Rock fragments are effusive andesite, guartz porphyry, siliceous and carbonate rocks. Andesite is moderately rounded, with distinct inclusions of plagioclase; the rock is often impregnated with gravish brown iron oxides. In semirounded fragments of quartz porphyry, inclusions of quartz and plagioclase in cryptopegmatoid enclosing matter are discernible. Moderately rounded fragments of siliceous rocks consist of crypto-grained, weakly polarizing silica. Carbonate fragments are moderately rounded. Cement of sandstone is carbonate, pored, impregnated with iron hydroxides.

Sandstone of cyclite IX (thin section 436/5) is greenish, fine-grained, psammitic, homogeneous in texture, consisting of fragments varying in composition and roundness (0.04-0.2 mm in size). Quartz (10%) is represented by colorless cracked angulate fragments. Plagioclase (20%) is weakly rounded, looking like andesite tablets, which are sericitized, saussuritized, possibly represented by andesite phenocrysts. Potassium feldspar (15%) is in the shape of grayish brown, pelitized, moderately rounded tablets. Biotite (5%) is in the shape of small brown-green, distorted chloritized scales. Andesite (25%) has been found in moderately rounded, strongly modified fragments, with saussiritized inclusions. Dacite (25%) has been found in moderately rounded fragments, with distinct not modified quartz and plagioclase inclusions. Fragments of cryptocrystalline silica are sparse. Cement of sandstone is pored, carbonate.

Mudstone (thin section 423/6) of cyclite III is ferruginate, consisting of mica scales (smaller than 0.01 mm in size) and angulate quartz grains (15%; 0.01–0.05 mm). The mica scales are subparallel, abundantly pigmented with iron hydroxides. Fragments of zircon (0.05 mm) and tourmaline (0.03 mm) are sparse.

The wood of tree stumps has also been studied microscopically (thin sections 442/2, 2a). It is substituted by chalcedonoid quartz of fine-grained or radial texture. In cement, abundant (up to 50%) oval formations are recognized, resembling macrospores in their concentric cellular structure (0.2–1.5 mm). Chalcedony substituting wood matter contains a considerable admixture of hematite.

Facial Associations and Paleoreconstructions

The Shar Teg sequence consists of seven facial associations, which form nine cyclites and the tenth upper sandstone layer, reflecting the deposit accumulation in different zones of the Shar Teg lake and adjacent parts of land (Fig. 21). The Shar Teg lake is characterized by mostly terrigenous sedimentation: carbonates and biogenic formations are extremely rare.

(1) Brown–grayish brown sandstone and yellow– white sandy siltstone (cyclite I; outcrop 441, Beds 1–2; outcrop 442, Beds 1–4; outcrop 443, Bed 2; and others). Sandstone (at most 10 m thick) and siltstone (at most 2 m thick) facies are abundant and constitute the visible base of the sequence, formed by normal



sedimentation processes. Sandstone is fine-grained, calcareous, massive, in places with many intersecting cracks, giving the rock a "block pavement" aspect (outcrop 443), or with eggshell parting (balls are up to 40 cm in diameter; outcrop 442). Sandy siltstone is usually massive, less often, with horizontal or streaked texture, accentuated by plant detritus. Grayish brown, brown, and yellow colors of the rocks are determined by the presence of limonite, common in sedimentation at the latitudes with temperate thermal regimes. The presence of cracks and calcareous cement in sandstone suggest that these facies represent deposits of sand beaches of a large lake or interchannel zones of a delta floodplain, where drying and flooding were frequent and soils were formed (Reading, 1986).

(2) Yellow sandstone (cyclites II-VIII; outcrop 423, Beds 1, 4, 6, 7, 9, 11, and 13; outcrops 426, 439; and others) is fine-grained, well-sorted, massive, or with streaked, lenticular, horizontal, diagonal texture, accentuated by either plant detritus or siltstone strata, which compose the bases of cyclites (0.5-20 m thick)and represent abundant facies of normal sedimentation processes. The texture is sometimes disturbed by landslides or breaks in interbeds (outcrop 423, Bed 1). The presence of diagonal textures is usually considered to be associated with river deltas (cyclite VI, Bed 9; outcrop 423). In sandstone of cyclite VI, outcrops 425 and 424, an admixture of psephitic matter in the form of gravel has been found, also suggesting sporadic inflows of coarse clastic matter. Carbonate or marcasite nodules occur frequently (outcrop 422, Bed 5: outcrop 423, Bed 13; outcrop 424, Bed 4; and others). This facial association is typical sediments of sand shoals of a large lake or a junction area between such a lake and the floodplain of a flatland river with mostly sandy bottom substrate (thick sandstone strata). Sedimentation developed under conditions of a semiarid climate with alternating dry and rainy seasons. This is evidenced by the vellow color of rocks, dynamic textures, carbonate and marcasite nodules, plant detritus, and absence of animal fossils (Twenhofel, 1926; Reineck and Singh, 1980; Reading, 1986; etc.).

(3) Green siltstone (cyclites I–VIII; outcrops 422, 443, 473, and others) is the most widespread facies in the section (abundant facies of normal sedimentation processes); it is characterized by horizontal or, less often, cloddy texture, considerable thickness (at most 25 m), and presence of abundant fossils ("conchostracans," ostracodes, insects, gastropods, fish, and plants). It represents sediments of shore areas of a large lake with a high water level. This situation is characterized by reducing conditions, resulting in the production of iron protoxide, which colors the rock green, as evidenced by the absence of traces of animal activity and cracks.

Green siltstone of cloddy texture is especially noteworthy as a unique facies of single sedimentation events. Fossils associated with this facies include turtles, labyrinthodonts, fishes, small gastropods, and ostracodes as well as scarce horsetails and charophyte oogonia. Cloddy textures are typical of sediments formed in quiet, periodically shallowing and even drying or overgrown water bodies; they are also typical of subsoils.

Other unique facies are composed of pale greenish blue siltstone with deep (at most 10 cm) cracks filled with bluish mudstone and containing stems, tubercles, and roots of horsetails (outcrop 424, Bed 4; outcrop 425, Bed 4). A distinctive feature of this type of deposits is the presence of 1-2-cm-thick red ferruginous crusts. This facies could have been formed on drying silty lake shoals overgrown with horsetails or in a delta floodplain of a flatland river. In the section of Bed 4, outcrop 424, where fossils of labyrinthodonts, turtles, lungfish, dinosaurs, and mammals have been recorded, facies and situations constitute the following sequence: green rocks of horizontal texture, sediments of the nearshore area of Shar Teg Lake; then, green rocks of cloddy texture, sediments of a shallowing lake; and then, green rocks with cracks and ferruginous crusts, sediments of a drying lake with cracked bottom. During rain torrents, the cracks were filled with clavey matter and became overgrown with horsetails, initially spreading their roots through available cracks and then forming horsetail thickets. The emergence of cracks and cloddy textures in siltstone deposits of Shar Teg Lake is a relatively rare phenomenon, present only at one stage of the lake's development (cyclite VII).

(4) Multicolored siltstone (cyclites III, V, VI, VIII, and IX; outcrops 422, 423, 424, 425, 428, 433, 434, 435, and others). Unique facies include purple siltstone (0.50-14 m thick), massive, vaguely layered, usually without fossils, except conifer leaves (outcrop 434, Bed 5), fern pinnae and sporangia, and, less often, gastropods and ostracodes (outcrop 423, Bed 11). Multicolored beds (up to 22 m thick) consisting of alternating green, yellow, grayish brown, and purple interbeds and beds (from a few millimeters to 1 m thick) with fine horizontal layered structure are also unique facies. Along the strike, multicolored beds are replaced by green siltstone containing fossil remains of lake animals. These facies are usually noncarbonate, except purple siltstone of cyclite VIII, in which carbonate nodules and hilly interbeds of whitish limestone have been recorded. The above-listed features characterize deposits of silty shoals of a large lake or its flat shores, common in humid or semihumid zones (Reading, 1986).

(5) Gray beds: gray siltstone (up to 1 m | thick) and coal-bearing siltstone (0.20-0.30 m thick) with thin interbeds of soot coals (0.01-0.02 m thick) (cyclites II, IV, and VII; outcrops 425, 439, 441, 442, and 443) are unique facies characterized by vaguely horizontal, streaked, and lenticular texture, accentuated by coalbearing plant detritus, which includes fossil horsetail stems, conifer and ginkgophyte leaves, fern pinnae, seeds, and coarse tree remains. These rocks were

formed by isolated sedimentation events. In Bed 5 of outcrop 441 and Bed 3 of outcrop 442, large (up to 3 m thick) siliceous tree stumps have been found. Fossils of lake animals represented by thin-wall bivalves, insects, and fishes are sparse. Along the strike, gray beds are replaced by green and purple rocks. These facies could have been formed in floodplains, possibly in the delta, where small lakes or dead channels separated from the river were gradually transformed into swamps and periodically overflowed with clastic and allochthonous plant matter.

(6) Carbonate sediments: marl and marlaceous siltstone (cyclites III and VIII; outcrops 423, 424, 425, 434, and 441) are sparse and thin (0.02–1 m thick) and represent unique facies of the association. They form interbeds within green siltstone and are characterized by massive or vague horizontally layered texture. Fossils found in marlaceous siltstone of Bed 4 of outcrop 441 include "conchostracans," insects, fish, horsetail stems, and seeds, whereas fossils found in marlaceous siltstone of Bed 7 of outcrop 423 include only horsetail stems. The presence of carbonate admixture is usually indicative of changes in clastic matter drift regime and increased evaporation in shallow shore areas of the lake.

(7) Green sandstone (Bed 10; outcrop 422, Bed 5; outcrop 423, Bed 15; outcrop 424, Bed 5; outcrop 425, Bed 9; and others; 0.5–6.0 m thick) completes the section of the Shar Teg sequence, overlying purple silt-stone of cyclite IX and overlain by caliche, carbonate weathering crust. The sandstone represented by well-sorted rocks of polymictic composition with clastic matter rounded to various degrees, carbonate cement, carbonate nodules, or interbeds of white limestone with hilly uneven boundaries (0.01–0.1 m thick), is formed by sediments of a lake that was gradually buried. Psammitic material was probably transported by flatland rivers. The presence of carbonate admixture indicates the start of the formation of caliche.

Cyclites of the Shar Teg sequence reflect both annual and long-term cycles of enlargement and shrinking of Shar Teg Lake, advances of flatland rivers onto the lake and, on the contrary, drying and soil formation on the lake shoals and delta floodplains. Relative symmetry is generally retained within each cyclite, i.e., the amounts of sandy and clayey material are approximately equal, with rare exceptions (cyclites IV and V), and show the dominance of normal sedimentation processes (river and lake regimes). The thickness of sandstone at the base of cyclites indicates the inflow of psammitic material by sandy rivers and formation of wide sandy beaches on the lake shores. Rivers transported plant detritus and huge tree stumps. The shore zones of the lake or oxbows in the lowermost reaches of the delta of the flatland river were partly transformed into swamps. The presence of purple siltstone and cracks gives evidence of drying on gentle shoals and their transformation into silty plains with forming soils. Decreasing sedimentation in Shar Teg Lake can be detected by green sandstone. Great thickness of this sandstone (up to 6 m thick) can only result from sandy flood masses flowing into the river. Subsequent evaporation and additional inflow of capillary carbonate brines created alkaline environment, which facilitated the formation of nodules and carbonate interbeds in the sandstone. Thus, the facial associations of the Shar Teg locality reflect varying levels of water in the lake: from high to low, with alternating stages of shallowing and periodic drying accompanied by the formation of soils in shore areas and then flooding of the newly formed soils and inflow of clastic matter via flatland rivers.

Dating the Shar Teg Sequence

Shar Teg deposits are characterized by abundant fossils, which, however, include relatively few species: plant remains, ostracodes, "conchostracans," gastropods, bivalves, fishes, turtles, and labyrinthodonts. Insects are more diverse, represented by both terrestrial and aquatic forms. The majority of fossil species collected in Shar Teg remain undescribed, making it more difficult to date the deposits.

Among lower plants, only charophytes have been identified to species. Charophyte gyrogonites were assigned by Gereltsetseg (1992) to two species of the genus Jurella, J. abshirica Kyansep-Romashkina, 1974 and J. ovalis Kyansep-Romashkina, 1974 (sample 425/4a), described from Jurassic deposits of the Fergana Depression (Middle Jurassic: Khodzhakelen Formation, Bathonian, and Balabansai Formation, Callovian). Therefore, Gereltsetseg dated the Shar Teg locality as Middle Jurassic, most probably Callovian. She believed that all charophyte fossils she studied from this locality, most of them identified by her to species described from the Balabansai Formation of the Callovian, had been collected in the Shar Teg sequence. However, the majority of the gyrogonites described were actually collected in the overlying Ulan Malgait sequence, separated from the Shar Teg sequence by a considerable gap in the lake deposit formation and distinguished by angle disconformity. A rather thick caliche was formed during this gap, showing that the gap must have been long and the two sequences could markedly differ in age. Gereltsetseg's statement that charophyte species found in the Upper Jurassic of Mongolia are different is most probably unjustified, since the Tormkhon Formation definitely belongs to the upper half of the Lower Cretaceous, rather than the Jurassic, and even if the Ikhes Nuur Formation belongs to the Upper Jurassic, it belongs to the uppermost horizons of this epoch, lying considerably above the deposits of Shar Teg.

Among higher plants, only two have been identified to species: the czekanowskian *Phoenicopsis angustifolia* Heer and the conifer *Pityophyllum nordenskioldii* (Heer) Nath.; both are widespread. The fern *Klukia*, in the opinion of Zh. Sodov, is close to Middle Jurassic forms. The abundance of *Neocalamites* and *Coniopteris* also gives evidence in favor of dating the sequence to the Middle Jurassic, whereas the presence of *Sphenopteris* and *Baisia* suggests a later age: Shar Teg is one of the earliest localities in which *Baisia* has ever been recorded.

"Conchostracans" are abundant and distributed almost over the entire section of the sequence, but represented only by one or two species of *Pseudestheria* (Lioestheriidae) and one species of *Palaeolynceus* (Lynceidae). The former genus is represented by species close to *Pseudestheria heckeri* (Raymond) from the Middle Jurassic Itat Formation of the environs of Krasnoyarsk; the latter is represented by a species close to *Palaeolynceus novojilovi* (Oleynikov) from the Upper Jurassic Unda–Daya Group.

Ostracodes form scattered, nested, and sheeted deposits in green and, less often, brown-grayish brown siltstone. The dominant ostracode species is Darwinula sarytirmensis Sharapova; the subdominants are D. nimia Sinitsa and D. oblonga (Roemer). Lycopterocypris sp., Mantelliana sp., and Darwinula aff. leguminella (Forbes) are rare. D. sarvtirmensis Sharapova has been described from Middle Jurassic deposits of the Karatau Range (Mount Sarytirmen') (Mandelshtam, 1947; Sharapova, 1947); it has also been reported from the Khamar-Khoburin Formation (Lower-Middle Jurassic) of the eastern Gobi (Neustrueva, 1974) and Unda–Dava Group of eastern Transbaikalia, which in my opinion belongs to the Upper Jurassic. D. nimia Sinitsa is known from deposits of the Turga Group of eastern Transbaikalia, the supposed age of which is debatable, varying from the Late Jurassic to Early Cretaceous (Sinitsa, 1993). D. oblonga (Roemer) and D. leguminella (Forbes) co-occur in deposits of the Lower Hauterivian to Lower Barremian of England (Anderson, 1966, Kilenvi and Neale, 1978), the Middle Purbeckian of France (Paris Basin) (Oertli, 1963) and Poland (zones C, D, and overlying) (Bielecka and Sztejn, 1966), Purbeckian-correlated deposits of Africa (Grekoff, 1957), serpulite of Germany (Martin, 1940), Jurassic and Lower Cretaceous of Scandinavia (Christensen, 1963), and Turga Group of eastern Transbaikalia (Sinitsa, 1993). Species of Mantelliana are common in the Purbeckian of Western Europe; they characterize Turga Group deposits in eastern Transbaikalia and Dund-Argalant Group deposits in Mongolia (Sinitsa, 1993). Species of Lycopterocypris have been described from Jurassic and Cretaceous of Europe and Asia (Sinitsa, 1993).

Insects are very diverse, although relative to the number of collected specimens their taxonomic diversity is markedly lower than in localities with maximum levels of diversity. In Mongolia, fossil insect diversity is the highest in Lower Cretaceous localities; in the Jurassic, it is markedly lower.

The dominance pattern of mayflies in Shar Teg is unusual: the dominant species belongs to the family Hexagenitidae (*Siberiogenites mongolicus*). Hexagenitiids prevailed only in Early Cretaceous oryctocoenoses, where they form single-species communities. Thus, mayfly fossils suggest that Shar Teg should be dated Late Jurassic or Early Cretaceous, although Late Jurassic appears more likely.

It is usually very productive to use homopterans for stratigraphic purposes, but the Homoptera of Shar Teg have not been studied at all.

Coleopterans, in turn, have been studied quite insufficiently, but make it possible to draw some stratigraphic conclusions. The greater abundance of cupedids compared to schizophoroids found in Shar Teg is typical of the Upper Jurassic, beginning from the very end of the Middle Jurassic. Cupedid fossils are absent in Lower and early Middle Jurassic localities of Mongolia. Fossils recorded in Shar Teg include elytra that belong to two cupedid species, Notocupes brachycephalus Ponomarenko, 1994 and N. exiguous Ponomarenko, 1994, described from the Bakhar locality, which can be dated as the late Middle Jurassic or early Late Jurassic. The genus *Anaglyphites* is only known from the Late Jurassic and Early Cretaceous. The latest known representative of the family Asiocoleidae has been recorded in the Daohugou locality; an isolated elytron collected in Shar Teg has been described as a new species of the same genus, Loculitricoleus. A rather high abundance of Coptoclavidae is typical of the Late Jurassic, but the genus Coptoclavella was previously known only from the Early Cretaceous. High abundance of Mesocinetidae is typical of deposits close to the boundary between the Jurassic and Cretaceous, and high abundance of Lasiosynidae is typical of the second half of Jurassic. It appears strange that buprestids are totally absent and elaterids and weevils are very scarce in Shar Teg. Summarizing all these relative indicators of the possible age of Shar Teg based on the recorded beetles, it appears that the most likely age of this locality is the second half of Late Jurassic, i.e., approximately the same as the age of Karatau. The difference in fossil faunas is probably explained by differences in the zonal and landscape position of these localities.

The most interesting data on the stratigraphic position of Shar Teg are probably those that refer to dipterans. They are expounded in a special section of this monograph authored by E.D. Lukashevich; hence, it is reasonable to provide only the conclusions here. "The dipterans of Shar Teg are especially similar to dipterans described from Karatau and Daohugou, localities that are probably close to Shar Teg in age (late Middle Jurassic or early Late Jurassic). This similarity can hardly be explained only by the quantitative and qualitative richness of dipterans in Karatau and Daohugou, two well-known Jurassic Lagerstätten, in which nearly everything is likely to be found eventually, although this factor should not be discarded. The faunal similarity of these localities probably reflects, above all, their similarity in age. To date, four dipteran species shared by Shar Teg and Karatau have been recorded (Praemacrochile ansorgei, Archirhyphus asiat*icus; Procramptonomyia kovalevi*, and *Archizelmira kazachstanica*). At the same time, it should not be forgotten that three of these four species are known in Karatau based on many complete insects, often of both sexes, whereas in Shar Teg, they are represented by single isolated wings, making the comparison less reliable."

Among other insects, seven genera are also known only from Karatau, and eight other taxa are considered especially similar to insects known from Karatau. Links with earlier Jurassic insects are fewer, but one of insect taxa, Plecoptera, is linked almost exclusively with Early and Middle Jurassic forms. Five insect genera recorded in Shar Teg have previously been recorded only in the Lower Jurassic; crickets of the family Baissogryllidae, represented in Shar Teg by locality-specific genera, belong to a family previously known only from the Lower Cretaceous. Cockroaches are more advanced than in any other Jurassic fauna; the advanced Mesoblattulidae and Blattulidae, along with the presence of mantids, are typical rather of the Lower Cretaceous, but Paleozoic relicts are also present. The oryctocoenosis includes simultaneously *Blattula*, typical of the Jurassic, and *Elisama*, which replaces it in the Early Cretaceous. Thus, the composition of cockroaches has a mixed Late Jurassic-Early Cretaceous aspect. Considering all above-said, it can be stated that insect in general suggest that the Shar Teg sequence should be dated Late Jurassic, probably the first half.

Fish fossils are mostly represented by scales and rarely by bones and other skeletal parts. Only large dental plates of lungfishes have been described (Krupina, 1994), belonging to four species, three of which were described as new from Shar Teg: *Ceratodus sharategensis*, *C. temporatus*, and *C. porrectus*; these three species are similar to Late Jurassic and Early Cretaceous forms known from China and North America.

The labyrinthodont *Gobiops* Shishkin (Shishkin, 1991) is especially similar to the Middle Jurassic *Sinobrachiops* Dong from China. Labyrinthodont fossils from the Balabansai Formation of Fergana (Nessov, 1990), from which charophytes recorded in Shar Teg were described, belong to quite different forms.

Caliche, the Calcareous Weathering Crust

In all known sections of the Shar Teg locality, caliche limestone is found between the Shar Teg and Ulan Malgait sequences. This limestone is a product of carbonate weathering crusts, which are usually formed in soils under semiarid climatic conditions with alternating dry and rainy seasons (Pettijohn, 1975; Reading, 1986; etc.; Figs. 17–20).

Two types of caliche sections have been described in the locality. The first type is most widespread, recorded in northern areas, where the top of the Shar Teg sequence section consists of green sandstone with interbeds of hilly limestone (outcrops 423, 425, 426, 434, 473, and others; Fig. 20). The following beds overlie the uneven surface of green limestone of the Shar Teg sequence, from base to top:

(1) White porous, sometimes brecciated limestone. Acute-angled limestone fragments (up to 1 cm thick) are cemented with porous calcareous matter.....0.5-1 m thick:

(2) White massive, dense limestone with sparse nodules of black silica and with "con in con" structures.....2 m thick;

(3) White massive or scaly limestone, often oolitic, with many nodules or rather extensive lenses of black silica......1.5–2 m thick.

The caliche of the first type is about 5 m thick.

The second type of caliche was studied in three sections, in which it overlies purple siltstone (outcrops 424, 456, and 465; Fig. 20) or, less often, green sandstone (outcrop 454). The following beds compose this type of caliche, from base to bottom (outcrop 424):

(1) White porous limestone with brecciated texture at the base and nodules of black silica at the top of the bed......2 m thick;

(2) Red–grayish brown sandy siltstone. 1 m thick;

(3) White dense limestone.....0.7 m thick.

A similar section of caliche has been studied in outcrops 456 and 454 (from base to top):

(1) White nodular limestone.....1 m thick;

(2) Grayish brown layered siltstone......1 m thick;

(3) White finely nodular limestone.....0.2 m thick.

The caliche section of outcrop 456 (Fig. 17) is somewhat different and includes the following beds, from base to top:

(1) Dense or porous limestone, sometimes brecciated at the base and with black silica nodules at the top of the bed.....1 m thick;

(2) Dark massive siltstone with uneven boundaries of the bed.....1 m thick;

(3) Partly alternating brecciated limestone (0.2 m thick), white and friable black limestone (0.05–0.4 m thick) and nodular excretions of black silica (up to 0.1 m thick).....up to 0.8 m thick;

In sum, the caliche is up to 3.8 m thick.

The presence of siltstone interbeds within the caliche is indicative of erosion of the crust, redeposition of erosion products, and subsequent reestablishment of caliche formation. Diagenesis of caliche in Shar Teg is rather strong, as evidenced by the dense, massive limestone broken with cracks containing nodules of silica. The caliche is invariably overlain by red beds of the Ulan Malgait sequence.

A microscopic study of the caliche (thin sections 432/16, 16a, 422/6, 434/7, and 436/6) has shown that it has oolitic structure. The oolites (0.03-1.5 mm in size; 70-90%) are situated in cryptomerous calcite (grain size is 0.001-0.004 mm), pigmented with yellow-grayish brown admixtures, possibly humic. At the periphery, the oolites are filled with granular calcite and



Fig. 22. Geological sections of outcrops 453 and 470.

include rhomboid dolomite crystals (0.008–0.02 mm in size). The central parts of oolites are formed by radial chalcedony with low refraction parameters. The oolites sometimes have radial structure; less often, they have concentric structure and consist of chalcedonic quartz. Radial aggregates of zeolites are sometimes found in central parts of such siliceous oolites. In section 422/6, small cracks are filled with rhomboid crystals of colorless dolomite.

As noted above, caliche (calcrete) is formed in soils under semiarid climatic conditions, with alternating dry and rainy seasons. Carbonates of underlying deposits are dissolved by groundwater and brought onto the surface, where in the course of drying, they form a calcareous cover on all exposures of the Shar Teg sequence. The layered structure of limestone and abundant nodules of silica are evidence of mature caliche and the presence of brecciated textures indicates repeated drying and breaking of calcareous crusts followed by secondary deposition (Wilson, 1975). Oolitic structure of limestone is typical of freshwater (vadose) pisolites (Wilson, 1975), formed in semiarid climates with seasonal rains during soil formation. The soil formation is accompanied by coagulation of colloids and formation of silica nodules.

The great thickness of the caliche shows that the period of the gap in lake sedimentation and weathering was rather long.

Ulan Malgait Sequence

Deposits of the Ulan Malgait sequence are much more widespread than deposits of the Shar Teg sequence. They lie with a slight disconformity on the caliche, or, less often, on deposits of the upper part of the Shar Teg sequence. The base of the sequence cyclically alternating sandstone and siltstone—has been studied in more detail, because it contains fossils of mollusks, ostracodes, fishes, turtles, crocodiles, dinosaurs, and plants. The upper part of the sequence consists of three subdivisions, with siltstone at the top and at the base and psephite in the middle. The sequence is overlain by weakly cemented boulder conglomerates, which could be Late Cretaceous or Cenozoic.

The most complete section of the Ulan Malgait sequence is situated north of Mount Ulan Malgait between the Western and Central gullies (Figs. 5, 22). In this area (outcrops 434 and 453), the hilly surface of the caliche limestone is overlain by a member (30 m thick) of red-gravish brown siltstone, shaly with sparse white carbonate lime nodules. At the base, this siltstone has spotted purple-grav coloration. It is overlain by 11 sandstone-siltstone cyclites, usually 3-10 m thick, at most 30 m thick. The sandstone beds at the bases of these cyclites are 0.1-0.3 m thick, rarely thicker, at most 1 m thick. Sandstone is usually redgrayish brown, massive, fine-grained, and poorly sorted, with a coarse sand-gravel, less often, rubble admixture. At the base and at the top of the cyclic member, there is coarse-grained gravel sandstone, sometimes layered in the same direction at an angle of 25° to the bed plain. Cracks up to 10 cm deep have been found at the base of sandstone beds in some of the cyclites; the base is sometimes uneven, hilly. The siltstone of the upper part of the cyclites is mostly redgravish brown, layered; sometimes, the cyclites are massive, with carbonate lime nodules.

The lower part of the sequence is 150 m thick; the cyclic part is 120 m thick.

The upper part of the Ulan Malgait sequence on the left bank of the Western gully (outcrop 470; Figs. 5, 22) has the following section:

(2) Interbedding red-grayish brown chlidolite (at most 1-2 m thick), gravelitic sandstone (at most 1 m thick), pebbly conglomerates (up to 1 m thick) and siltstone with carbonate lime nodules (up to 10 m thick). Chlidolite contains gravel and small detritus of effusive rocks (at most 30%) in the basically siltstone mass. Pebbles (at most 2 cm thick) in the conglomerates have the same composition and are well rounded. The cement is sandy siltstone......100 m thick;

(3) Crimson and red siltstone with white and pinkish carbonate lime nodules......130 m thick.

The upper part is up to 430 m thick.

The Ulan Malgait sequence in this area is up to 600 m thick.

The Ulan Malgait sequence has a cyclic structure. Cyclites usually consist of two subdivisions, sandstone and siltstone; less often, they consist of three subdivisions: conglomerate, sandstone, and siltstone. The cyclites are typically strongly asymmetrical: the basal part, which consists of sandstone or conglomerates, is usually rather thin (at most 3 m thick), while the upper part, which consists of red or multicolored siltstone, is at most 30 m thick. The cyclites are from 0.5 to 31 m thick.

Fossils recorded in the Ulan Malgait sequence include mollusks, ostracodes, fish, turtles, tritylodontids, dinosaurs, and crocodiles; charophyte oogonia also occur, but less often.

Ostracodes form scattered deposits; they have been identified as *Darwinula* sp., *Cypridea* sp., *Lycoptero-cypris* sp., *Mantelliana* sp., *Timiriasevia* aff. *cristiformis* Mandelstam, and *Timiriasevia* sp. Such combinations of ostracode genera are common in Turga or Dund–Argalant associations, the age of which is debatable: terminal Jurassic, terminal Jurassic to the beginning of the Cretaceous, or the beginning of the Cretaceous alone (Sinitsa, 1993).

The charophyte gyrogonites have been identified by Gereltsetseg (1992) as *Jurella abshirica* Kyansep-Romashkina, *J. ovalis* Kyansep-Romashkina, *J. ferganensis* Kyansep-Romashkina, and *J. karierika* Kyansep-Romashkina. A similar assemblage of species was recorded by Kyansep-Romashkina in Khodzhakelen and Balabansai Formations of southeastern Fergana. These formations are dated as the Middle Jurassic: the former as Bathonian and the latter as Callovian. The last two of the above-listed species have only been recorded in Balabansai deposits. Therefore, Gereltsetseg believes that the age of the Ulan Malgait sequence is also Middle Jurassic, most probably Callovian. However, the majority of these charophyte species have been recorded in both the Shar Teg and Ulan Malgait sequences, which are separated by a considerable time gap, during which the caliche was formed. Consequently, the stratigraphic range of these species cannot be narrow, and they cannot be used for precise correlation of these deposits with deposits of the Fergana Depression.

2. GENERAL DESCRIPTION OF THE BIOTA OF SHAR TEG

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2.1. Plants

Records of terrestrial plants in deposits of the Shar Teg sequence are extremely rare. According to the identifications of M.P. Doludenko, E.L. Lebedev, and Zh. Sodov, these plants belong to ferns, proangiosperms, ginkgophytes, czekanowskians, conifers, and horsetails, which are dominants and often represented by complete small plants with preserved root systems. These horsetails probably grew in shallow areas, beyond which they were washed out by waves. Abundant plant remains have only been recorded in the Elstiyn-Am area, where, in addition to the abovelisted plants, Bennettitales have been recorded. Aquatic plants are represented by Xanthophyta (coenobia of Bothriococcus) and charophytes, the liverworts *Riccites* (rosettes and very thin isolated thalli), and lycopods of the Limnoniobe type. The above-listed plants could compose floating aggregates. Charophyte gyrogonites were attributed by Gereltsetseg (1992) to two species described by Kyansep-Romashkina from Bathonian deposits of the Fergana Depression. Conclusions about the age of the Shar Teg sequence based on plants are ambiguous: some plants are close to Middle Jurassic taxa, while others are close to Late Jurassic and Early Cretaceous forms.

In one of the samples studied with SEM, fossil plants have been found that may represent a destroyed plant aggregate that sank onto the bottom (Fig. 23).

¹ This section was compiled by A.G. Ponomarenko, unless indicated otherwise.



Fig. 23. Fossil plant: (1) ?lycopod of the *Limnoniobe* type: (a) stipe (under a beetle), (b) leaves; (2) ?liverworts *Ricciopsis*; (3) ? coenobium *Bothryococcus* (Xanthophyta); specimen PIN, no. 2470/1535.

They include a stipe and leaves of a lycopod of the *Limnoniobe* type, very narrow thalli of the liverwort *Ricciopsis* sp., and coenobia of *Bothryococcus* (Chloro-coccalis).

2.2. Arthropods

Chelicerates

Chelicerates are represented by a rather small horseshoe crab, a very strange find for continental water bodies, and by spiders.

Crustaceans

Crustaceans are represented by "conchostracans" and ostracodes. "Conchostracans" belong to the most abundant components of the oryctocoenosis; "conchostracan" remains, especially those of the lioestheriid *Pseudestheria*, occur over the entire section of the Shar Teg sequence; *Palaeolynceus* is considerably rarer. *Pseudestheria* is more typical of the Middle Jurassic, whereas *Palaeolynceus* is more typical of the Upper Jurassic and beginning of the Early Cretaceous. Abundant and widespread ostracodes are the Jurassic *Darwinula sarytirmensis* Sharapova, *D. oblonga* (Roemer), and *D. nimia* Sinitsa; mostly Cretaceous *Lycopterocypris* and *Mantelliana* are much rarer, especially in the Shar Teg sequence.

Insects

Insects are the most diverse component of the oryctocoenosis in the Shar Teg locality. They are represented by at least 22 orders, 110 families, 131 genera, and more than 140 species. The true number of genera and species is certainly much higher, many hundreds, although relative to the number of collected fossils, the insect diversity of this locality is not very high. It is higher than in Early to Middle Jurassic faunas, but markedly lower than in most Late Jurassic and Early Cretaceous faunas. Insects are represented by almost all orders known from Mesozoic oryctocoenoses, including such rare orders as Lepidoptera, Megaloptera, Miomoptera, and Lophioneurida. Insect fossils have only been found in deposits of the Shar Teg sequence; they have not been preserved in deposits of the Ulan Malgait sequence because of the coarse nature of sediments and acidophilic conditions of sedimentation. However, caddisfly cases had to be preserved even under such conditions; their absence is evidence of some distinguishing features of the Ulan Malgait water body compared to the Shar Teg water body.

Order Ephemeroptera

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Mayfly fossils do not form rich burials in Shar Teg. A total of 92 specimens have been collected, almost all of them are nymphs: 30 nymphs and one adult in section 434/2 (cyclite VII) and 60 nymphs and one adult in section 443/1 (cyclite III). Some specimens have not been identified to species; 32 remained unidentified, because they are fragmentary or poorly preserved. Since species described based on nymphs are represented by several specimens, they are most probably autochthonous and developed in the same lake in which insect-bearing deposits accumulated. The beds containing mayflies correspond to the maximum transgression of Shar Teg Lake.

The mayflies belong to six species of five genera and four families. All species and the genus *Sharephemera* Sinitshenkova, 2002 are endemic to Shar Teg. The other genera are widespread in the Jurassic of Asia, but their combination is unique to this locality. Shar Teg is comparable in species diversity of mayflies to Chernovskie Kopi (75 specimens; seven species of six genera and three families) and Khutel-Khara (73 specimens; five species of five genera and five families).

Family Mesonetidae Tshernova, 1969

This family is represented in Shar Teg by three species of two genera, *Clavineta* Sinitshenkova, 1991 and *Furvoneta* Sinitshenkova, 1990. *C. cantabilis* Sinitshenkova, 1991 was described based on four nymphs. A characteristic feature of the genus *Clavineta* is the presence of a dense fringe of long setae on the internal



Fig. 24. Mayflies of Shar Teg: (1) Furvoneta lucida Sinitshenkova, 2002, holotype PIN, no. 4270/322, nymph; (2) Epeoromimus umbratus Sinitshenkova, 2002, specimen PIN, no. 4270/259, nymph. Scale bar, 2 mm.

surface of the profemora and protibiae remarkably close to the head. This leg structure is evidence of filtering feeding type. To date, members of this genus have been recorded in Chernovskie Kopi, in the Jiulongshan Formation (Zhouyingzi locality, Hebei Province) (Zhang, 2006c), and in the Yixian Formation, northern China (Huang et al., 2011).

The genus *Furvoneta* is represented by two species, F. lucida Sinitshenkova, 2002 and F. sobria Sinitshenkova, 2002. F. lucida (Fig. 24.1) was described based on 14 specimens and F. sobria, from three. The genus is known from the Glushkovo and Ukurei formations (Upper Jurassic to Lower Cretaceous) of Transbaikalia and from the Ulugei Formation (Upper Jurassic to Lower Cretaceous) of Mongolia (Mandal-Obo) (Sinitshenkova, 1990a). F. relicta Zhang, 2006, which is close to F. lucida, has been recorded in the Haifanggou Formation (Middle to Upper Jurassic; Yushudonggou locality, Liaoning Province) (Zhang, 2006c). Another species, especially close to F. domefacta from Mongolia (Mandal-Obo), has recently been found in the Jiulongshan Formation (Middle-Upper Jurassic) of northeastern China (Daohugou) (Zhang, 2006c).

Family Epeoromimidae Tshernova, 1969

One species of this family, *Epeoromimus umbratus* Sinitshenkova, 2002, was described based on 14 nymphs. It is similar in the shape of the large rounded gills to

E. cretaceus Sinitshenkova, 1976 from the Balei and Glushkovo formations of Transbaikalia (Sinitshenkova, 1990) and to *E. infractus* Sinitshenkova, 1989 from the Tsagan-Tsab Formation (Lower Cretaceous) of Mongolia (Khutel-Khara) (Sinitshenkova, 1989) and sharply differs from E. kazlauskasi Tshernova, 1969 from the Abashevo Formation of Siberia. Because of the unsatisfactory preservation of specimens, the strong median rib on the gills was neither mentioned in the original description of *E. umbratus* nor shown in the figure of the holotype (Sinitshenkova, 2002, p. 46, text-fig. 1e). In a recently prepared specimens (PIN, nos. 4270/259), the gill shape is clearly visible (Fig. 24.2). The median rib on the gills probably strengthened the gill plate, helping the nymph to remain afloat in the water column, and could help it swim by moving the gills.

Family Hexagenitidae Lameere, 1917

The species *Siberiogenites mongolicus* Sinitshenkova, 2002 is dominant in Shar Teg; it was described based on 22 nymphal specimens. Species of the genus *Siberiogenites* are known from the Ichetui Formation (Lower–Middle Jurassic) of Transbaikalia (Novospasskoe), Zhargalant Formation of western Mongolia (Oshin-Boro-Udzyur-Ula), Chernovskie Kopi sequence of eastern Transbaikalia (Chernovskie Kopi), and Tsagan-Tsab Formation (Lower Cretaceous) of Mongolia (Khutel-Khara). In addition, a new species, *Siberiogenites branchicillus* Huang et al., 2011, was recently found in Yixian. Species of the genus *Siberiogenites* are dominant in none of the above-listed localities.

Family Sharephemeridae Sinitshenkova, 2002

The species *Sharephemera cubitalis* Sinitshenkova, 2002 was described based on a single forewing fragment. Other representatives of the family were recently described from the Middle Triassic of Germany (*Hammephemera* Sinitshenkova, 2011) (Bashkuev et al., 2012) and from Permian–Triassic intertrappean deposits of the Tunguska Basin, Siberia (*Tunephemera* Sinitshenkova, 2013).

The mayfly assemblage of Shar Teg has an unusual pattern of dominance: the dominant species (S. mongolicus) belongs to the family Hexagenitidae, and the subdominant species belong to the families Mesonetidae (F. lucida) and Epeoromimidae (E. umbratus). Hexagenitids are dominant only in Early Cretaceous oryctocoenoses and form singlespecies mayfly communities in lakes of Siberia and Mongolia (Ephemeropsis Eichwald, 1864) and in western Mongolia (Mongologenites Sinitshenkova, 1986; Sinitshenkova, 1986). Ephemeropsis and Mongologenites are more advanced in gill shape than Siberiogenites. Advanced hexagenitids were recently found in China, in the Lower Cretaceous Yixian Formation (Epicharmeropsis Huang et al., 2007: Huang et al., 2007a); this formation also contains nymphs of Siberiogenites and Clavineta. Another surprising feature of the Shar Teg mayfly assemblage is complete absence of the family Siphlonuridae, which is widespread in Jurassic and Cretaceous deposits. Adult and nymphal siphlonurids are also present in the Jiulongshan Formation (Zhang, 2006a; Huang, 2008) and Yixian Formation of China (Huang et al., 2007b).

Thus, mayfly fossils suggest the Late Jurassic to Early Cretaceous age of Shar Teg, with the Late Jurassic appearing more likely. A peculiar feature of the oryctocoenosis of this locality is the absence of Siphlonuridae. Mayfly fossils are found in the most finegrained and thin-layered sediments of the profundal zone of the Shar Teg Lake (according to A.G. Ponomarenko's opinion), sediments that were not bioturbated. Therefore, it is unlikely that these fossils are benthic forms. It is also unlikely that they represent dead bodies transferred by currents. The small thickness of the sediments excludes the existence of bottom currents, and the strictly limited area of deposition excludes transportation by surface currents. The mayflies of this assemblage were probably components of the biome of floating islets. Mayfly nymphs found in Shar Teg include small-detritus collectors and filterfeeders. Based on the combination of genera, the insect-bearing beds were dated Upper Jurassic (Sinit-shenkova, 2002).

Order Odonata

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The odonate fossils of the Shar-Tag locality are rather scarce: only 24 specimens have been collected, most of them are fragmentary. The fragments are wellpreserved: their margins are cut as if with scissors. Odonate larvae have not been found. The taxonomic position of 12 specimens can be summarized as follows: they include representatives of four of five odonate suborders that existed in the Mesozoic; two specimens are described as new species; and a total of six species of six families are recorded. The odonate fauna of Shar Teg is especially similar in composition to that of the Upper Jurassic Karatau locality and includes two genera in common, one of them is endemic to these two localities. The odonates of Shar Teg are described in more detail in the Section Systematic Paleontology.

Order Hemiptera

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True bugs and their allies (Hemiptera) are represented in Shar Teg by almost all main groups: Auchenorrhyncha, Psylloidea, Aleyrodoidea, Aphidoidea, Coleorrhyncha, and aquatic and terrestrial Heteroptera. The most widespread family of Auchenorrhyncha is Procercopidae: several species of the genus Sinocercopis are represented in almost all points of the locality in which any insect fossils have been found. The second most widespread family is Archijassidae, represented mostly by the Jurassic subfamily Karajassinae and by the earliest record of the Cretaceous subfamily Dellasharinae (Dellashara). The rarest families are Palaeontinidae, Tettigarctidae, and Hylicellidae. Psylloidea are represented by the families Liadopsyllidae and Protopsyllidiidae (Subaphidilum, Cicadopsyllidium, and Aphidulum). All these genera are Jurassic, except Cicadopsylidium, which includes a species from Bon-Tsagan which is the only species of this genus known from the Cretaceous. Aleyrodoidea and aphids are represented by a few specimens. The strong dominance of Psyllomorpha over aphids is typical of the second half of the Jurassic; the earliest Coccoidea are known from the Early Cretaceous. Coleorrhyncha



Fig. 25. Hymenopterans: (1) *Shartexyela mongolica* Rasnitsyn, 2008, holotype PIN, no. 4270/119; (2) *Praeaulacus sharteg* Rasnitsyn, 2008, PIN, no. 4270/1544; (3) *Cleistogaster gobialtaica* Rasnitsyn, 2008, holotype PIN, no. 4270/1548; (4) *Praescopinus excellens* Rasnitsyn, 2008, holotype PIN, no. 4270/1550. Scale bar, 1 mm.

are rather scarce and represented only by the genus *Onokhoia* of the family Progonocimicidae. Strangely, representatives of the family Karabasiidae are absent.

Heteroptera are represented by terrestrial, coastal, and aquatic forms. The most abundant family of aquatic Heteroptera is Corixidae. Amphibiotic Leptopodomorpha are represented by Archegocimicidae, relatively rare, but diverse: *Saldonia formosa* Ryzhkova, 2011, *S. insoluta* Ryzhkova, 2011, *Shartegocimex rasnitsyni* Ryzhkova, 2011, *S. distans* Ryzhkova, 2011, and *Shartegocorpus paranotalis* Ryzhkova, 2011. The hemipterans of Shar Teg are described in more detail in the Section *Systematic Paleontology*.

Orders Psocoptera, Lophioneurida, and Miomoptera

Records of Psocoptera and Lophioneurida are rather scarce. The record of Miomoptera is one of the latest or the latest known.

Order Hymenoptera

Hymenopterans are relatively rare in Shar Teg compared to other localities of the same age. This is especially true of Symphyta. The first fossil described

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was Sepulca mongolica (Rasnitsyn, 1993); others were described later also by Rasnitsyn (2008). The summary provided below is based on the latter publication. Only two sawflies have been recorded (Xyelidae: Gigantoxyelini: Shatexyela mongolica Rasnitsyn, 2008 and Sepulcidae: Sepulca mongolica Rasnitsyn, 1993). Parasitoid wasps are more diverse (Ephialtitidae: Altephialtites altaicus Rasnitsyn, 2008; Megalyridae: Cleistogastrinae: Cleistogaster gobialtaica Rasnitsyn, 2008; Mesaulacinus mongolicus Rasnitsvn. 2008: Praeaulacidae: Praeaulacinae: Praeaulacus patiens Rasnitsyn, 2008; P. sharteg Rasnitsyn, 2008; and Anomopterellinae: Anomopterella gobi Rasnitsyn, 2008; Pelicinidae: Iscopininae: Praescopinus excellens Rasnitsyn, 2008) (Fig. 25). All nine recorded species and three of eight recorded genera were described as new. Five previously known genera are Jurassic; Asiephialtites, the closest relative of Altephialtites, is also Jurassic; Gigantoxyelini and Iscopininae were previously described only from the Lower Cretaceous, but undescribed representatives of these taxa are also known from the Jurassic. Fossil Aculeata, which appeared in the Early Cretaceous, have not been found in Shar Teg. Representative hymenopteran associations have been collected only in two localities similar in age: Karatau in south-



Fig. 26. Cupedid beetles of the tribe Notocupedini: (1a–1c) *Notocupes brachycephalus* Ponomarenko, 1994: (1a, 1b) specimen PIN, no. 2470/888, part and counterpart, (1c) specimen PIN, no. 2470/45; (2) *N. exiguus* Ponomarenko, 1994, specimen PIN, no. 2470/892; (3) *Zygadenia giebeli* sp. nov., holotype PIN, no. 2470/46; (4) *Z. handlirshi* sp. nov., holotype PIN, no. 2470/886.

ern Kazakhstan (Rasnitsyn, 1980) and Daohugou in northeastern China (Rasnitsyn and Zhang, 2004). Praeaulacidae and Megalyridae make up more than half of all fossil hymenopterans collected in Shar Teg, 34% in Karatau, and only 6% in Daohugou.

Order Coleoptera

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Fossil remains of beetles (Coleoptera) occur in the locality especially frequently: a total of about 700 specimens have been collected, including 150 specimens of supposedly aquatic forms. They have also been found in the Elisutain Am area. Beetle fossils compose more than half of the oryctocoenosis, but almost all of them are isolated sclerites, mostly elytra. The order Coleoptera is also the most diverse of all insect orders found in Shar Teg. It is probably represented by about 25 families and some 200–300 species, of which about 30 have been described. Whole fossil beetles are barely present, and none of them are supposedly aquatic. The group of beetles represented by the greatest number of whole fossils, with legs and



Fig. 27. Cupedid beetles of the tribe Mesocupedini: (1a, 1b) *Anaglyphites crassipygus* sp. nov., holotype PIN, no. 2470/885; (2a-2c) *A. minutissimus* sp. nov.: (2a, 2b): holotype PIN, no. 2470/1014, (2c) paratype PIN, no. 2470/889.

antennae, is the Mesozoic family Mesocinetidae, which combines features of Eucinetidae and Scirtidae. The larvae of extant scirtids live in water, but the fossil mesocinetids collected in Shar Teg include only adult beetles. Extant eucinetids live in rotting wood. Thus, we can find no explanation for the abundance and good preservation of Mesocinetidae in Shar Teg, where it is the most abundant of all beetle families. The majority of isolated elytra, which can only be treated as representatives of formal genera of unclear taxonomic position, remain undescribed.

The proportion of Archostemata is only about 2.5%; the frequencies of Cupedidae and Schizophoroidea are approximately equal. Cupedids (Fig. 26) are rather common and diverse, although they have not been found in Mongolia in the second half of the Jurassic. The dominant cupedid genus is *Notocupes*;

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three specimens, two of them isolated elytra, are assigned to *N. brachycephalus* Ponomarenko, 1994 and *N. exigius* Ponomarenko, 1994; other records of which are dated late Middle–early Late Jurassic of central Mongolia (Bakhar Group). Several other elytra of similar structure could not be attributed to any known species of Notocupedinae and are described in the formal genus *Zygadenia* Handlirsch, 1906. Two more species are described in the genus *Anaglyphites* Ponomarenko, 1964 (Fig. 27).

The relict Asiocoleidae (including Tricoleidae) are represented by several isolated elytra; one of them is described as a new species of the genus *Loculitricoleus* (Fig. 28), known from the Jurassic of China. It is the latest known record of this family.

The Schizophoridae are represented almost exclusively by isolated elytra; two most complete specimens



Fig. 28. Beetle of the family Asiocoleidae: *Loculitricoleus mongolicus* sp. nov.: (a, b) holotype PIN, no. 2470/898; (c) paratype PIN, no. 2470/896.

are described as the new genus *Sodovia* and a new species of the genus *Tersus* Martynov, 1926 (Fig. 29). Judging from the size and structure of isolated elytra, the collection also includes two or three other species of Schizophoridae.

Adephagans compose more than 10% of all beetle specimens (it is difficult to determine the proportion more precisely because of many isolated elytra that cannot be identified). Almost all adephagan specimens are aquatic forms; ground beetles are represented by less than ten specimens. One elytron may belong to a whirligig (Gyrinidae) of the genus Mesogyrus Ponomarenko, 1973, widespread in the terminal Jurassic and basal Cretaceous (Fig. 30). Relatively small Coptoclavidae are more abundant, but this identification cannot be formally proved even for almost complete specimens, because none of them retains legs with swimming setae. The most complete specimens are described in the genera Coptoclavella Ponomarenko, 1980 and Timarchopsis Brauer, Redtenbacher et Ganglbauer, 1889 (Fig. 31). Incomplete fossil specimens with similarly shaped metacoxae are traditionally described in the latter genus; the former genus is distributed mostly in the Early Cretaceous; the latter is distributed in the Jurassic. Coptoclavid larvae have not been found. The collection also includes several elytra, fragments of abdomens, and a protarsus of large adephagan beetles that probably also belong to Coptoclavidae. Thus, the total number of coptoclavid species may be as high as five. The majority of adephagan specimens belong to the Jurassic family Liadytidae (Fig. 32) and the genus Memptus, which has an unclear taxonomic position. Ground beetles are represented by both Trachypachydae (Eodromeinae) and Carabidae –(Protorabinae) (Fig. 33). A rather small well-preserved elytron with punctate grooves and elytra combined in the formal genus Allognosis almost certainly belong to Protorabinae. The posterior half of a rather large beetle and an isolated elytron are described in Eodromeinae. They are assigned to the genus *Procalosoma*, previously known only from the Solnhofen locality, Germany. This genus belongs to a group of long-legged ground beetles with long, protruding, asymmetrical mandibles and tuberculate elytra, often bearing a pale (probably desclerotized) spot preapically on the external margin. They are similar to extant mollusk-eating ground beetles, such as Cychrus, and known in Upper Jurassic and basal Cretaceous localities of Western Europe, Central Asia, western Mongolia, and Transbaikalia, but absent among the abundant Jurassic and Cretaceous ground beetles known from China.

The family Jurodidae, which presently exists as a relict, is represented by the genus *Jurodes*, widespread in the Late Jurassic and Early Cretaceous, but always as a minor component. Two poorly preserved speci-



Fig. 29. Beetles of the family Schizophoridae: (1a, 1b) *Tersus minor* sp. nov., holotype PIN, no. 2470/899; (2a–2c) *Sodovia sharotegica* sp. nov., holotype PIN, no. 2470/95; (3–5) Schizocoleidae gen. spp.: (3) specimen PIN, no. 2470/979; (4) specimen PIN, no. 2470/897; (5) specimen PIN, no. 2470/895.

mens of a new species of this genus have been found in Shar Teg (Fig. 34).

Almost all Polyphaga, which include the overwhelming majority of beetles collected in Shar Teg, belong to the lower groups. Cucujiformia and Rhynchophora compose only a few percent. Staphyliniformia are also rather scarce, represented mostly by hydrophils, the family Spercheidae, recorded as fossils for the first time (Fig. 35), and by the extant genus Helophorus, very common among fossils (Fig. 36). Abundant elytra assigned to the formal genera Hydrobiites, Polysitum, and Platycrossos (Fig. 37), or at least some of them, may also belong to hydrophils. Hydrophils occur in Shar Teg almost exclusively in basal horizons of the lake section. Very few (less than ten) specimens of Staphylinidae have been found. Such a low abundance of staphylinids is usually typical of temperate faunas of Siberia, whereas in localities of the lower latitudes and in volcanogenic deposits, staphylinid fossils are much more frequent. One speci-



Fig. 30. Beetle of the family Gyrinidae: *Mesogyrus elongatus* sp. nov., holotype PIN, no. 2470/47, photograph and drawing.



Fig. 31. Beetles of the family Coptoclavidae: (1a–1c) *Coptoclavella jurassica* sp. nov., holotype PIN, no. 2470/1007; (2a, 2b) *Timarchopsis longus* sp. nov., (2a) holotype PIN, no. 2470/947, (2b) no. 2470/936; (3) male protarsus of Coptoclavidae inc. sed., specimen PIN, no. 24740/906.



Fig. 32. Beetle of the family Liadytidae: Liadytes aspidytoides Prokin, Petrov, Wang et Ponomarenko, holotype PIN, no. 2470/942.



Fig. 33. Beetles of the superfamily Caraboidea: (1a, 1b) *Procalosoma incertum* sp. nov.: holotype PIN, no. 4270/946, (2) specimen PIN, no. 4270/981; (3) Protorabinae inc. sed.: specimen PIN, no. 4270/949; (4) Caraboidea inc. sed.: specimen PIN, no. 4270/948.

men (*Mesagyrtoides fulvus* Perkovsky, 1999) belongs to the family Leiodidae, which is very rare among fossils.

Several fossil remains of very small beetles could have belonged to Hydraenidae (Fig. 38).

The Scirtoidea are surprisingly abundant. Most of them have been described in the family Mesocinetidae (Fig. 39). These beetles were previously assigned to the family Eucinetidae, but examination of better-preserved material from Shar Teg has shown that features of both Eucinetidae and Scirtidae can be found in their structure (Kireitshuk and Ponomarenko, 2010). with some species closer to Eucinetidae and others, to Scirtidae. The specimens described are assigned to eight species of five genera (Mesocinetes Ponomarenko, 1986, Shartegus Kirejtshuk et Ponomarenko, 2010, Parashartegus Kirejtshuk et Ponomarenko, 2010, Manopsis Kirejtshuk et Ponomarenko, 2010, and Manoelodes Kirejtshuk et Ponomarenko, 2010). Almost all mesocinetids found in Shar Teg are assigned to the genus *Mesocinetes*; other genera are represented by single specimens. There are no other localities in which mesocinetids are known to be as abundant and diverse as in Shar Teg. Eucinetids live in dead wood; scirtids have aquatic larvae, but fossil scirtids are abundant only in the Late Eocene Bembridge locality (England). Mesocinetids are rather frequent in localities of the second half of the Jurassic and Lower Cretaceous, but they are not among the dominants in any of these localities. Crowson (1975) suggested that the earliest known representative of Eucinetidae could be *Ooperiglyphus* Bode, 1954 from the Upper Lias of Germany, but now it appears more likely that it belongs to Mesocinetidae. Interestingly, almost all mesocinetids found in Shar Teg are nearly complete beetles, while most other beetle remains found in this locality are fragmentary. One specimen was found together with abundant remains of Corixidae in a fish coprolite. The genus *Microcarpoides* could also belong to Scirtoidea.

Only two specimens of Scarabaeoidea have been found in Shar Teg. Such scarcity of this group is typical of the Late Jurassic and contrasts with Cretaceous localities: scarabaeoids are quite widespread and abundant from the very beginning of the Cretaceous. One scarabaeoid specimen from Shar Teg was described as *Paralucanus mesozoicus* Nikolaev, 2000, the only representative of a new subfamily of Lucanidae (Paralucaninae).



Fig. 34. Beetle of the family Jurodidae: *Jurodes shartegiensis* sp. nov.: (1a, 1b) holotype PIN, no. 4270/1010; (2) paratype PIN, no. 4270/1006.

The most common representatives of Polyphaga in Shar Teg are Elateriformia. The Byrridae are, as usual, rather scarce (Fig. 40). However, if we consider the isolated elytra of *Dzeregia* as belonging to Byrridae, this family will be quite abundant. The genus *Dzeregia* is rather widespread, at least in Siberian faunas. The Elateridae, even considering the possibility that the isolated elytra of *Agrilium* belong to this family, have an extremely low abundance, as usual in Siberian faunas and in contrast to more southern faunas of the same age, in which elaterids are dominant.

The Lasiosynidae, including those with the structure of elytra typical of the formal genus *Artematopodites* (over 200 specimens), are dominant among elateriform beetles. Two species (*Lasiosyne shartegensis* Yan, 2012 and *L. insculpta* Yan, 2012) were described based on almost complete specimens (Fig. 41); three (*Artematopodites maximus* Yan, 2010, *A. crispulus* Yan, 2010, and *A. lepidus* Yan, 2010) were described based on isolated elytra that could belong to beetles of this family. Several beetles found in Shar Teg may belong to Anobiidae. Dermestoids are absent, as usual.

Typically of the Late Mesozoic, Cleroidea are dominant among cucujiform beetles (Fig. 42); one specimen belongs to the family Cleridae (*Shartegopsis* *miranda* Kirejtshuk, 2012) (Fig. 43). The Heteromera are rather diverse and include forms that display characters of Rhipiphoridae, Scraptiidae, Mordellidae, and Melandryidae (Fig. 44). Only one specimen represents Rhynchophora, abundant and diverse in lowlatitude faunas, but absent in Siberian faunas. This specimen was described in the family Eccoptarthridae (*Gobicar ponomarenkoi* Gratshev et Zherichin, 1999), known from the Late Jurassic on, especially widespread in the Early Cretaceous, and existing up to the present time as a relict in Australia and South America.

Order Megaloptera

Megaloptera is represented by a single record, mature larva of *Sharasialis fusiformis* Ponomarenko, 2012, Sialidae (Fig. 45). The good preservation of the specimen suggests that, in spite of its singularity, it was not allochthonous and lived in Shar Teg Lake. It is the earliest known record of such larvae.

Order Raphidioptera

Snakeflies are represented in Shar Teg by two records of rather poorly preserved specimens (Fig. 46). Jurassic snakeflies are absent in the Siberian region,



Fig. 35. Beetle of the family Spercheidae: *Prospercheus cristatus* Prokin, 2009, holotype PIN, no. 4270/1012: (a, b) photographs, counterpart and part; (c, d) drawings, dorsal and ventral views; (e) anterior head end; (f) head.

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Fig. 36. Beetles of the family Helophoridae: (1a–1d) *Helophorus inceptivus* Ficacek et al., holotype PIN, no. 4270/1008: (1a) photograph, (1b) photograph under alcohol, (1c) dorsal view, (1d) ventral view; (2a, 2b) *H. costalis* sp. nov.: (2a) holotype PIN, no. 4270/997, (2b) paratype PIN, no. 4270/988; (3a–3c) *Helophorus* spp.: (3a) specimen PIN, no. 4270/990, (3b) specimen PIN, no. 4270/1003, (3c) specimen PIN, no. 4270/1004.

but abundant at low latitudes, although their diversity is low.

Order Neuroptera

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A total of 35 specimens of Neuroptera have been collected in Shar Teg; they belong to at least five families: Osmylidae, Grammolingiidae, Prohemerobiidae, Kalligrammatidae, and Polystoechotidae. Representatives of six genera were described from this locality: *Leptolingia* Ren, 2002 (Grammolingiidae), *Jurakempynus* Wang et al., 2011 and *Sogjuta* O. Martynova, 1958 (Osmylidae), *Prohemerobius* Handlirsch, 1906 (Prohemerobiidae), *Frustumopsychops* Khramov gen. nov. (Polystoechotidae), and *Dimidiosmylus* Khramov gen. nov. (Incerta familia). Two of them, *Leptolingia* and *Jurakempynus*, are typical of the Mid-dle–Upper Jurassic of Asia.

Order Mecoptera

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Scorpionflies are rather abundant in Shar Teg, although their diversity is relatively low (Fig. 48). They are represented by two families widespread in the Mesozoic, Orthophlebiidae Handlirsch, 1906 and Bittacidae Handlirsch, 1906. According to the estimation of Novokshonov and Sukatsheva (2003), 86 of 88 specimens collected belong to Orthophlebiidae and

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Fig. 37. Beetles Hydrophiloidea inc. sed.: (1a, 1b) *Polysitum sharotegense* sp. nov., holotype PIN, no. 4270/1005; (2a–2d) *Hydrobiites mongolicus* sp. nov.: (2a, 2b) holotype PIN, no. 4270/1002, photograph and habitus, (2c, 2d) paratype PIN, no. 4270/998, photograph and habitus; (2e, 2f) *Hydrobiites minor* sp. nov.: holotype PIN, no. 4270/985, photograph and habitus.

two belong to Bittacidae (Novokshonov, 1993a, 1993b; Novokshonov and Sukatsheva, 2003). Subsequent revision of the collection has shown that the proportion of Orthophlebiidae was somewhat overestimated: only 67 specimens can be assigned to this family, ten belong to Bittacidae, and the rest of the specimens are fragmentary and cannot be identified to family. Almost all mecopteran specimens are represented by isolated wings, mostly forewings.

Two species have been described from Shar Teg in the genus *Orthophlebia* Westwood, 1845 of the family Orthophlebiidae: *O. gubini* Novokshonov et Sukatsheva, 2003 and *O. shartegica* Novokshonov et Sukatsheva, 2003. The former species is only represented by the holotype, whereas the second, in the opinion of Novokshonov and Sukatsheva, is represented, in addi-

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tion to the type series of 18 specimens, by about 50 wings. Thus, the proportion of *O. shartegica* among all scorpionflies collected in Shar Teg was estimated as 77%.

However, at most 25 undescribed specimens can be more or less reliably assigned to *O. shartegica*, which, in combination with the type series, makes the proportions of this species 50% among all scorpionflies and 64% among orthophlebiids. The other wings either clearly belong to other species or cannot be identified because of poor preservation.

The described species of Orthophlebiidae differ mainly in size and pattern of the wing. The wings are 6.5 to 9.3 mm long in *O. shartegica* and 20.5 mm long in *O. gubini*. At the same time, the material includes some wings 10 to 15 mm long and a few wings that are



Fig. 38. Beetles assigned to the family Hydraenidae: (1a-1c) specimen PIN, no. 4270/999; (1d-1f) specimen PIN, no. 4270/1015; (2a, 2b) specimen PIN, no. 4270/1013.

larger (20 mm long and longer), but clearly differ from *O. gubini* in coloration pattern (Figs. 48.4, 48.5).

The problem of identification of orthophlebiid species based on isolated wings, caused by lack of diagnostic characters (often in direct dependence on preservation) and by insufficiently known interspecies variation, was pointed out by Novokshonov and Sukatsheva (2003), but the scale of this problem seems somewhat overestimated. The presence in Shar Teg of some species that remain undescribed is beyond doubt and the total number of orthophlebiid species in this locality is probably at least five or six. However, it would be untimely to describe new orthophlebiid taxa from Shar Teg before a full-fledged revision of the genus *Orthophlebia*.

Two species have been described from Shar Teg in the family Bittacidae: *Orobittacus minutus* Novokshonov, 1993 and *Sharabittacus mongolicus* (Novokshonov, 1993), each based on a single impression. As noted by Novokshonov and Sukatsheva (2003), "very closely related species of these two genera are also known from the Upper Jurassic Karatau locality, a fact that supports the Late Jurassic age of Shar Teg." In addition, the revision revealed eight incomplete bittacid wings, previously assigned to Orthophlebiidae. The wings are incompletely preserved and cannot be identified to genus.


Fig. 39. Beetles of the family Mesocinetidae: (1a–1e) *Mesocinetes aequalis* Kirejtshuk et Ponomarenko, 2010: (1a–1d) holotype PIN, no. 4270/48: (1a) photograph, (1b) dorsal view, (1c) ventral view, (1d) leg, (1e) paratype PIN, no. 4270/1071; (2) *Mesocinetes angustitibialis* Kirejtshuk et Ponomarenko, 2010, holotype PIN, no. 4270/1067, photograph; (3a–3c) *Shartegus transversus* Kirejtshuk et Ponomarenko, 2010, holotype PIN, no. 4270/1069: (3a) photograph, (3b) dorsal view, (3c) ventral view; (4a–4d) *Manoelodes gratiosus* Kirejtshuk et Ponomarenko, 2010: (4a, 4b) holotype PIN, no. 4270/1082: (4a) photograph, (4b) ventral view; (4c, 4d) paratype PIN, no. 4270/1087: (4c) dorsal view, (4d) ventral view; (5) *Parashartegus distinctus* Kirejtshuk et Ponomarenko, 2010, holotype PIN, no. 4270/1313.



Fig. 40. Beetles assigned to the family Byrridae: (1a, 1b) specimen PIN, no. 4270/1104; (2) specimen PIN, no. 4270/1106; (3a, 3b) specimen PIN, no. 4270/1109; (4) specimen PIN, no. 4270/1110.



Fig. 41. Beetles of the family Lasiosynidae: (1a, 1b) *Lasiosyne shartegiensis* Yan, 2012, holotype PIN, no. 4270/1246; (2a, 2b) *L. insculpta* Yan, 2012, paratype PIN, no. 4270/1184, (3a, 3b) *L. longitarsa* Yan, 2012, holotype PIN, no. 4270/1228; (4a, 4b) *Artematopodites maximus* Yan, 2010, holotype PIN, no. 4270/1130 (photograph) and reconstruction of elytron (drawing); (5a, 5b) *A. crispulus* Yan, 2010 holotype PIN, no. 4270/1222 (photograph) and reconstruction of elytron (drawing); (6a, 6b) *A. lepidus* Yan, 2010 PIN, no. 4270/1143.



Fig. 42. Beetles Cleroidea inc. sed.: (1a, 1b) specimen PIN, no. 4270/1531, (2a, 2b) specimen PIN, no. 4270/1535: (2a) dry, (2b) under alcohol.

Order Trichoptera

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Caddisflies are represented in Shar Teg by rather few (27) adult specimens, most of them belonging to

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the common family Philopotamidae (*Baga pumila* Sukatcheva [Sukatsheva] and gen. sp. cf. *Archiphilopotamus*) and the rare families Hydrobiosidae (*Bullivena grandis* Novokshonov et Sukacheva [Sukatsheva], 1995 and Dysoneuridae (*Oncovena sharategensis* Ivanov et Novokshonov, 1995). The genera *Bullivena* and *Oncovena* are endemic to Shar Teg and have similar morphological features, swellings of forewing veins that could contain pheromone glands.



Fig. 43. Beetle of the family Cleridae: *Shartegopsis miranda* Kirejtshuk, 2012: (a–d) holotype PIN, no. 4270/1116: (a, b) habitus, (c, d) maxilla, SEM image.



Fig. 44. Beetles assigned to Heteromera: (1a, 1b) specimen PIN, no. 4270/1117; (2a, 2b) specimen PIN, no. 4270/1124. Scale bar, 1 mm.



Fig. 45. Megalopteran larva of the family Sialidae: *Sharassialis fusiformis* Ponomarenko, 2012: (a–c) holotype PIN, no. 4270/1493: (a) SEM image, (b) photograph, (c) habitus.



Fig. 46. Snakeflies: (1a, 1b) specimen PIN, no. 4270/131; (2a, 2b) specimen PIN, no. 4270/1402.



Fig. 47. Neuropteran *Leptolingia shartegica* Khramov, 2010, holotype PIN, no. 4270/5001: (a, c) forewing; (b, d) hind wing. Scale bar, 10 mm.

The genus *Baga* is also known from the Middle– Upper Jurassic of Mongolia (Bakhar locality). These are the earliest known records of Philopotamidae.

Caddisfly cases are rather rare in Shar Teg; only about 100 specimens have been collected. They are less abundant not only compared to Cretaceous localities, but also compared to other Jurassic localities. Nevertheless, they are rather diverse. The following species have been recorded: *Terrindusia* cf. *minuta* Vialov et Sukatsheva, 1976, *Folindusia digna* Sukatsheva, 2000, *F. adumbrata* Sukatsheva, 2000, *F. pilarius* Sukatsheva, 2000, *F. megasporae* Sukatsheva, 2000, *Secrindusia expressa* Sukatsheva, 2000, *Ostracindusia callida* Sukatsheva, 2000, and *Conchindusia longaeva* Sukatsheva, 2000 (Fig. 49). Adult specimens do not include forms usually associated with case-building

Mesozoic larvae. Species of the genera Terrindusia, Conchindusia and Folindusia have been found in deposits of cyclites I-III. Cases are built mostly of sand in Terrindusia, "conchostracan" shell fragments in Conchindusia, and plant remains in Folindusia. Caddisfly larvae most probably collected the building material in coastal environments, and the cases were then transported to fossilization areas on floating aggregates. In cyclites VII and VIII, deposited in a shallowing lake, sparse cases of Conchindusia and Ostracindusia are found; they were probably buried here in the same environments in which they lived. However, even in these cyclites, cases buried in the finest-grain interbeds were probably transported to deeper areas of the water body. Remarkably, although caddisfly cases are distributed over the entire section,



Fig. 48. Scorpionflies: (1, 2) Orthophlebia shartegica Novokshonov et Sukatsheva, 2003, (1) holotype PIN, no. 4270/1552, (2) forewing, paratype PIN, no. 4270/1621, forewing; (3) Orthophlebia gubini Novokshonov et Sukatsheva, 2003, holotype PIN, no. 4270/1594, forewing; (4) Orthophlebia sp., specimen PIN, no. 4270/129, forewing; (5) Orthophlebia sp., specimen PIN, no. 4270/1596, forewing reconstructed from photographs, positive and flipped negative; (6) Sharabittacus mongolicus (Novokshonov, 1993), holotype PIN, no. 4270/126, forewing.

they are especially frequent in the finest-grain interbeds, where empty cases could not be transported over the bottom and no traces of crawling larvae can be found. Cases built of sand grains occur in fine-grain sediments lacking this matter and cases built of "conchostracan" shell fragments and ostracode shells frequently occur in beds lacking any remains of these animals. Since there are no traces showing that the cases were transported over the bottom, it can only be suggested that the cases were transported on floating aggregates, while most of the cases still contained living larvae. This can be viewed as another evidence supporting the conclusion that caddisfly larvae did not live on the bottom because of asphyxial conditions. One case was built by the larva using megaspores of the lycopod Limnoniobe (identified by V.A. Krassilov), macroremains of which have not been found in Shar Teg. This plant had a submerged or floating mode of life; if it was floating, it could serve as a frame for floating aggregates.

Order Lepidoptera

Lepidopteran fossils are rather scarce and remain unstudied (Fig. 50).

Order Diptera

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Dipterans compose one of the most diverse insect orders in Shar Teg. They are known from several cyclites: II (sample 442/2), III (samples 423/6, 9, 441/4, and 443/1), VII (sample 434/2), VIII (sample 452/2)—and from sample 451/3, the position of which in the section remains uncertain. The most abundant material comes from two samples, 423/6 and 443/1, of the same bed, which was formed according to Sinitsa (see Chapter 1. Geological Description ... in this volume) in sandy shoals of a large lake (at a high water level) or at the junction area between such a lake and floodplain of a flatland river with mostly sandy bottom. All dipteran families known from Shar Teg, without exceptions, have been recorded in these two sections (Table 1). Only rare finds of exclusively aquatic families have been recorded in sample 434/2, the environment of which is reconstructed as a silty beach shoal of a periodically shallowing, drying, and



Fig. 49. Caddisflies: (1) family Philopotamidae, *Baga pumila* Sukatcheva, 1992, holotype PIN, no. 4270/121; (2) family Hydrobiosidae, *Bullivena grandis* Novokshonov et Sukatcheva, 1995, holotype PIN, no. 4270/123. Caddisfly cases: (3) *Secrindusia expressa* Sukatsheva, 2000, holotype PIN, no. 4270/1743; (4) *Ostracindusia martinovae* Sukatsheva, 2000, holotype PIN, no. 4270/125; (5) *Conchindusia longaeva* Sukatsheva, 2000, holotype PIN, no. 4270/1736; (6) *Folindusia* (s. str.) *pilarius* Sukatsheva, 2000, holotype PIN, no. 4270/1701; (7) *F*. (s. str.) *megasporae* Sukatsheva, 2000, polotype PIN, no. 4270/1684; (8) *F*. (s. str.) *digna* Sukatsheva, 2000, holotype PIN, no. 4270/1684; (9) *F*. (s. str.) *admirata* Sukatsheva, 2000, holotype PIN, no. 4270/1685.



Fig. 50. Lepidopterans: (1) specimen PIN, no. 4270/1756; (2) specimen PIN, no. 4270/1751.

423/6 434/2441/4 442/2443/1 451/3452/2 Family Limoniidae Speiser, 1909 423/6 434/2 441/4 443/1 451/3 452/2 Architipulinae Handlirsch, 1906 Architipula krzeminskii Lukashevich, 2009 ++Architipula ampla Lukashevich, 2009 ++Cretolimonia jurassica Lukashevich, 2009 +Cretolimonia pygmaea Lukashevich, 2009 + Mesotipula sigmoidea Lukashevich, 2009 ++?Mesotipula brevicella Lukashevich, 2009 + Mesotipula (Metatipula) continents Luk., 2009 ++Tipunia undata Lukashevich, 2009 ++Tipunia jorgi Lukashevich, 2009 +Eotipulinae Kalugina, 1985 Eotipulina sharategica Lukashevich, 2009 ++Eotipulina paula Lukashevich, 2009 +Eotipulina evidens Lukashevich, 2009 +*Eotipuloptera* sp. + Family Trichoceridae Rondani, 1841 423/6 442/2443/1?Undaya lenae Krzeminska et al., 2009 + ?Undaya lukashevichae Krzeminska et al., 2009 + Zherikhinina alastos Krzeminska et Luk., 2009 + + + Family Tanyderidae Osten-Sacken, 1880 434/2 443/1 ?Nannotanvderus incertus Lukashevich. 2011 +Praemacrochile ansorgei Luk. et Krzeminski, 2009 +Protanyderus nebulosus Luk. et Krzeminski, 2009 + + Protanyderus vetus Kalugina, 1992 + Protanyderus senilis Kalugina, 1992 +Family Ptychopteridae Schiner, 1864 423/6 443/1Proptychopterininae Lukashevich, 1995 Proptychopterina sharategica Kalugina, 1992 +Eoptychopterinae Handirsch, 1906 Eoptychoptera tempestilla Lukashevich, 1998 +Eoptychoptera spp. ++Crenoptychoptera liturata Lukashevich, 2011 ++*Nedoptychoptera* sp. +Eoptychopterininae Lukashevich, 1995 Eoptychopterina kaluginae Lukashevich, 2004 +Eoptychopterina sp. + Family Dixidae Schiner, 1868 443/1 Eucorethrina convexa Lukashevich, 1996 + Eucorethrina sp. +Family Chaoboridae Edwards, 1912 434/2 423/6 441/1443/1Chaoburmus amphilogos Lukashevich, 2011 + +Mesocorethra cincta Lukashevich, 2011 +

Table 1. Diptera recorded in Shar Teg

Table 1. (Contd.)

	423/6	434/2	441/4	442/2	443/1	451/3	452/2
Family Chironomidae Newman, 1834	423/6	434/2	441/4		443/1		
Aenneinae Ansorge, 1999							
Cretaenne rasnicyni Lukashevich et Przhiboro, 2011					+		
Podonominae Thienemann et Edwards, 1937							
Podonomius blepharis Luk. et Przhiboro, 2011					+		
Podonomius macromastix Luk. et Przhiboro, 2011	+						
?Podonomius robustus Luk. et Przhiboro, 2011					+		
Oryctochlus brundini Lukashevich, 2012		+					
Oryctochlus kaluginae Lukashevich, 2012					+		
Podonominae or Tanypodinae Skuze, 1889							
Jurochlus trivittatus Lukashevich et Przhiboro, 2012					+		
Jurochlus limbatus Lukashevich et Przhiboro, 2012					+		
Jurochlus lineatus Lukashevich et Przhiboro, 2012					+		
Tanypodinae Skuze, 1889					+		
Family Perissonmatidae Colless, 1962					443/1		
Palaeoperissomma ornatum Lukashevich, 2011					+		
Rasnicynomma additum Lukashevich, 2011					+		
Family Protorhyphidae Handlirsch, 1906	423/6				443/1		
Protorhyphus rohdendorfi Lukashevich, 2012	+				+		
Archirhyphus asiaticus Rohdendorf, 1964					+		
Family Anisopodidae Knab, 1912			441/4		443/1		
Olbiogastrinae Hennig, 1973							
Mesorhyphus handlirschi Lukashevich, 2012			+		+		
Mesorhyphus hennigi Lukashevich, 2012					+		
Pachyrhyphus sp.					+		
Teginae Lukashevich, 2012							
Tega penna Blagoderov et al., 1993					+		
Family Procramptonomyiidae Kovalev, 1985	423/6		441/4		443/1		
Procramptonomyia kovalevi Lukashevich, 2012	+		+		+		
Procramptonomyia ponomarenkoi Luk., 2012					+		
Family Paraxymyiidae Rohdendorf, 1946			441/4		443/1		
Paraxymyiinae Rohdendorf, 1946							
Paraxymyia mongolica Blagoderov, 1999			+		+		
Eomycetophilinae Ansorge, 1996							
Complecia clara Blagoderov, 1999					+		
Family Archizelmiridae Rohdendorf, 1962	423/6				443/1		
Archizelmira kazachstanica Rohdendorf, 1962	+				+		
Family Archisargidae Rohdendorf, 1962					443/1		
Mesosolva longivena Mostovski, 1996					+		
Sharasargus ruptus Mostovski, 1997					+		

overgrowing water body; in other areas of the outcrop, dipterans have been collected only sporadically.

A total of about 600 specimens of Diptera have been collected, most of them are adults. At least 50 genera of 25 dipteran families occur in Shar Teg (see list in Section 2.5). Systematic description of this material started more than 20 years ago (Kalugina, 1992), but remains far from completed. A total of 36 genera of 14 families have been described: Trichoceridae (two genera), Limoniidae (six), Tanyderidae (three), Ptychopteridae (five), Chaoboridae (two), Dixidae (one), Chironomidae (four), Perissommatidae (two), Protorhyphidae (two), Anisopodidae (three), Paraxymyiidae (two), Procramptonomyiidae (one), Archizelmiridae (one), and Archisargidae (two). The material includes many undescribed specimens of Protopleciidae, Pleciofungivoridae, Antefungivoridae, and Mesosciophilidae and some Bolitophilidae and probably Sciaridae. Brachycerans are rather scarce (about 20 specimens), but diverse: more than half of them belong to Rhagionidae; the others include described Archisargidae (Mostovski, 1996, 1997), undescribed Eremochaetidae, and probably Rhagionempididae, Therevidae, Vermileonidae, and Empididae, but the last four families cannot be identified with certainty based on available isolated wings. The mode of life reconstructed for larvae of the extinct families Archisargidae and Eremochaetidae is parasitism on invertebrates (adults were probably aphagous); the majority of extant rhagionids are predaceous: their predaceous larvae live in moist ground and in accumulations of decomposing plant remains, often at water edge. Almost all undescribed specimens are different, suggesting that actual diversity was undoubtedly higher than that of preserved fossils.

The dominant families are Limoniidae, which probably had semiaquatic larvae (about 100 imprints and six pupae: Lukashevich, 2009; Fig. 51), and probably Chironomidae, which had aquatic immature stages (about 50 adults and about 20 pupae; most of the chironomid specimens are too poorly or too fragmentarily preserved to be assigned with certainty to any subfamily). The previously described chironomids belong to the extinct subfamily Aenneinae (Fig. 52.3) and extant subfamilies Podonominae and Tanypodinae (Lukashevich and Przhiboro, 2011, 2012; Lukashevich, 2012b). Materials collected in Shar Teg do not include representatives of the more advanced subfamilies Prodiamesinae and Orthocladiinae, known from Early Cretaceous Lebanese amber (Veltz et al., 2007), to say nothing of the subfamily Chironominae, which has never been recorded in the Early Cretaceous.

Jurassic and Early Cretaceous lacustrine deposits of Asia are often dominated by Chaoboridae, usually because of abundance of immatures (Kalugina and Kovalev, 1985; Kalugina, 1986; Lukashevich, 2008). However, chaoborids collected in Shar Teg are only represented by scarce isolated wings, while neither pupae nor larvae have been recorded (Lukashevich, 2011). Similar situations are found in other Jurassic Lagerstätten of Asia: Kubekovo, Karatau, and Daohugou (my unpublished data). No deposits containing abundant fossils of any immature Diptera have been found in Shar Teg; only scarce pupae of limoniids and chironomids have been collected (Fig. 51.3; Lukashevich, 2009, 2012b) as well as tanyderid larvae, found in the fossil record for the first time (Fig. 52.2; Lukashevich and Krzeminski, 2009).

Semiaquatic (developing at the water edge) and aquatic families are rather few (Limoniidae, Tanyderidae, Ptychopteridae, Dixidae, Chaoboridae, and Chironomidae), and their dominance in abundance is not overwhelming because of the absence of abundant specimens of immature Culicomorpha. High diversity at the generic level combined with rather low abundance has been recorded not only in Brachycera, but also in semiaquatic families of Psychodomorpha sensu Hennig. For instance, all three genera of Tanyderidae known from the Mesozoic have been recorded in Shar Teg, although this family is represented in the collection by only six impressions of adults and two larvae (Figs. 52.1, 52.2). As for Ptychopteridae, of some thirty Mesozoic localities in which this family has been recorded, Shar Teg has the greatest number of genera: five genera represented by 14 specimens (Lukashevich et al., 1998; Lukashevich, 2004, 2011).

The diversity of described Bibionomorpha with primitive venation is not high (one or two genera in each family), but all three families with four-branched median and discoidal cell have been recorded: the extinct Protorhyphidae and Procramptonomyiidae (Fig. 53) and extant Anisopodidae, known beginning from the Early Jurassic (Lukashevich, 2012a). Larvae of most bibionomorph families have not been found, but they probably were phytosaprophagous (like trichocerids and some limoniids) and lived in accumulations of decomposing organics: accumulations of algae brought onto the shore, rotting wood, decaying leaf litter or fruit bodies of fungi. Two genera of Perissommatidae found in Shar Teg were probably also associated with decaying litter or fungi; this family is extremely rare in the fossil record and includes only one extant genus, which lives only in Australia and Chile (Lukashevich, 2011). Similar biogeographic associations are found in the trichocerid Zherichinina Krzeminska et al., 2009, which is similar to only one extant genus, Nothotrichocera Alexander, 1926. This Recent genus presently has a circum-Antarctic range, but it has been shown to have Laurasian roots in the Mesozoic (Krzeminska and Lukashevich, 2009).

The dipteran fauna of Shar Teg proved surprisingly unoriginal at the generic level (Table 2), showing that Jurassic dipterans of Eurasia are rather well studied. Only two genera endemic to Shar Teg have been described to date in systematically processed dipteran families: the paraxymyiid *Complecia* Blagoderov, 1999 and the perissommatid *Rasnicynomma* Lukashevich,



Fig. 51. Dipterans Limoniidae: (1a, 1b) *Eotipulina sharategica* Lukashevich, 2009, holotype PIN, no. 4270/2109; (2) *Tipunia undata* Lukashevich, 2009, holotype PIN, no. 4270/2144; (3) pupae Limoniidae inc. sed. PIN, no. 4270/2433. Scale bar, 1 mm.



Fig. 52. Dipterans Tanyderidae and Chironomidae: (1) wing of *Protanyderus vetus* Kalugina, 1992, holotype PIN, no. 4270/181; (2) larva of ?*Protanyderus* sp., PIN, no. 4270/237; (3) *Cretaenne rasnicyni* Lukashevich et Przhiboro, 2011: (3a) habitus, holotype PIN, no. 4270/2379, (3b) head, paratype PIN, no. 4270/2367.



Fig. 53. Dipterans Protorhyphidae and Procramptonimiidae: (1) *Protorhyphus rohdendorfi* Lukashevich, 2012, wings, holotype PIN, no. 4270/2263; (2) *Procramptonomyia ponomarenkoi* Lukashevich, 2012, habitus, holotype PIN, no. 4270/2267. Scale bar, 1 mm.

2011; monotypic subfamilies have been established for both genera (Blagoderov, 1999; Lukashevich, 2011). Several genera recorded in Shar Teg were previously known only from Lower Cretaceous deposits: the limoniid Cretolimonia Kalugina, 1986 (Western Mongolia), chaoborid Chaoburmus Lukashevich, 2000 (Burmese amber), and chironomid Cretaenna Azar et al., 2008 (Lebanese amber). Several genera from Shar Teg are only known from Jurassic deposits: the ptychopterid Nedoptychoptera Lukashevich, 1998, chironomid Podonomius Kalugina, 1985, archisargids Mesosolva Hong, 1983, and Sharasargus Mostovski, 1997. All other genera are stratigraphically and geographically widespread in Eurasia; most of them are known from a broad age range, from the Early Jurassic to Early Cretaceous; two genera have even been recorded in the Triassic: the limoniid Architipula Handlirsch, 1906 (Krzeminski, 1992) and ptychopterid *Eoptychoptera* Handlirsch, 1906 (Barth et al., 2011; Ansorge, pers. comm.). The number of more or less thoroughly studied Mesozoic localities in other modern continents is insufficient for representative comparison, but, for instance, the anisopodid genus Mesorhyphus Handlirsch, 1920, presently known in Eurasia only from Jurassic localities (including Shar Teg) was recorded in Upper Cretaceous American amber (Grimaldi and Engel, 2005). In addition, it should not be forgotten that, even in Eurasia, only a few families can be considered sufficiently thoroughly studied (e.g., Trichoceridae and Ptychopteridae); representatives of other families are usually described selectively; thus, the level of originality of the Shar Teg fauna can prove to be even lower than it appears now.

Dipterans of Shar Teg are especially similar to dipterans described from Karatau and Daohugou, localities that are probably close to Shar Teg in age (late Middle Jurassic or early Late Jurassic). This similarity can hardly be explained only by the quantitative and qualitative richness of dipterans in Karatau and Daohugou, two well-known Jurassic Lagerstätten, in which almost everything is likely to be found eventually, although this factor should not be discarded. The faunal similarity of these localities is probably acounted for by similar age. Four dipteran species shared by Shar Teg and Karatau are known to date (Praemacrochile ansorgei, Archirhyphus asiaticus, Procramptonomyia kovalevi, and Archizelmira kazachsta*nica*). At the same time, it should not be forgotten that three of these four species are known from Karatau based on numerous complete insects, often of both sexes, whereas from Shar Teg they are only represented by scarce isolated wings, making the comparison less reliable.

It would have been preferable to date localities using mostly those genera that have limited stratigraphic range, but such genera are relatively rare. For instance, *Tipunia* Krzeminski et Ansorge, 1995, a very peculiar limoniid genus from Shar Teg, was previously known only from precisely dated Upper Jurassic and Lower Cretaceous marine deposits of Europe (Solnhofen and Wealden of England). This distribution makes this genus considerably more informative than, for example, the cosmopolitan ptychopterid *Eoptychoptera* Handlirsch, 1906, known from the Late Triassic of Europe, Jurassic and Early Cretaceous localities distributed over the whole of Eurasia, and even from the Early Cretaceous of South America (the only presently known record of fossil Ptychopteridae in the Southern Hemisphere; Krzeminski et al., 2014).

Descriptions of dipterans from precisely dated Early Cretaceous localities of England have considerably expanded our knowledge of the distribution of particular genera and even families; as a result, it became clear that many of these taxa are less important diagnostically than previously believed. For instance, dating the Glushkovo Formation, which has a debatable age, Kovalev (1990) proceeded from the fact that protorhyphids were only known from Jurassic deposits; therefore, when this family was recorded in Daya, it was used as an argument in favor of dating this locality as Late Jurassic. However, reliably identified protorhyphids were later recorded in deposits of the Purbeck Group of England (Jarzembowski and Coram, 1997). Species described from Purbeck include, for instance, the dixid *Eucorethra* Kalugina, 1985 (Lukashevich et al., 2001) and the procramptonomyiid Procramptonomyia Kovalev, 1985 (Krzeminski and Krzeminska, 1994; Coram and Jarzembowski, 1999), genera previously known only from the Jurassic of Asia. Such finds change our notions of geographical and stratigraphical distribution of genera and give evidence of the smooth way, in which nematocerans crossed the boundary between the Jurassic and Cretaceous, a boundary that proved to be rather unimportant for them. As a result, Shar Teg cannot be dated more precisely based on nematocerans; it can only be stated that genera typical of the second half of the Jurassic are dominant, but the Early Cretaceous picture remains too fragmentarily to perform a representative analysis.

However, the data on changes in brachyceran faunas during the Jurassic and Cretaceous provided by Mostovski (2009) make it possible to date Shar Teg with certainty as Jurassic, since it displays all characters of the Jurassic: the proportion of brachycerans among nonaquatic dipterans is very small; rhagionids undoubtedly dominate (loosing the dominant position in the Cretaceous); archisargids are present (becoming extinct by the Cretaceous); and the proportion of empidids is very small.

Order Blattodea

Cockroaches and their derivative mantids of Shar Teg were studied by Vršanský (2003, 2004). Based on 171 specimens, he described eight or nine cockroach species of six genera and four families. The cockroaches proved to be quite advanced, more so than in

Taxon	\mathbf{J}_1	J ₁₋₂	J ₂₋₃	J ₃ –K ₁	K ₁	References
Zherikhinina	-	+	+		+	Krzeminska et al., 2009
Undava				+		Krzeminska et al. 2009
Architipula	+	+	+			Handlirsch, 1906; Krzeminski and Zessin, 1990; Kalugina and Kovalev, 1985; Zhang, 2004a, 2006b
Mesotipula	+	+				Handlirsch, 1920; Kalugina and Kovalev, 1985
Mesotipula						
(Metatipula)						
Tipunia				+	+	Krzeminski and Ansorge, 1995; Jarzembowski, 1991
Cretolimonia					+	Kalugina, 1986
Eotipulina		+	+			Kalugina and Kovalev, 1985; Zhang, 2006a
Eotipuloptera			+			Kalugina and Kovalev, 1985; Zhang, 2006a
Praemacrochile	+	+	+			Bode, 1953; Kalugina and Kovalev, 1985; Ansorge and Krzeminski, 2002; Krzeminski and Ren, 2001
Protanyderus		+	+	+	+	Kalugina, 1988; Zhang, 2004a; Lukashevich and Krzeminski, 2009
Nannotanyderus	+		+		+	Ansorge, 1994; Coram and Jarzembowski, 1998; Ansorge and Krzemin- ski, 2002: Krzeminski et al., 2010: Krzeminski et al., 2013
Proptychopterina	+	+	+	+		Kalugina and Kovalev, 1985; Kalugina, 1988; Lukashevich, 1993, 2000a; Lin and Lukashevich, 2006
Eoptychoptera	+	+	+		+	Handlirsch, 1906, 1920, 1939; Kalugina and Kovalev, 1985; Bode, 1953; Kalugina, 1988; Kalugina, 1989; Lukashevich, 1993, 2000a; Ansorge, 1996: Lukashevich et al., 1998, 2001: Ren and Krzeminski, 2002
Crenoptychoptera	+	+	+	+	+	Kalugina and Kovalev, 1985; Kalugina, 1989; Krzeminski and Ansorge, 1995; Lukashevich, 1995; Lukashevich et al., 1998
Nedoptvchoptera			+			Lukashevich et al., 1998
Eoptychopterina		+	+	+	+	Kalugina and Kovalev, 1985; Kalugina, 1989; Lukashevich, 1993, 2004; Coram and Jarzembowski, 1998; Lukashevich et al., 2001; Ren and Krzeminski, 2002; Zhang, 2004b; Hao et al., 2009
Eucorethrina		+	+	#	+	Kalugina and Kovalev, 1985; Lukashevich, 1996; Lukashevich et al., 2001
Chaoburmus					+	Lukashevich, 2000b
Mesocorethra				+		Kalugina, 1993
Cretaenne					+	Azar et al., 2008
Oryctochlus			+	+		Kalugina and Kovalev, 1985; Zhang, 1991; Kalugina, 1993; Luka- shevich, 2012b
Podonomius	+	+	+	+		Kalugina and Kovalev, 1985; Ansorge, 1996
Jurochlus			+		+	Kalugina and Kovalev, 1985; Lukashevich and Prziboro, 2012
Rasnicynomma						
Palaeoperissomma		+		+		Kalugina and Kovalev, 1985; Kovalev, 1990
Protorhyphus	+	+	+	+		Handlirsch, 1906, 1939; Rohdendorf, 1962, 1964; Kalugina and Kovalev, 1985; Hong, 1983; Kovalev, 1990; Ansorge, 1996; Zhang, 2007
Archirhyphus	+		+		#	Handlirsch, 1939; Rohdendorf, 1962, 1964; Ansorge, 1996; Jarzembowski and Coram, 1997; Lukashevich, 2012a
Tega		#	+			Blagoderov et al., 1993
Mesorhyphus	+			+		Handlirsch, 1920, 1939; Rohdendorf, 1962, 1964, Kovalev, 1990; Ansorge and Krzeminski, 1995; Ansorge, 1996
Pachyrhyphus				+	+	Kovalev, 1986, 1990; Jarzembowski and Coram, 1997
Paraxymyia		+	+			Rohdendorf, 1946, Blagoderov, 1999
Complecia						
Archizelmira			+		+	Rohdendorf, 1962, 1964; Grimaldi et al., 2003
Procramptonomyia		+	+		+	Kalugina and Kovalev, 1985; Krzeminski, Krzeminska, 1994; Coram and Jarzembowski, 1999; Lukashevich, 2012a
Mesosolva		+	+			Hong, 1983; Mostovski, 1996; Zhang and Zhang, 2003; Zhang et al., 2010
Sharasargus			+			Zhang et al., 2008

Table 2. Occurrence of dipteran genera recorded in Shar Teg

 (J_1) Sogyuty, Charmouth, German Liassic, Krasnoyarsk, Ust'-Balei; (J_{1-2}) Shurab, Novospasskoe, Kubekovo (J_2) , Haifanggou Formation (J_2) ; (J_{2-3}) Uda, Karatau, Daohugou, Bakhar, Beipiao, Solnhofen (J_3) , Khoutiyn Khotgor (J_3) ; (J_3-K_1) Unda, Daya, Shev'ya, Tergen', Olovskaya Depression, Kempendyai; (K_1) Khutel-Khara, Baisa, Bon-Tsagan, Onokhoi, Zhigansk, English Early Cretaceous, Lebanese amber, Burmese amber (K_{1-2}) ; (#) undescribed, but mentioned in published studies.

any other Jurassic fauna; advanced Mesoblattulidae and Blattulidae as well as the presence of mantids are typical of the Early Cretaceous; however, Paleozoic relicts are also present. Nevertheless, it should be pointed out that the only reliable mantis from Shar Teg, Juramantis initialis Vršanský, 2002, is represented by a very fragmentary wing and, according to Grimaldi (2003), lacking features specific to Mantodea. The oryctocoenosis includes the genus *Blattula*, typical of the Jurassic and, at the same time, the genus *Elisama*, which replaced *Blattula* in the Early Cretaceous. Thus, the composition of cockroaches has a mixed Late Jurassic-Early Cretaceous aspect. The nature of their preservation gives evidence of fish-mediated decomposition and rotting in warm water rather than destruction in the course of transportation by flowing waters. It is possible that some ecological stress factor was present, often resulting in fused veins of wings.

Order Orthoptera

Orthopterans are more abundant in Shar Teg than cockroaches. Tuphellidae (Paracyrtophyllites popovi Gorochov, 1992), Aboilidae, and Elcanidae have been recorded. The genus Paracyrtophyllites is known from the Tithonian Solnhofen locality. Crickets are especially abundant: Protogryllidae (Aenigmagryllus indistinctus Gorochov, 1992, A. obscurus Gorochov, 1992), Baissogryllidae—Sharategiinae (Sharategia rasnitsyni Gorochov, 1992, Neosharategia paradoxa Gorochov, 1992), and Baissogryllinae (Ponomarenkoana probontzagania Gorochov, 1992 and Storozhenkoana parvispeculum Gorochov, 1992) have been recorded (Fig. 54). Protogrvllidae is an exclusively Jurassic family; the subfamily Baissogryllinae was previously known only from the Lower Cretaceous. The subfamilv Sharategiinae is endemic to Shar Teg.

Order Grylloblattida

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Grylloblattids are rare in the Jurassic; they are represented in Shar Teg by a single impression of *Sinosepididontus shartegicus* (Aristov, Wappler et Rasnitsyn, 2009) of the family Geinitziidae (Aristov et al., 2009; Cui et al., 2012). This family is known beginning from the Permian (Aristov, 2009); in the Mesozoic, it is one of the most common families of Grylloblattida (Storozhenko, 2002). In addition to Shar Teg, the genus *Sinosepididontus* Huang et Nel, 2008 has only been recorded in the Middle Jurassic Daohugou locality in China (Cui et al., 2012). *S. shartegicus* is the latest described species of Geinitziidae and one of the latest winged representatives of Grylloblattida.

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A distinguishing feature of the Shar Teg stonefly assemblage is its high taxonomic diversity (Sinitshenkova, 1990b; Sinichenkova, 1995). A total of 37 stonefly specimens have been collected in Shar Teg; representatives of both suborders, Perlina and Nemourina, have been described from this locality. Stoneflies of Shar Teg include eight species of eight genera and four families; two genera (Sharaperla Sinitshenkova, 1990 and Mongolonemoura Sinitshenkova, 1995) and all species are endemic to this locality. Species of Perlina have been described based on nymphs; both nymphs and adults have been described for Sharaperla obligua Sinitshenkova, 1990 of the family Siberioperlidae (Gripoptervgomorpha). Most of the Nemourina species are known only from adults (Perlariopseidae); nymph has been described only for Mesoleuctroides derelictus Sinitshenkova, 1995 (Mesoleuctridae).

Suborder Perlina Latreille, 1802

Infraorder Gripopterygomorpha Enderlein, 1909

Family Siberioperlidae Sinitshenkova, 1983

One species of Siberioperlidae has been described from Shar Teg, *Sharaperla obliqua* Sinitshenkova, 1990 (Fig. 55.1) (nine nymphs and two adults). *Sharaperla* is especially similar in wing venation to *Sinosharaperla* Liu et al., 2007 from the Yixian Formation (Late Jurassic to Early Cretaceous) of northern China (Liu et al., 2007) and clearly differs from *Siberioperla* Sinitshenkova, 1983 in the advanced venation pattern; nymphs of *Sharaperla* are markedly distinguished from all known Siberioperlidae by the short and dilated femora and tibiae, similar in shape to that of *Platyperla* Br., Rdtb. et Gglb., 1889 (Sinitshenkova, 1982). The genus *Siberioperla* is known from the Early–Middle and Upper Jurassic of Siberia and Mongolia.

Infraorder Perlomorpha Latreille, 1802

Family Platyperlidae Sinitshenkova, 1982

The family Platyperlidae is represented in Shar Teg by one species, *Platyperla mendosa* Sinitshenkova, 1995 (six nymphs), close to *P. rigida* Sinitshenkova, 1987 from the Kushmurun Formation (Lower–Middle Jurassic) of western Kazakhstan (Turgaiskaya Vpadina locality) and *P. caudiculata* Sinitshenkova, 1985 from the Osinovka Formation (Lower–Middle Jurassic) of the Kuznetsk Basin (Ters' locality).



Fig. 54. Orthopterans Tuphellidae, Protogryllidae, and Baissogryllidae: (1) *Paracyrtophyllites popovi* Gorochov, 1992, holotype PIN, no. 4270/29; (2) *Aenigmagryllus indistinctus* Gorochov, 1992, holotype PIN, no. 4270/212; (3) *Sharategia rasnitsyni* Gorochov, 1992, holotype PIN, no. 4270/31; (4) *Neosharategia paradoxa* Gorochov, 1992, holotype PIN, no. 4270/210a; (5) *Ponomarenkoana probontzagania* Gorochov, 1992, holotype PIN, no. 4270/205; (6) *Storozhenkoana parvispeculum* Gorochov, 1992, holotype PIN, no. 4270/217.

Perlomorpha inc. sed.

Two genera of uncertain family position have been found in Shar Teg, *Trianguliperla* Sinitshenkova, 1985 and *Bestioperlisca* Sinitshenkova, 1990. *Trianguliperla optanda* Sinitshenkova, 1995 (four nymphs collected in Shar Teg) clearly differs from congeners in the structure of the thorax in the nymph. The genus *Trian*- guliperla includes eight known species from the Upper Triassic (two species; Kenderlyk and Garazhovka), Lower to Middle Jurassic (two species; Novospasskoe and Oshin-Boro-Udzyur-Ula), Upper Jurassic to Lower Cretaceous (in addition to the species recorded in Shar Teg, two species from Chernovskie Kopi), and Early Cretaceous (one species; Khutel-Khara).





Fig. 55. Stoneflies: (1) *Sharaperla obliqua* Sinitshenkova, 1990, holotype PIN, no. 4270/8, forewing; (2) *Bestioperlisca inulta* Sinitshenkova, 1990, holotype PIN, no. 4270/9, nymph. Scale bar, 2 mm.

The genus *Bestioperlisca* is represented by nymphs combining morphological features of perlomorphs (wide head, narrow mandibles with apically acute teeth, and short basal tarsomeres) and nemourin stoneflies (long and narrow wing primordia). *Bestioperlisca inulta* Sinitshenkova, 1990 (Fig. 55.2) was described based on a single nymph.

Suborder Nemourina Newman, 1853

Family Mesoleuctridae Sinitshenkova, 1987

Only one nymph of the family Mesoleuctridae, *Mesoleuctroides derelictus* Sinitshenkova, 1995, has been found in Shar Teg. The genus *Mesoleuctroides* includes three species. *M. derelictus* is close to *M. saturatus* Sinitshenkova, 1985 from the Ichetui Formation (Lower–Middle Jurassic) of western Transbaikalia (Novospasskoe, Ichetui II, Koltygei, Darasatui). The third species, *M. latus* Sinitshenkova, 1985, was described from the Zhargalant Formation (Lower– Middle Jurassic) of western Mongolia (Oshin-Boro-Udzyur-Ula) (Sinitshenkova, 1985).

Family Perlariopseidae Sinitshenkova, 1985

The family Perlariopseidae is represented exclusively by adults, which belong to three genera: *Dicronemoura* Sinitshenkova, 1985, *Karanemoura* Sinitshenkova, 1987, and *Mongolonemoura* Sinitshenkova, 1995.

The genus *Dicronemoura* includes ten species from the Triassic, Jurassic, and deposits dated as the Late Jurassic to Early Cretaceous. Species of this genus mostly occur in Siberia, Central Asia, and Mongolia; one species is known from the Upper Jurassic of northern Germany. *D. attenuata* Sinitshenkova, 1995 (two specimens) from Shar Teg is close to *D. dira* Sinitshenkova 1987 from the Madygen Formation (Middle–Upper Triassic) of Kyrgyzstan (Dzhailyaucho) and *D. muscosa* Sinitshenkova, 1992 from the deposits dated Upper Jurassic to Lower Cretaceous of Yakutia (Kempendyai) (Sinitshenkova, 1992).

The genus *Karanemoura* includes ten species found in the Lower, Middle, and Upper Jurassic and deposits dated as the Late Jurassic to Early Cretaceous. The geographical range of this genus covers Yakutia, central Transbaikalia, southern Kazakhstan, Central Asia, Eastern Mongolia, and northeastern China (Daohugou) (Liu et al., 2009). *K. perpropinqua* Sinitshenkova, 1995 from Shar Teg was described based on four specimens.

The genus *Mongolonemoura* resembles *Fritaniopsis* Sinitshenkova, 1987 and *Tritaniella* Sinitshenkova, 1987 from the Triassic of Central Asia (Dzhailyaucho and Sai-Sagul) in the archaic venation pattern. *M. inversa* Sinitshenkova, 1995 from Shar Teg was described based on a single wing impression.

Most of the stonefly specimens found in Shar Teg have been collected in outcrop 443, Bed 1 (A.G. Ponomarenko, pers. comm.). These finds are limited to the maximum transgression stage of large Shar Teg Lake. In other beds (outcrop 423, Bed 6, and outcrop 442, Bed 2), the same species rarely occur in grayish pelites similar to that of outcrop 443.

The Shar Teg locality is only comparable in taxonomic diversity to Kempendyai, where 20 of 52 specimens collected were identified to species. A total of 12 species of nine genera and six families have been recorded in Kempendyai. Kempendyai differs from Shar Teg in the dominance of remains of adults (isolated wings) and scarcity of nymphs among stonefly fossils.

Stonefly fossils are usually rare in oryctocoenoses and, if remains of a species are represented by several specimens, it is very likely that the species is taphonomically autochthonous. In Shar Teg, this is true of three species represented by nymphs, *Sharaperla obliqua, Platyperla mendosa*, and *Trianguliperla optanda*, probably autochthonous lake stoneflies. Nymphs of the first two species have short dilated femora and tibiae adapted for swimming, so that they were probably swimming pelophiles. *Mesoleuctroides derelictus* can be interpreted as an open-living pelophile, but it is represented by only one nymph. Both modes of life are typical of Mesozoic stonefly nymphs that lived on soft silty substrates (Sinitshenkova, 1987).

All stonefly families known from Shar Teg (Siberioperlidae, Platyperlidae, Mesoleuctridae, and Perlariopseidae) and the genus *Trianguliperla* Sinitshenkova, 1985 (Perlomorpha inc. sedis) are widespread in Jurassic deposits of Asia. The general aspect of the stonefly assemblage of Shar Teg is typical Jurassic, without Early Cretaceous elements; the insect-bearing deposits were previously dated as probably Middle Jurassic (Sinitshenkova, 1995), but the characters of some species suggest that the Late Jurassic age of these deposits is also probable.

The abundance and diversity of stoneflies also characterize the insect fauna of Shar Teg as temperate, although it includes not only forms typical of the Jurassic of Siberia, but also *Karanemoura* represented in some localities with hot climates.

2.3. Insects in Ecosystems

2.3.1. Aquatic Insects

The composition of aquatic insects in Shar Teg has a typical Jurassic appearance, with many species of stoneflies (represented not only by adults, but also by nymphs), rather small mayflies of more than one species, abundant beetles of the genus *Memptus*, and small coptoclavid beetles. Only the abundance and diversity of caddisfly cases are more typical of the Lower Cretaceous, but there are some localities of the second half of the Jurassic (e.g., Bakhar in Central Mongolia), where caddisfly cases are rather abundant in some facies. The abundance of corixids is typical of lakes of the Late Jurassic and basal Cretaceous, but the only corixid species recorded in Shar Teg, *Coryphocorixa zhangi* Popoy, sp. nov. occurs in terminal Jurassic localities of eastern and central Mongolia. By contrast, one of tanyderid species recorded in Shar Teg was described from Karatau, a locality of the first half of the Upper Jurassic. All the above strongly suggests that the deposits of Shar Teg should be assigned to the middle part of the Upper Jurassic.

Let us now discuss the biome-related position of the locality. Two climatically distinguished regions existed in the Jurassic in the territory that is now a part of Asia, except Gondwanan India: the warm temperate Siberian region and the Euro-Sinic region, which had a hot seasonally aridized climate. At the end of the Jurassic, the boundary between the two biomes very rapidly shifted northerly from the great bend of the Yellow River deep into Siberia. Freshwater insects are characterized by a great number of species and often dominance of stoneflies in the former region and exceptionally high abundance of corixids, usually of one species, in the latter. The composition of freshwater insects found in Shar Teg is intermediate. They include, on the one hand, many diverse stoneflies and, on the other hand, rather abundant (but not dominant in most assemblages of the locality) corixids Coryphocorixa zhangi Popov, sp. nov. (the absolute dominant in most of the terminal Jurassic localities). In addition to stoneflies, "Siberian" groups apparently include mayflies, liadytid beetles, and beetles of the formal genus *Memptus*; and "Euro–Sinic" groups include corixids, whirligigs, coptoclavids, corydalids, case-building caddisflies, and most of the odonates. This composition gives evidence that Shar Teg represents an ecotone: the locality was formed during the northward shift of the boundary between biomes; comparison of the Shar Teg, Elisatuin, and Ulan Malgait sequences reveals some signs of warming climate.

Regarding the ecology, the aquatic insect assemblage of Shar Teg should probably be considered rather uniform. Fossil remains of the majority of aquatic insects occur in the most fine-grain and thin-layered sediments without traces of bioturbation. These deposits formed during the periods of maximum transgression of the lake and at relatively great depths. The absence of bioturbation of sediments and, hence, the absence of benthic fauna suggests that these sediments were formed under asphyxial conditions. There are no traces of benthic epi- and in-fauna nor transportation of caddisfly cases over the bottom. The fine-grain structure of sediments also gives evidence of the absence of currents sufficiently strong for transportation of insect remains. The gray color of sediments is determined by the protoxide state of iron and presence of unoxidized organic matter, although in minor amounts. Interestingly, fossil insects breathing oxygen dissolved in water (stoneflies, mayflies, caddisflies, and corydalids) are confined to the finest-grain deposits of the profundal zone, while air-breathing insects (corixids, coptoclavids, and hydrophiloids) are considerably more widespread and their remains are occur in coarser shallow-water or nearshore sediments. The distribution of insects breathing oxygen dissolved in water also shows a negative correlation with the distribution of such oxyphilic taxa as ostracodes and bivalves. Certainly, it can also be hypothesized that insect remains have simply not been preserved in the relatively mobile environment, in which oxyphilic sediments accumulated, but some beds of such sediments contain remains of terrestrial insects and almost no caddisfly cases, which would have been preserved even under such conditions. All the above suggests that the majority of aquatic insects, including those that lived on substrate, judging from their morphology, were not benthic. It seems plausible that they lived on floating aggregates of aquatic plants. The frameworks of these aggregates were formed by submerged lycopods of the genus Limnoniobe and liverwort Thallites and colonized by diverse algae. Lycopod macrofossils have not been found, but some caddisfly cases collected in Shar Teg are built of Limnoniobe megaspores. This fact is additional argument against the possibility that most caddisfly larvae of Shar Teg were benthic. It is difficult to imagine a benthic animal of the nearshore zone using the megaspores of a floating plant to build a case that subsequently is transported into the profundal zone. The trophics of the lake was rather low and considerable amounts of organic were not deposited. The insects fed mostly on plant material immediately on liverwort-algal aggregates and organic matter of disintegrated aggregates was consumed by ostracodes under more oxyphilic conditions and by "conchostracans" under less oxyphilic conditions. Amphibiotic leptopodomorph heteropterans (Archegocimicidae) could be predators on floating aggregates. It is possible that cladocerans also participated in processing both planktonic and aggregate organic substances, although cladoceran fossils have not been found. Judging from the relatively low abundance of chaoborids, the main consumers of cladocerans, this trophic mode played a minor role.

The aquatic insects most widespread over the section are corixids; moreover, in shallow-water and nearshore facies, they compose a considerably larger proportion of oryctocoenoses than in other environments. Adult coptoclavids are also rather widespread. Hydrophiloids and caddisfly cases have also been found in nearshore and shallow-water facies (cyclites I–VIII), but they are visibly rarer here and their presence could well be explained by transportation by means of floating algal aggregates.

Not a single odonate larva has been recorded; L.N. Pritykina (pers. comm.) believes that larval Protomyrmeleontidae, which belonged to an early, mostly Paleozoic, group lived on land. Odonate larvae from other families were rather active aquatic predators, moved using their strong caudal fin, and breathed with the rectal gill. Larvae are usually much more abundant than adults in oryctocoenoses of temperate localities, whereas in oryctocoenoses of the hot zone larvae are either rare or absent. Therefore, odonate larvae probably did not live in the lake itself.

2.3.2. Terrestrial Insects

Ecological interpretation of fossils found in Shar Teg is much more difficult for terrestrial insects than for aquatic ones. This is especially true of completely extinct taxa. Thus, we can make more or less certain conclusions about the ecology of Eucinetidae and Scirtidae, two families rather different ecologically: the former is xylobiont, while the latter has aquatic larvae. But what was the ecology of the Mesozoic family Mesocinetidae, which combines the characters of both? The version that the primary mode of life of scirtoids was terrestrial seems more likely than the version that the terrestrial eucinetids evolved from aquatic forms. However, the family Mesocinetidae is the most abundant beetle family in Shar Teg; the number of mesocinetid specimens in the collection is even greater than the number of all aquatic beetles taken together. Furthermore, mesocinetids are represented mostly by more or less complete specimens, while certainly aquatic beetles are mostly represented by fragments, especially isolated elytra. How did mesocinetids reach such high frequencies in oryctocoenoses? The second most abundant beetle family is Lasiosynidae, the ecology of which is also impossible to reconstruct from any reliable data. Based on the fact that lasiosynids belong to Byrrhoidea, Yan et al. (2013) hypothesized that they could have lived on shore plants, like extant Eulichadidae, Ptilodactylidae, and Chelonariidae. Their larvae were probably aquatic, lived in submerged wood, and probably also colonized organic remains accumulating at the water edge, where they fed on rotting plants. It is most likely that adult lasiosynids also fed on plants.

Terrestrial insects are much more diverse in Shar Teg than aquatic insects, as they almost always are. They include all main Mesozoic groups: very rare leafchewing phytophages, abundant and diverse sucking phytophages, diverse and rather abundant xylophiles (mostly associated with rotting wood), detritophages, predators, parasites of insects, and a few anthophiles.

Judging from the composition of primary consumers, phyllophages are almost absent in the locality. Neither leaf beetles nor other known phyllophages have been recorded. Leaves of gymnosperms and ferns only slightly differ from wood in regard to their nutritive value. But consumption of leaves weakens the producing part of ecosystems, while consumption of wood only spurs the cycle of matter and energy. The idea that sauropods fed on leaves and branches of trees, widely disseminated by popular books and films, is based on a simple misconception. The dental system of sauropods is absolutely unfit for processing such food, especially in the required huge amounts. Green parts of leaves were mainly damaged by sucking homopterans. Auchenorrhyncha were especially abundant; Psylloidea were also rather abundant; Aphidoidea and Coccoidea were rare.

Fossil insects that could be identified with certainty as consumers of living wood, such as buprestids, have not been found, but consumers of dead wood and wood partly processed by fungi are rather abundant among fossil insects found in Shar Teg, especially among beetles and dipterans. Among xylophilous beetles, cupedids are rather diverse, although most of them belong to the same genus, *Notocupes*. Such a composition is more typical of Siberian localities. Mordellid-like Heteromera found in Shar Teg could also belong to consumers of relatively weakly decomposed wood. Insects feeding on strongly decomposed wood are considerably more abundant, represented by diverse beetles, dipterans, and cockroaches.

Predators and parasites of invertebrates are rather diverse in Shar Teg. Odonates, aerial predators, have a rather low abundance compared to many other Late Jurassic localities, but their diversity is rather high and different taxa are represented rather evenly. The dominance of protomyrmeleontids is considerably weaker than the dominance of isophlebiids in terminal Jurassic localities of Eastern Asia. Terrestrial predators are represented by rather rare ground beetles and staphylinids. Clerids, which could be xylophilous predators, are especially abundant. Hymenopterans include egg parasitoids and parasitoids of xylophilous insects.

2.4. Vertebrates

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One of the most important advantages of the faunal paleoassemblage of Shar Teg is the extremely broad diversity of tetrapods. Tetrapod fossils are distributed over almost the entire section of this locality; most of them are associated with the lower part, the Shar Teg sequence (Gubin and Sinitza, 1996).

Fish

Lungfishes collected in the "labyrinthodont" bed (cyclites VI and VII, Shar Teg sequence): Gubin and Sinitza, 1996, p. 314) are represented by dental plates of at least three species of the genus *Ceratodus*. *C. sharatensis* Krup. is similar to Chinese *Ceratodus* species from the Middle Jurassic of Sichuan and North American Upper Jurassic *C. felchi* and *C. quentheri*. *C. temporatus* Krup. is closer to *C. guentheri* and *C. frazieri* (Lower Cretaceous, United States), and *C. porrectus* Krup. is similar to *C. gustasoni* from the Cenomanian of North America (Krupina, 1994).



Fig. 56. Amphibian *Gobiops desertus* Shishkin: (a) reconstruction of postorbital cranium, dorsal view; (b, c) specimen PIN, no. 4174/106, left dentale: (b) dorsal and (c) external views (after Shishkin, 1991).

Fossil Palaeoniscomorpha (scales and rare fragments of skeletons) have been recorded in both sequences. In addition, an isolated icthyodorulite of a hybodont shark was found in one outcrop of the Shar Teg Formation at the level of Bed 3. Fish remains have also been collected in gray fine-grained sandstone and siltstone at the base of the Shar Teg Formation section on the northern slope of Mount Ulan Malgait.

Amphibians

Many isolated bones of skulls and postcranial skeletons of brachyopid amphibians described as *Gobiops desertus* Shishkin (Fig. 56) have been collected in cyclites VI and VII of the Shar Teg sequence. According to M.A. Shishkin, *G. desertus*, which reaches 1–1.5 m in length, is characterized by a strongly flattened skull, resembling that of late plagiosaurs and implying benthic mode of life. It is very similar to *Sinobrachyops placenticephalis* from the Middle to Upper Jurassic of



Fig. 57. Turtle *Shartegemys laticentralis* Sukhanov et Narmandakh, PIN, no. 4636, reconstruction of carapace based on one plate and almost complete plastron: (a) dorsal and (b) ventral views. Scale bar, 20 mm (after Sukhanov, 2000).

Sichuan, China, and is the latest known representative of Brachyopidae (Shishkin, 1991; Caroll, 2009).

Turtles

The study of turtles, which occur almost in all beds of the Shar Teg section (Gubin and Sinitza, 1996), is not yet completed; therefore, the list of recorded forms can become considerably longer in the future.

All turtles known from the Shar Teg locality belong to the same family, Xinjiangchelydae, widespread in Middle to Upper Jurassic assemblages of Central Asia, Mongolia, and China (Sukhanov, 2000; Sukhanov and Narmandakh, 2006).

Each stratigraphic member is characterized by its own composition of species and genera of these animals, and the differences between members can be related to differences in ecology. Representatives of *Shartegemys laticentralis* Sukhanov et Narmandakh (Fig. 57) (Sukhanov and Narmandakh, 2006), close to Callovian *Xinjiangchelys latimarginalis* (northern Fergana) and "*Plesiochelys*" *latimarginalis* from the Middle to uppermost Upper Jurassic of Sichuan, have been recorded in the "labyrinthodont" bed (cyclites VI and VII, Shar Teg sequence).

Annemys, represented by two species, A. latiens Sukhanov et Narmandakh and A. levensis Sukhanov et Narmandakh (Fig. 58) (Sukhanov and Narmandakh, 2006), also of the Jurassic habitus, have been recorded in the Ulan Malgait part of the section (448/1–3 and 456/4). Turtles recorded in Shar Teg are morphologically close in some characters to late Macrobaenidae



Fig. 58. Turtle *Annemys latiens* Sukhanov et Narmandakh, holotype Institute of Geology and Mineral Resources, Mongolian Academy of Sciences, carapace: (a) dorsal and (b) ventral views. Scale bar, 20 mm (after Sukhanov, 2000).

(Cretaceous–Paleogene) (Narmandakh, 1991; Sukhanov, 2000).

Crocodiles

Crocodile fossils have only been recorded in the Ulan Malgait part of the section (448/1-3 and 456/4).

Regarding the ecology, crocodiles are clearly divided into two groups. The first includes the aquatic goniopholid *Sunosuchus shartegensis* Efimov, 1988 (Fig. 59), which reached 3 m in length and had a typical ichthyophagous specialization (Efimov, 1988a). Similar forms are known from the Hukou Group (Late Jurassic–Early Cretaceous; Gansu, China), Early Jurassic of Thailand, and Callovian of Kyrgyzstan (Averianov, 2000).

The second group is represented by small longlegged crocodiles of terrestrial ecological adaptation, which probably fed on nearshore mollusks, small fish, and insects, and are included in the family Shartegosuchidae (*Shartegosuchus asperopalatum* Efimov, 1988; Fig. 60), and two species of the genus *Nominosuchus, N. manirinus* Efimov, 1996 (Fig. 61) and



Fig. 59. Crocodile Sunosuchus shartegensis Efimov, holotype, PIN, no. 4174/1, skull, dorsal view. Scale bar, 40 mm.



Fig. 60. Crocodile *Shartegosuchus asperopalatum* Efimov, holotype PIN, no. 4174/2, skull: (a) lateral, (b) dorsal, and (c) ventral views. Scale bar, 10 mm (after Efimov et al., 2000).

N. arcanus Efimov, 2003 (Efimov, 1988b, 1996; Kurzanov et al., 2003). Close to this group are representatives of the genus *Adzhosuchus* (*A. fuscus* Efimov, 2000) (Fig. 62), small forms, with the skull about 40 mm long (Efimov et al., 2000). They are morphologically similar to archaic crocodiles from the Jurassic of the United States and Late Jurassic of Sichuan. Shartegosuchids (*Kyasuchus saevi*) are also known from the Lower Cretaceous of southern Siberia (Efimov and Leshchinsky, 2000). As a result of adaptive radiation of

Protosuchia, accompanied by increasing competitive pressure from other terrestrial predators, shartegosuchids occupied the niches of small predators living near water, partly overlapping the niches of large lizards.

Dinosaurs

Dinosaurs are represented by two groups. The first group includes a theropod (not identified more precisely), represented by only one tooth from the "laby-



Fig. 61. Crocodile *Nominosuchus manirinus* Efimov, holotype PIN, no. 4174/4, skull: (a) dorsal, (b) ventral, and (c) right lateral views. (*Mx*) maxillare, (*V*) vomer, (*Ch*) choana, (*Pal*) palatinum; (*Pt*) pterygoideum (after Efimov, 1996).

rinthodont" bed (cyclite VI of the Shar Teg sequence). The second includes separate sauropod bones collected in the middle and upper parts of the section of the Ulan Malgait sequence (448/1 and 456/4) on the slopes of Mount Shar Teg. Watabe et al. (2004, p. 102) mentioned theropod bones collected in the Ulan Mal-



Fig. 62. Crocodile *Adzhosuchus fuscus* Efimov, holotype PIN, no. 4174/5, incomplete skull with lower jaw, ventral view. Scale bar, 10 mm (after Efimov et al., 2000).

gait sequence, but provided no information about the composition and subsequent fate of those fossils. In the list of collected materials provided by Watabe et al. (2004, p. 111), these fossils are missing. In addition, scattered postcranial elements of large sauropod skeletons were found here in six areas in lenses of finegrained bluish sandstone and siltstone in the lower part of the Ulan Malgait sequence (Gubin and Sinitza, 1996). According to S.M. Kurzanov (pers. comm.), these sauropods could be close to the diplodocid Mamenchisaurus from the Kimmeridgian of Sichuan. In 2002, the Japanese-Mongolian Expedition collected in this part of the section isolated sauropod vertebrae, ribs, pelvic bones, and a large femur; some of these bones could be associated with each other (Watabe et al., 2004). It was noted that the neural spine of the vertebrae were forked and, hence, could be assigned to diplodocids.

Synapsids

According to the report of the Japanese–Mongolian Expedition, the lower and upper jaws of a tritilodontid synapsid, identified as a new species, *Bienotheroides shartegensis* (Fig. 63), were collected above the base of the Ulan Malgait sequence, which overlies the deposits of the Shar Teg sequence (Mount Ulan Malgait), in the lower 100 m of the section (Watabe et al., 2004, p. 102; the part of the section was later specified as the lower 10 m: Watabe et al., 2007). Representatives of the family Tritilodontidae are known from the Late Triassic to Early Cretaceous, and the genus *Bienotheroides* is typical of the Middle to terminal Late Jurassic of Sichuan and Xinjiang, China.



Fig. 63. Synapsid *Bienotheroides shartegensis* Watabe et al., holotype MPS-Nd 10/301, skull: (a) ventral view, (b) schematic drawing (after Watabe et al., 2007, text-fig. 8).

Mammals

One tooth of the mammal *Tegotherium gubini* Tatarinov, 1994, representing the new order Tegotheridia of the superorder Symmetrodonta, was found among bone remains collected in the "thin" fraction of the "labyrinthodont" bed (cyclite VI). According to Tatarinov (1994), *Tegotherium* is related to *Shuotherium dongi* from the Late Jurassic of Sichuan. However, Hopson (1995) disagreed with this, considering *Tegotherium* closer to *Simpsonodon* from the Late Jurassic of Portugal and *Borealestes* from the Middle Jurassic (Bathonian) of Scotland and forming a separate clade of docodontids.

Discussion

It is clear from the data provided above that the age range of vertebrates close to those known from the Shar Teg locality is rather broad, from the Middle Jurassic to Late Cretaceous. However, forms of Late Jurassic relations are clearly dominant in Shar Teg. The similarity of vertebrates of Shar Teg with the fauna of Sichuan is well pronounced. The latest records of dinosaurs in Mongolia (*Mamenchisaurus* sp.) were known from the Dariv locality (western Mongolia), dated as either Middle to Late Jurassic (Sinitsa, 1986)

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or Late Jurassic (Graham et al., 1997). Shar Teg is probably close in age to Dariv and it there is reason to hope that vertebrate assemblages of these localities are also similar in other components.

> 2.5. List of Plants and Animals Recorded in the Shar Teg Locality (precise localization of fossils and numbers of specimens indicated if known)

Plantae Xanthophyta Heterotrichales ?cenobium *Bothryococcus*; nos. 2470/1535, 443/1 Charophyta Charales

Characeae: Jurella abshirica Kyansep-Romashkina, 1974: nos. 425/4a, 446/1, 453/8, 456/4, 467/2; J. ovalis Kyansep-Romashkina, 1974: nos. 425/4a, 446/1, 453/8; J. ferganensis Kyansep-Romashkina, 1974: nos. 453/8, 467/2; J. karierica Kyansep-Romashkina, 1974: no. 446/1

Bryophyta

Hepaticae

Ricciopsis sp.: 423/6, 433/3, 443/1; no. 2470/1535, 443/1

Pteridophyta Lycopsida Selaginella sp.: 460/1, 2, 462 cf. Limnoniobe: no. 2470/1535, 443/1 Sphenopsida *Equisetites* sp.: 423/6, 443/1, 466 Neocalamites ex. gr. pinetoides (Chachl.) Chachlov: 443/1, 452, 459, 460/1, 2 Pteropsida Klukia sp.: 433, 453 Sphenopteris sp.: 423/6, 443/1 Coniopteris atassiensis Sodov: 443/1 Coniopteris ajibogdensis Sodov: 460/1, 2 Coniopteris spp.: 460/1, 2 Cladophlebis nebbensis (Brogn.) Nathorst: 458 Cladophlebis sp.: 458, 460/2 Gingkoales Ginkgo ex. gr. sibirica Heer: 458, 460/1 Czekanowskiales Phoenicopsis ex. gr. angustifolia Heer: 423/6 Czekanowskia ex. gr. rigida Heer: 460/1, 2; C. sp.: 459 Coniferales Pityophyllum nordenskoioldi (Heer) Nathorst: 423/6, 443/1, 458, 459, 460/1, 2 *Pityospermum* sp.: 443/1 Samaropsis sp.: 423/6 Schizolepis sp.: 460/1 Podozamites sp.: 459 *Conites* sp.: no. 460/2 **Bennittitales** Anomozamites sp.: 460/1, 2

Baisia hirsuta Krassilov: 423/6, 433, 443/1, 466 Animalia Mollusca Bivalvia

433/2

454/2

Gastropoda

Crustacea

Conchostraca

Lioestheriidae: *Pseudestheria* sp.: 422/1, 4, 423/1, 2, 4, 6, 9, 425/4, 7 435/1, 439/2, 441/2, 4, 442/1, 3, 443/1, 3, 451/2, 452/2

Lynceidae: *Palaeolynceus* sp.: 423/9, 433/2, 442/1 Ostracoda

Darwinula sarytirmensis Sharapova, *D. oblonga* (Roemer), *D. nimia* Sinitsa: 423/1, 2, 6, 8, 11, 424/4, 6, 425/4, 428 433/3, 441/2, 4, 442/1, 443/1, 3, 451/2 *D.* aff. *leguminella* (Forbes): 454/2 *Lycopterocypris* sp.: 423/6, 428, 441/4, 443/1, 3,

454/2 Mantelliana sp.: 425/4

Insecta

Ephemeroptera

Mesonetidae: *Furvoneta lucida* Sinitshenkova, 2002: nos. 4270/322, 434/2, 295, 297, 298, 326, 327, 351, 355, 363, 366, 367, 372, 379, 380, 443/1; *F. sobria* Sinitshenkova, 2002: nos. 4270/358, 314, 369, 371, 443/1; *Clavineta cantabilis* Sinitshenkova, 1991: nos. 4270/1, 3, 4, 434/2, 441/4, 443/1

Epeoromimidae: *Epeoromimus umbratus* Sinitshenkova, 2002: nos. 4270/353, 443/1, 296, 311, 434/2, 317, 318, 319, 342, 347, 356, 360, 443/1

Hexagenitidae: *Siberiogenites mongolicus* Sinitshenkova, 2002: nos. 4270/373, 443/1, 300, 302, 303, 305, 309, 434/2, 320, 324, 325, 328, 334, 341, 343, 344, 350, 354, 362, 364, 376, 383, 2778, 443/1

Sharephemeridae: *Sharephemera cubitalis* Sinitshenkova, 2002: no. 4270/357, 443/1

Leptophlebiidae: *Clavineta cantabilis* Sinitch., 1991: 423/6, 434/2, 441/4, 443/1.

Fam. gen. sp. imagines: Sinitshenkova, 2002: no. 4270/313, 434/2

Odonata

Meganeurida (=Protodonata + Odonata p.p.) Kennedyina

Protomyrmeleontidae: *Protomyrmeleon* sp. indet.: nos. 4270/863, 864, 866, 868, 423/6; 876, 443/1

Libellulida (=Odonata p.p.)

Libellulina

Libellulina inc. sed.: no. 4270/881, 883, 443/1; 865, 423/6

Heterophlebiina

Heterophlebiidae: *Erichschmidtia* sp. indet.: nos. 4270/862, 867, 423/6

Oreopteridae gen. sp.: no. 4270/879, 443/1

Euthemistidae: *Mongolothemis gobicus* Pritykina et Vassilenko, sp. nov.: no. 4270/873, 443/1

Calopterigina

Hemiphlebiidae: *Enteropia mongolica* Pritykina et Vassilenko, sp. nov.: no. 4270/884, 443/1

Psocoptera

Lophineurida

Lophioneuridae: nos. 4270/1929, 423/6, 1930, 1931, 1932, 1933, 443/1

Hemiptera

Homoptera

Archijassidae: Karajassinae: 423/6, 434/2, 443/1, 451/3 Dellasharinae: *Dellashara tega* Shcherbakov, 2012:

no. 4270/811, 443/1

Palaeontinidae: 434/2, 443/1

Tettigarctidae

Procercopidae: *Sinocercopis* spp.: 423/6, 443/1, 451/3, 452/2, 465/2, 441/4, 443/1, 451/3, 452/2,

465/2 Hylicellidae: 443/1

Liadopsyllidae: 443/1, 2

Protopsyllidiidae: 423/6, 434/2, 443/1, 453/3: *Subaphidulum ponomarenkoi* Klimaszewski, 1995: no. 4270/846, 840, 841, 844, 443/1; *S. gobicum* Klimaszewski, 1995: nos. 4270/843, 839, 443/1

Cicadopsyllidium mongolicum Klimaszewski, 1995: no. 4270/1572, 443/1

Aphidulum bemigdium Klimaszewski, 1995: no. 4270/850, 443/1

Aleyrodoidea: no. 443/2

Palaeoaphidoidea: Juraphididae: *Pterotella shartegensis* Zyla, Blagoderov et Wegierek, 2014: no. 4270/2787, 423/6

Coleorrhyncha

Progonocimicidae: *Onokhoia* sp.: 422/4, 434/2, 443/1

Heteroptera

Nepomorpha

Corixidae: Velocorixinae: *Coryphocorixa zhangi* Popov, sp. nov.: nos. 4270/510, 426, 458, 462, 464, 496, 504, 443/1; in addition, 60 adults and over 100 nymphs: 443/1, 422/4, 423/11, 423/6, 441/4, 442

Naucoridae: *Jurategia laticlavalis* Popov, sp. nov.: nos. 4270/580, 567, 578, 593, 563, 573, 579, 581, 583, 587, 591, 443/1, 557, 582, 423/6; *J. yaoi* Popov, sp. nov.: no. 4270/565, 443/1

Shartegonaucoris weitingae Popov, sp. nov.: nos. 4270/572, 566, 571, 574, 575, 590, 592, 597, 443/1

Gerromorpha

Mesoveliidae: gen. sp., no. 4270/548, 423/6

Veliidae: gen. sp., no. 4270/549b, 423/6

Leptopodomorpha

Archegocimicidae: *Saldonia formosa* Ryzhkova, 2011: no. 4270/553, 443/1

S. insoluta Ryzhkova, 2011: no. 4270/556, 443/1

Shartegocimex rasnitsyni Ryzhkova, 2011: no. 4270/555, 443/1

S. distans Ryzhkova, 2011: no. 4270/552, 443/1

Shartegocorpus paranotalis Ryzhkova, 2011, nos. 4270/554, 443/1

Pentatomomorpha

Pachymeridiidae: gen. sp.

Cimicomorpha

Nabidae: Velocipedinae: gen. sp.: no. 4270/609, 443/1

?Nabidae: gen. sp.: no. 4270/589, 443/1

Vetanthocoridae: no. 4270/600, 443/1

Coreoidea: gen. sp. 1: no. 4270/576, 443/1; gen. sp. 2: no. 4270/622, 443/1

?Miomoptera

Hymenoptera

Xyelidae: Macroxyelinae: Gigantoxyelini: *Shatexyela mongolica* Rasnitsyn, 2008: no. 4270/119, 434/2

Sepulcidae: *Sepulca mongolica* Rasnitsyn, 1993: no. 4270/120, 434/2

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Praeaulacidae: Praeaulacinae: *Praeaulacus patiens* Rasnitsyn, 2008: no. 4270/1545, 441/4; *P. sharteg* Rasnitsyn, 2008: no. 4270/1544, 441/4

Anomapterellinae: *Anomapterella gobi* Rasnitsyn, 2008: no. 4270/1549, 443/1

Megalyridae: Cleistogastrinae: *Cleistogaster gobialtaica* Rasnitsyn, 2008: no. 4270/1548, 443/1; *Mesaulacinus mongolicus* Rasnitsyn, 2008: no. 4270/1547, 443/1

Pelicinidae: Iscopininae: *Praescopinus excellens* Rasnitsyn, 2008: no. 4270/1550, 443/1

Ephialtitidae: *Altephialtites altaicus* Rasnitsyn, 2008: no. 4270/1546, 443/1, 423/6, 441/4, 443/1-2

Apocrita inc. sed.: no. 4270/1551, 443/1

Proctotrupoidea: 443/1

Coleoptera

Archostemata

Cupedidae: *Notocupes brachycephalus* Ponomarenko, 1994: no. 2470/888, 441/4; no. 2470/45, 434/2; no. 2470/891, 443/1; *N. exiguus* Ponomarenko, 1994: no. 2470/892, 443/1

Zygadenia giebeli Ponomarenko, sp. nov.: no. 2470/46, 434/2; *Z. handlirshi* Ponomarenko, sp. nov.: no. 2470/886, 434/2

Anaglyphites crassipygus Ponomarenko, sp. nov.: no. 2470/885, 434/2; A. minutissimus Ponomarenko, sp. nov.: no. 2470/1014, 423/6, 889, 443/1

Asiocoleidae: *Loculitricoleus mongolicus* Ponomarenko, sp. nov.: no. 2470/898, 451/3; *L*. sp.: no. 2470/896, 443/1

Schizophoridae: *Tersus minor* Ponomarenko, sp. nov.: no. 2470/899, 443/1

Sodovia sharotegica Ponomarenko, sp. nov.: no. 2470/95, 434/2

Schizocoleidae gen. spp.: no. 2470/895, 425/4; nos. 2470/896, 897, 930, 935, 1227, 443/1; no. 2470/979, 423/11

Adephaga

Gyrinidae: *Mesogyrus elongatus* Ponomarenko, sp. nov.: no. 2470/47, 434/2

Coptoclavidae: *Coptoclavella jurassica* Ponomarenko, sp. nov.: no. 2470/1007, 443/1

Timarchopsis longus Ponomarenko, sp. nov.: no. 2470/947, 423/6, ?nos. 2470/936, 443/1, 982, 441/4

Coptoclavidae gen. sp.: nos. 2470/74, 80, 434/2, 903, 906, 443/1

Liadytidae: *Liadyties asidytoides*: no. 2470/942, 441/4; nos. 4270/938, 423/6, 945, 451/3

Trachypachidae: Eodromeinae: *Procalosoma incertum* sp. nov.: no. 4270/946, 423/6; no. 4270/981, 423/6

Carabidae: Protorabinae: Protorabinae inc. sed.: no. 4270/949, 441/4

Caraboidea inc. sed.: no. 4270/948, 441/4

Jurodidae: *Jurodes shartegiensis* Yan, sp. nov.: nos. 4270/1010, 1006, 443/2

Polyphaga Hydrophiloidea

Spercheidae: *Prospercheus cristatus* Prokin, 2009: nos. 4270/1012, 442/2, 994, 423/6

Helophoridae

Helophorus (Mesosperchus) inceptivus Fikáček, Prokin, Angus, Ponomarenko, Jue, Ren et Prokop, 2012: nos. 2470/1008, 1009, 443/1, nos. 2470/996, 423/6; *H. (M.) costalis* Ponomarenko sp. nov.: nos. 2470/997, 443/1, 988, 990, 423/6; *H.* spp.: nos. 2470/1003, 1004, 443/1, no. 2470/989, 423/6

Polyphaga incertae sedis propria Hydrophiloidea

Polysitum sharategense sp. nov., no. 2470/1005, 443/1

Hydrobiites mongolicus sp. nov.: nos. 4270/1002, 998, 443/1, 984, 423/6, 996, 424-II/5, 1314, 423/6; *H. minor*: nos. 2470/986, 423, 985, 987, 423/6

Histeridae: 441/4

Hydraenidae: nos. 2470/999, 443/1, 1015, 423/6, 1013, 423/6

Staphylinidae: 443/1

Leiodidae: Leiodinae: *Mesagyrtoides fulvus* Perkovsky 1999: no. 4270/1033, 441/4

Mesocinetidae: *Mesocinetes aequalis* Kirejtshuk et Ponomarenko, 2010: nos. 4270/48, 434/2, 1071, 1078, 1079, 1065, 1066, 1070, 1077, 1084, 1089, 1090, 1092, 1094, 1097, 1099, 1100, 443/1, 1103, 422/2; *M. angustitibialis* Kirejtshuk et Ponomarenko, 2010: no. 4270/1067, 443/1; *M. elumbis* Kirejtshuk et Ponomarenko, 2010: no. 4270/1088, 443/1; *M. subjectus* Kirejtshuk et Ponomarenko, 2010: nos. 4270/1075, 1068, 1074, 443/1

Shartegus transversus Kirejtshuk et Ponomarenko, 2010: nos. 4270/1069, 1086, 1091, 443/1

Parashartegus distinctus Kirejtshuk et Ponomarenko, 2010: no. 4270/1313, 423/6

Manopsis concavicollis Kirejtshuk et Ponomarenko, 2010: no. 4270/1110, 443/1

Manoelodes gratiosus Kirejtshuk et Ponomarenko, 2010: nos. 4270/1082, 1083, 1087, 443/1

Byrridae: nos. 4270/999, 1013 1015, 443/1; 423/6, 441/4, 443/1, 452/2

Lucanidae: *Paralucanus mesozoicus* Nikolaev, 2000: no. 4270/1111, 443/1

Scarabaeidae: 443/1

Lasiosinidae: *Lasiosyne shartegensis* Yan, 2012: nos. 4270/1176, 443/1, 62, 84, 434/2, 1157, 452/2, 1225, 1246, 1279, 443/1; *L. insculpta* Yan, 2012: nos. 4270/1198, 443/1, 52, 57, 62, 65, 68, 434/2, 905, 906, 1119, 1168, 1171, 1172, 1179, 1184, 1189, 1206, 1213, 1215, 1235, 1241, 1256, 1276, 1279, 2787, 443/1, 1149, 443/2, 1156, 452/2, 1161, 423/6; *L. longitarsa* Yan, 2012: no. 4270/1228, 443/1

Elateridae: 423/11, 441/4, 443/1

Cleroidea: nos. 4270/1531, 1535, 443/1, 451/3

Cleridae: ?Tillinae: *Shartegopsis miranda* Kirejt-shuk, 2012, no. 4270/1116, 443/1

Heteromera

nos. 4270/1117, 1122, 443/1

Rhynchophora

Eccoptarthridae: *Gobicar ponomarenkoi* Gratshev et Zherikhin, 1999: no. 4270/1125, 443/1

Polyphaga incertae sedis

Agrilium: 442/2, 443/1

Allognosis: 442/2

Artematopodites maximus Yan, 2010: nos. 4270/1130, 423/11, 1166, 1209, 1195, 1205, 1210, 443/1, 2786, 425/7; *A. crispulus* Yan, 2010: nos. 4270/1194,1222, 443/1, 50, 54, 70, 434/2; *A. lepidus* Yan, 2010: nos. 4270/1143, 1158, 1258, 443/1, 51, 83, 434/2, 422/4, 423/6, 9, 11, 425/2, 425/4b, 434/2, 435/1, 441/4, 442/2, 443/1, 2, 451/3, 452/2; *A. latis-*

simus Ponomarenko, sp. nov.: no. 2470/992, 423/6

Chimaerocoleites: 423/6, 425/4b, 443/2

Platycrossos mongolicus Ponomarenko, sp. nov.: no. 2470/1323, 443/1; *P. latus* Ponomarenko, sp. nov.: no. 2470/1320, 423/6; *P. longus* Ponomarenko, sp. nov.: no. 2470/1331, 423/6; *P. ovum* Ponomarenko, sp. nov.: no. 2470/1321, 423/6; *P. loxonicus* Ponomarenko, sp. nov.: no. 2470/1334, 423/6; 422/4, 434/2, 441/4, 442/2, 451/3

Dzeregia platis Ponomarenko, sp. nov.: no. 2470/1324, 423/6; sp. 1: nos. 4270/992, 993, 1324; sp. 2: nos. 4270/995: 423/6, 424/II-6, 441/4, 442/2, 443/1, 2, 451/3, 452/2

Microcarpoides: 423/6, 442/2

Prostecogmus: 443/1

Strongulites: 441/4, 451/3

Megaloptera

Sialidae: *Sharasialis fusiformis* Ponomarenko: no. 4270/1493, 443/1

Raphidioptera

Gen. spp.: no. 4270/131, 1402, 443/1 Neuroptera

Osmylidae: *Jurakempynus sublimis* Khramov, 2014: no. 4270/1522, 452/2

Sogjuta shartegica Khramov, 2011: no. 4270/5010, 443/1

Osmylidae inc. sed: no. 4270/1513, 443/1

Prohemerobiidae: *Prohemerobius minor* Khramov, 2011: nos. 4270/1509, 1512, 443/1

Grammolingiidae: *Leptolingia shartegica* Khramov, 2010: no. 4270/5001, 443/1

Polystoechotidae: *Frustumopsychops pectinatus* Khramov, gen. et sp. nov.: no. 4270/1503, 441/4

Kalligrammatidae: gen. spp.: nos. 4270/130, 518, 1514, 443/1

Familia incerta: *Dimidiosmylus ramosus* Khramov, gen. et sp. nov.: no. 4270/1494, 443/1

Mecoptera

Orthophlebiidae: *Orthophlebia gubini* Novokshonov et Sukatsheva, 2003: no. 4270/1594, 443/1, and *O. shartegica* Novokshonov et Sukatsheva, 2003:

nos. 4270/1552, 1553, 1578, 1580. 1581, 1583, 1585, 1586, 1590, 1591, 1597, 1601, 1609, 1612, 1615, 1621,1635, 1638, 423/6, 441/4, 443/1,2,

Orthophlebiidae: gen. Spp.: nos. 4270/225, 1582, 1599, 1610, 443/1

Bittacidae: *Scharabittacus mongolicus* Novokshonov, 1993: no. 4270/126, 434/2

Orobittacus minutus Novokshonov, 1993: no. 4270/224, 443/1

Trichoptera

Philopotamidae: *Baga pumila* Sukatsheva, 1992: no. 4270/121, 443/1

Hydrobiosidae: *Bullivena grandis* Novokshonov et Sukatcheva, 1995: no. 4270/123, 443/1

Dysoneuridae: *Oncovena sharategensis* Ivanov et Novokshonov, 1995: no. 4270/1665, 433/1

Trichoptera dominulae

Terrindusia cf. *minuta* Vialov et Sukatsheva, 1976: 422/4, 425/7, 431/1, 452/2

Folindusia digna Sukatsheva, 2000: 425/4c, nos. 4270/1677, 4270/1676, 1678, 1680, 1681, 1683, 425/4, 1686, 1687, 1690, 1691, 11695, 1699, 1703, 1705, 1718, 443/1, 1725, 1727, 1728, 1731, 435/1; F. adumbrata Sukatsheva, 2000: nos. 4270/1685, 443/1, 1698, 1710, 1719, 443/1, 1722, 1724, 1729, 1730, 422/4; F. pilarius Sukatsheva, 2000: nos. 4270/1701, 443/1, 1688, 1689, 1692, 1693, 1694, 1697, 1700, 1706, 1707, 1709, 1713, 1714, 1716, 1717, 2730, 2731, 443/1, 1726, 422/4, 1732, 435/1; F. megasporae Sukatsheva, 2000: nos. 4270/1671, 423/6, 1669, 1670, 1671, 1672, 423/6, 1673, 1674, 1675, 1679, 1682, 425/4c, 1684, 1704, 1712, 1720, 443/1, 1733, 435/1, 1740, 423/6; Folindusia spp.: 422/4, 423/6, 425/4b, 7, 435/1, 441/4, 443/1, 2

Secrindusia expressa Sukatsheva, 2000: no. 4270/1743, 423/11; *Secrindusia* spp.: 423/6, 11, 424/II-5, 425/4b, 443/2

Ostracindusia callida Sukatsheva, 2000: no. 4270/125, 441/3, 1746, 452/2; *Ostracindusia* spp.: 435/1

Conchindusia longaeva Sukatsheva, 2000: nos. 4270/1736, 425/4c, 1735, 1737, 434/2, 1738, 442/1, 1739, 451/3; *Conchindusia* spp.: 425/4b, 434/2, 442/1, 451/3

Lepidoptera

Gen. spp.: nos. 4270/1751, 1756, 423/6, 434/2 Diptera

Limoniidae: *Architipula krzeminskii* Lukashevich, 2009: nos. 4270/ 2100, 2118, 2121, 2293, 443/1, 451/1; *A. ampla* Lukashevich, 2009: nos. 4270/2070, 2098, 2106, 2137, 2149, 423/6, 443/1

Cretolimonia jurassica Lukashevich, 2009: no. 4270/2066, 423/6; *C. pygmaea* Lukashevich, 2009: no. 4270/2476, 423/6

Mesotipula sigmoidea Lukashevich, 2009: nos. 4270/2096, 2490, 423/6, 443/1; ?*M. brevicella* Lukashevich, 2009: no. 4270/2068, 423/6; *M. (Metatipula) continents* Lukashevich, 2009: nos. 4270/2073, 2091, 423/6, 443/1

Tipunia undata Lukashevich, 2009: nos. 4270/2097, 2144, 441/4, 443/1; *T. jorgi* Lukashevich, 2009: nos. 4270/2294, 452/2

Eotipulina sharategica Lukashevich, 2009: nos. 4270/2074, 2083, 2092, 2094, 2108, 2109, 2113, 2117, 2125, 2127, 2142, 2134, 2311, 423/6, 443/1; *E. paula* Lukashevich, 2009: no. 4270/2594, 423/6; *E. evidens* Lukashevich, 2009: no. 4270/2090, 443/1

Eotipuloptera sp.: no. 4270/2099, 443/1

Limoniidae inc. sed.: nos. 4270/160, 161, 162, 228, 2067, 2069, 2072, 2076, 2079, 2085, 2087, 2088, 2093, 2095, 2101, 2103, 2104, 2107, 2110, 2111, 2114, 2115, 2116, 2120, 2123, 2128, 2131, 2133, 2139, 2143, 2146, 2147, 2155, 2180, 2253, 2310, 2425, 2433, 2470, 2480, 2493, 2494, 2495, 2499, 2514, 2516, 2560, 2568, 2729, 423/6, 443/1

Trichoceridae: *?Undaya lenae* Krzeminska et al., 2009: no. 4270/2150, 423/6; *?U. lukashevichae* Krzeminska et al., 2009: no. 4270/2151, 423/6

Zherikhinina alastos Krzeminska et Lukashevich, 2009: nos. 4270/2148, 2152, 2153, 2154, 2156, 2157, 2159, 2160, 2161, 423/6, 442/2, 443/1

Tanyderidae: *Protanyderus vetus* Kalugina, 1992: no. 4270/181, 443/1; *P. senilis* Kalugina, 1992: no. 4270/186, 443/1; *P. nebulosus* Lukashevich et Krzeminski, 2009: nos. 4270/1573, 2141, 434/2, 443/1; ?*Protanyderus* sp.: nos. 4270/230, 237, 443/1

Praemacrochile ansorgei Lukashevich et Krzeminski, 2009: no. 4270/233, 443/1

?Nannotanyderus incertus Lukashevich, 2011: no. 4270/2075, 434/2

Ptychopteridae: *Proptychopterina sharategica* Kalugina, 1992: no. 4270/178, 443/1

Eoptychoptera tempestilla Lukashevich, 1998: no. 4270/2297, 423/6; *Eoptychoptera* spp.: nos. 4270/2071(2468), 2129, 2140, 2298, 2299, 2469, 2471, 423/6, 443/1

Eoptychopterina kaluginae Lukashevich 2004: no. 4270/232, 443/1; *Eoptychopterina* sp.: no. 4270/236, 443/1

Crenoptychoptera liturata Lukashevich, 2011: nos. 4270/235, 2466, 423/6, 443/1

Nedoptychoptera sp.: no. 4270/231, 443/1

Dixidae: *Eucorethrina convexa* Lukashevich, 1996: nos. 4270/2284, 2308, 443/1; *Eucorethrina* sp.: no. 4270/2313, 443/1

Chaoboridae: *Chaoburmus amphilogos* Luka-shevich, 2011: nos. 4270/2320, ?2246, 423/6, 441/4

Mesocorethra cincta Lukashevich, 2011: no. 4270/2309, 443/1

Chaoboridae inc. sed.: nos. 4270/2312, 2349, 434/2, 443/1

Chironomidae: *Cretaenne rasnicyni* Lukashevich et Przhiboro, 2011: nos. 4270/2367, 2379, 2459, 443/1

Podonomius blepharis Lukashevich et Przhiboro, 2011: no. 4270/2357, 443/1; *P. macromastix* Lukashevich et Przhiboro, 2011: no. 4270/2314, 423/6; *?P. robustus* Lukashevich et Przhiboro, 2011: no. 4270/2254, 443/1

Oryctochlus brundini Lukashevich, 2012: no. 4270/2343, 434/2; *O. kaluginae* Lukashevich, 2012: no. 4270/2442, 443/1

Jurochlus trivittatus Lukashevich et Przhiboro, 2012: nos. 4270/2540, 2581, 443/1; *J. limbatus* Lukashevich et Przhiboro, 2012: no. 4270/2584, 443/1; *J. lineatus* Lukashevich et Przhiboro, 2012: nos. 4270/348, 2544, 443/1

Tanypodinae inc. sed.: nos. 4270/2324, 2384, 2431, 423/6, 443/1

Perissommatidae: *Rasnitsynomma additum* Luka-shevich, 2011: no. 4270/2553, 443/1

Palaeoperissomma ornatum Lukashevich, 2011: no. 4270/2278, 443/1

Protorhyphidae: Archirhyphus asiaticus Rohdendorf, 1964: nos. 4270/2168, 2261, 2262, 443/1

Protorhyphus rohdendorfi Lukashevich, 2012: nos. 4270/1600, 2263, 2265, 2166, 423/6, 443/1

Anisopodidae: Mesorhyphus handlirschi Luka-

shevich, 2012: nos. 4270/2165, 2266, 441/4, 443/1; *M. hennigi* Lukashevich, 2012: no. 4270/2171, 443/1

Pachyrhyphus sp. : no. 4270/2515, 443/1

Tega penna Blagoderov et al., 1993: no. 4270/2172, 443/1

Procramptonomyiidae: *Procramptonomyia kovalevi* Lukashevich, 2012: nos. 4270/2164, 2167, 2264, 2268, 2269, 423/6, 441/4, 443/1; *P. ponomarenkoi* Lukashevich, 2012: no. 4270/2267, 443/1

Paraxymyiidae: *Paraxymia mongolica* Blagoderov, 1999: nos. 4270/2173, 2174, 441/4, 443/1

Complecia clara Blagoderov, 1999: no. 4270/2176, 443/1

Archizelmiridae: *Archizelmira kazachstanica* Rohdendorf, 1962: nos. 4270/2242, 2243, 2244, 426/3, 443/1

Archisargidae: *Mesosolva longivena* Mostovski, 1996: no. 4270/2275, 443/1

Sharasargus ruptus Mostovski, 1997: no. 4270/2274, 443/1

Eremochaetidae: no. 4270/2276, 423/6 Identified by V. Blagoderov: Protopleciidae: *Archipleciomima*: 423/6 *Protoligoneura* sp.: no. 4270/2178, 423/6 *Mesoplecia*: no. 4270/2180, 443/1 *Mesopleciella*: no. 4270/2200, 443/1

Earlasiidaa 422/6

Eopleciidae: 423/6

Pleciofungivoridae: no. 423/6, 443/1: *Pleciofungi-vora*: nos. 4270/2181, 2182, 2186, 2187, 2188, 2191,

2192, 2194, 2196, 2198, 2201, 2234, 2235, 2295,

423/6, 434/2, 443/1

Bryanka: no. 4270/2203, 423/1

Ghilaroviana: no. 4270/2183, 423/6

Pleciofungivorella: nos. 4270/2179, 2189, 2199, 2247, 443/1, 443/3 Fungivorites: nos. 4270/2190, 2193, 443/1 Fungivoriplecia: no. 4270/2202, 443/1 Antefungivoridae: 423/6, 443/1: Pleciomima: nos. 4270/2204, 2207, 2209, 2210, 2212, 2214, 2230, 423/6, 435/1, 443/1 Sciaromima: nos. 4270/2206, 2217, 423/6, 443/1 Paralvcoriomima: nos. 4270/2205. 2208. 2219. 2224, 2228, 2236, 423/6, 443/1, 441/1 Lycoriomimodes: nos. 4270/2215, 2226, 2227, 2229, 2232, 443/1 Antiquamedia: nos. 4270/2222, 2225, 443/1 Mesosciophilidae: no. 4270/2195, 443/1 Bolitophilidae: 443/1 Identified by M. Mostovski: Rhagionidae: nos. 4270/2271, 2272, 2273, 2285,

2286, 2287, 2288, 2289, 2290, 2291, 423/6, 443/1, 443/3

Vermileonidae: 443/1

Rhagionempedidae: 443/1

Therevidae: 443/1

Empididae: 423/6, 443/1

Blattodea

Phyloblattoidea

Caloblattinidae: *Sharategoblattina elongata* Vršanský, 2004: nos. 4270/1846, 443/1, 20, 1785, 434/2, 1800, 451/3, 1803, 452/2, 1804, 465/2, 1807, 443/2, 1814, 1818, 1853, 1863, 1865, 1875, 1889, 1907, 1913, 443/1

Polyphagoidea

Liberiblattinidae: *Elismoides mantiformis* Vršanský, 2004: nos. 4270/1828, 1844, 1865, 443/1

Blattulidae: *Blattula mongolica* Vršanský, 2004: nos. 4270/1798, 451/3, 28, 434/2, 1767, 423/6, 1826, 1866, 443/1; *B. vidlickai* Vršanský, 2004: nos. 4270/1897(1919), 443/1, 14, 21. 25, 434/2, 1759, 1763, 1764, 1768, 1769, 1771, 1773, 423/6, 1777, 423/5, 1780, 1782, 1783, 1784, 1786, 1788, 1792, 434/2, 1793, 441/4, 1799, 451/3, 1811, 443/2, 1815, 1816, 1819, 1829, 1834, 1847, 1850, 1854, 1858, 1861, 1871 (1903), 1872, 1873, 1874, 1878, 1881, 1885, 1891, 1893, 1905, 1909, 443/1

Elisama pterostigmata Vršanský, 2004: nos. 4270/1916, 443/1, 10, 16, 22, 24, 26, 434/2, 1758, 1765, 1770, 1774, 1775, 423/6, 1781, 434/2, 1794, 441/4, 1797, 442/2a, 1801, 1802, 451/3, 1828, 1832, 1835, 1841, 1845, 1848, 1851, 1855, 1859, 1875, 1894, 1899, 1920, 441/1

Mesoblattinoidea

Mesoblattinidae: *Breviblattina minor* Vršanský, 2004: nos. 4270/1801, 451/3, 1868, 1906, 1912, 441/3

Mongoloblatta accura Vršanský, 2004: nos. 4270/1849, 441/3, 11, 434/2, 1761, 1766, 423/6, 1796, 434/2, 1806, 465/2, 1827, 1831, 1833, 1838, 1839, 1856, 1857, 1864, 1877, 1898, 1900, 1908, 443/1

Mantodea

Juramantis nitialis Vršanský, 2003: no. 4270/1842, 443/1

Orthoptera

Tuphellidae: *Paracyrtophyllites popovi* Gorochov, 1992: no. 4270/29, 434/2

Aboilidae: 434/2

Elcanidae: 434/2

Protogryllidae: *Aenigmagryllus indistinctus* Gorochov, 1992: no. 4270/212, 443/1; *A. obscurus* Gorochov, 1992: no. 4270/206, 434/2

Baissogryllidae-Sharategiinae: *Sharategia rasnitsyni* Gorochoy, 1992: no. 4270/31, 434/2

Neosharategia paradoxa Gorochov, 1992: no. 4270/210a, 423/6

Baissogryllinae: *Ponomarenkoana probontzagania* Gorochov, 1992: no. 4270/205, 423/6

Storozhenkoana parvispeculum Gorochov, 1992: nos. 4270/217, 443/1, 210b, 423/6

Grylloblattida

Geinitziidae: *Sinosepididontus shartegicus* (Aristov et al., 2009): no. 4270/1939, 451/3

Plecoptera

Siberioperlidae: *Sharaperla obliqua* Sinitshenkova, 1990: nos. 4270/8, 245, 272, 275, 277, 278, 291, 292, 294, 382, 443/1; 2775, 423/6

Platyperlidae: *Platyperla mendosa* Sinitshenkova, 1995: nos. 4270/268, 273, 274, 279, 281, 290, 443/1

Perlomorpha inc. sed.: *Triangulaperla optanda* Sinitshenkova, 1995: nos. 4270/247, 265, 280, 443/1, 2774, 423/6

Bestioperlisca inulta Sinitshenkova, 1990: no. 4270/9, 423/6

Mesoleuctridae: *Mesoleuctroides derelictus* Sinitshenkova, 1995: no. 4270/257, 443/1

Perlariopseidae: *Dicronemoura attenuata* Sinitshenkova, 1995: nos. 4270/283, 286, 443/1

Karanemoura perpropingua Sinitshenkova, 1995: nos. 4270/252, 284, 287, 289, 443/1i

Mongolonemoura inversa Sinitshenkova, 1995: no. 4270/285, 443/1

Prothelytroptera Dermaptera Chelicerata Limulida Aranea Vertebrata Pisces Selachia Hypodontida Dipnoi

Ceratodus sharategensis Krupina, 1994; *C. temporatus* Krupina, 1994; *C. porrectus* Krupina, 1994: 423, 424

Actinopterigia

(423/1, 2, 425/7 441/2, 442/1, 454/2) scales of Palaeoniscomorpha and Pholidophoroidea, coprolites with scales, agglomerate of incompletely digested insects (mostly Corixidae)

Amphibia

Brachyopidae: Gobiops desertus Shishkin, 1991: 423/1

Reptilia

Chelonia

Xinjiangchelidae: *Shartegemis laticentralis* Sukhanov et Narmandakh, 2006: 423, 424

Annemys latiens Sukhanov et Narmandakh, 2006; A. levensis Sukhanov et Narmandakh, 2006: 448, 456

Crocodilia

Gonofolidae: *Sunosuchus shartegensis* Efimov, 1988: 448, 456

Shartegsuchidae: *Shartegsuchus asperopalatum* Efimov, 1988: 448, 456

Nomiosuchus matutinus Efimov, 1988; N. arcanus Efimov, 1988: 448, 456

Dinosauria

Theropoda

Gen. sp.: 423, 424, 448

Sauropoda

Diplodocidae: Mamenchisaurus sp., 448

Synapsida

Tritylodontidae: *Bienotherioides shartegensis* Watabe, 2007: 448

Mammalia

Symmetrodontida vel Docodontida

Tegoteriidae: *Tegotherium gubini* Tatarinov, 1994: 423

3. SYSTEMATIC PALEONTOLOGY

3.1. Odonata

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Odonate fossils are rather scarce in oryctocoenoses of the Shar Teg locality (our collection includes only 24 specimens, less than 1% of all insect fossils). Odonates are represented by wings (mostly fragments, often rather small) or, less often, segments of adult bodies. The fossils are well preserved, but since many of them are fragmentary, reliable identification to genus and species is often impossible. However, the practice of paleodontological studies shows that the most interesting results can be obtained from comparisons at the level of higher-rank taxa. Therefore, even fragmentary material that we have at our disposal

Shar Teg Karatau 6% 2% 39% 38% 55% 12% *Calopterigina* (=*Zygoptera*) *Heterophlebiina* (=*Anisozygoptera*) *Kennedyina* (=*Protozygoptera* + *Archizygoptera*) *Libellulina* (=*Anisoptera*)

Fig. 64. Proportions of specimens of different odonate suborders in the Shar Teg and Karatau localities.

deserves detailed treatment and allows drawing some conclusions.

Specimens representing four of five odonate suborders that existed in the Mesozoic have been recorded in the locality. Two of these specimens are sufficiently well preserved and have enough diagnostic characters for describing new genera and species; seven are only identified to genus; two are identified family; and others are identified to suborder.

Comparison of the Shar Teg odonate assemblage with other Jurassic odonate assemblages reveals some peculiar features. There are two types of Late Jurassic odonate faunas. The first is the isophelbiid type, typical of Siberian and Baikal faunas, reconstructed as showing signs of taxonomic depletion, probably accompanied by simplification of the ecological structure of assemblages. Only representatives of the suborder Heterophlebiina have been recorded in faunas of this type. Although heterophlebiin odonates are also dominant in Shar Teg, it is not quite correct to compare the fauna of Shar Teg with the above-described depleted faunas. The second type of Jurassic odonate faunas is the Karatau type. These faunas are characterized by high diversity of the suborder Heterophlebiina and presence of other suborders in different proportions. The rich odonate assemblage of Solnhofen contains a considerable proportion of the suborder Libellulina and the proportion of Heterophlebiina is considerably lower than in Shar Teg or Karatau, making Solnhofen dissimilar to these two localities. In addition, Solnhofen, in contrast to Shar Teg and Karatau, reflects a specific paleoecological and taphonomical environment of the lagoon type.

The Upper Jurassic Karatau locality in Central Asia is especially similar to Shar Teg in the dominance pattern of odonate suborders. In both localities, the suborder Heterophlebiina is dominant, followed in decreasing order by Kennedyina, Libellulina, and

Calopterigina (Fig. 64). The similarity between the two localities is not restricted to the dominance pattern of higher taxa. A new genus and new species of the family Euthemistidae are described here from Shar Teg; representatives of this family are also known from the Upper Jurassic of Karatau (Pritykina, 1968) and Lower Cretaceous of England (Nel and Jarzembowski, 1996). In addition, the faunas of Shar Teg and Karatau share two genera, Erichschmidtia and Proto*myrmeleon*; the former is only known from these two localities, and the latter also occurs in the Lias of Germany and Wealden Group of England. In general, the suborders Libellulina and Heterophlebiina are more diverse in Karatau than in Shar Teg and the suborder Calopterigina is represented in Karatau and Shar Teg by endemic genera (Auliella and Enteropia, respectively), which could be expected, considering the mode of life typical of this suborder (represented mostly by small ambush predators that are relatively weak and slow fliers).

The system of higher taxa used below was proposed by Pritykina (1989).

Order Meganeurida (=Protodonata + Odonata p. p.)

Suborder Kennedyina (=Protozygoptera + Archizygoptera)

Family Protomyrmeleontidae Handlirsch, 1906

The family Protomyrmeleontidae is a relict group in the Late Jurassic odonate fauna, phylogenetically associated with the Permian Protozygoptera. It comprises highly specialized odonates with a narrow petiole and reduced wing venation. The petiolate wing is considered to be an adaptation for rather slow, but highly maneuverable flight, especially typical of insects living among dense thickets (e.g., extant Calopterygina, Tipuloidea, Bittacidae). The same is probably true of fossil petiolate-winged odonates of the suborder Kennedyina.

Protomyrmeleon sp. indet.

Specimen. PIN, no. 4270/864, basal part of wing.

D e s c r i p t i o n (Fig. 65.1). The wing is narrow, petiolate. Sc is supported by one crossvein; C has a distinct sinuation at this level. The nodal vein is simple, oriented perpendicular to the wing axis, not aligned with the vein in the second space; two antenodal veins (Ax1 and Ax2) are located considerably proximal to the arculus; the postnodal veins in the first and second spaces are not aligned with each other; CuP is weakly zigzagging distally; IR₂ is weakened and strongly zigzagging over its entire length, forming additional branches.

Measurements, mm. Length of fossil, 17; wing width at level of nodus, 3.







Fig. 65. Odonates of the suborder Kennedyina, genus *Protomyrmeleon*: (1) specimen PIN, no. 4270/864, (2) specimen PIN, no. 4270/863, (3) specimen PIN, no. 4270/866, (4) specimen PIN, no. 4270/876.

M a t e r i a l. In addition to specimen PIN, nos. 4270/864, specimens PIN, nos. 4270/863, 866, 868: fragments of apical wing fragments with preserved pterostigmata, characteristic of *Protomyrmeleon* (Figs. 65.2, 65.3); specimen PIN, nos. 4270/876, anterior wing fragment with characteristic nodal and postnodal complexes (Fig. 65.4).

Order Libellulida (=Odonata p.p.)

Suborder Libellulina (=Anisoptera)

Late Jurassic Libellulina faunas of Central Asia and Europe display considerable taxonomic diversity compared to the known depleted Lias assemblages. Among Jurassic assemblages, odonates of this suborder are especially abundant in Solnhofen. The Libellulina fauna of Karatau also shows some similarity to that of Solnhofen (two shared genera and one closely related genus) (Pritykina, 1968).

Three specimens from Shar Teg that cannot be identified more precisely are assigned to the suborder Libellulina: PIN, no. 4270/881, rather small fragment of posterior wing part (containing discernible cell rows of characteristic type, not found in other suborders, Fig. 66.1); PIN, no. 4270/865, medium-sized fragment of median—cubital complex area, with regular rows of cells characteristic of Libellulina (Fig. 66.2); PIN, no. 4270/883, apical fragment of a medium-sized wing (Fig. 66.3). It is visible in the last specimen that the pterostigma is positioned proximally and IR₂ diverges distal to Pt. We do not know such a wing apex structure in known Jurassic Libellulina.

Suborder Heterophlebiina (=Mesozoic Anisozygoptera)

Family Heterophlebiidae Handlirsch, 1906

Representatives of this family are medium-sized dragonflies with moderately narrow, nonpedunculate wings (except the genus *Erichschmidtia*, in which the base of the forewing is pedunculate), and dense venation. The family is known mostly from the Lower Jurassic of Europe and together with other Heterophlebiina constitutes the bulk of the typical Jurassic odonate fauna of Europe.

Erichschmidtia sp. indet.

S p e c i m e n. PIN, no. 4270/862, distal one-third of wing.

Description (Fig. 67.2). The pterostigma is distinct, moderately long, with one short supporting vein; the posterior margin of Pt is weakly convex: veins R_1 and R_2 are closely set behind Pt and slightly diverge more distally; the first space distal to Pt contains two cell rows. Crossveins in the first and second spaces are not aligned with each other; the distal part of the wing, beginning from the level of Pt, is covered with a dense network of crossveins and additional intercalary veins.

M e a s u r e m e n t s, mm. Length of fossil, 14; wing width at level of proximal margin of pterostigma, 5.

M a t e r i a l. In addition to specimen PIN, no. 4270/862, specimen PIN, no. 4270/867, distorted and fragmentary wing without anterior part and with crumpled pterostigmal area (Fig. 67.1). The distal wing part has the same distinctive features as in specimen PIN, no. 4270/862.



Fig. 66. Odonates of the suborder Libellulina: (1) specimen PIN, no. 4270/881, (2) specimen PIN, no. 4270/865, (3) specimen PIN, no. 4270/883.

Family Oreopteridae Pritykina, 1968

The family was described from the Karatau locality (Pritykina, 1968) and originally assigned to the suborder Calopterigina (=Zygoptera), but later transferred to Heterophlebiina (=Anisozygoptera) based on peculiar features of the discoidal area and antenodal complex (Dolin et al., 1980; Ansorge, 1996). Seven genera from Kazakhstan and Central Asia (Pritykina, 1968, Dolin et al., 1980) and one genus from the Lias of Germany have been described in this family. The family is distinguished by the high diversity; at the same time, it is rather strongly specialized. These specifics are probably linked with the trend displayed by many Heterophlebiina towards shifting to habitats hidden from predators among thickets. Under such conditions, a small body size and narrow pedunculate wings prove especially efficient.

We assign to the family Oreopteridae a wing fragment that cannot be identified more precisely, which includes a preserved area of the subdiscoidal cell (specimen PIN, no. 4270/879, Fig. 67.3).

Family Euthemistidae Pritykina, 1968

Odonates of the family Euthemistidae have narrow medium-sized nonpedunculate wings. Euthemistids, like heterophlebiids, probably belong to the ecological group of medium-sized predators hunting at small heights and capable of flights for a moderate distance. The family was described from Karatau, where it is represented by one genus. Another genius was established based on the material from the Lower Cretaceous of England (Nel and Jarzembowski, 1996). The new genus described here is close to *Euthemis* from Karatau and considerably differs from*Proeuthemis* from England.

Genus Mongolothemis gen. nov.

Etymology. From Mongolia and the generic name *Euthemis*.

Type species. Mongolothemis gobicus sp. nov.

Diagnosis. Wings medium-sized; nodus (N) shifted towards wing base; antenodal costal—subcostal complex represented, in addition to two isolated basal veins, by small series (about 20) of nonaligned cross-


Fig. 67. Odonates of the suborder Heterophlebiina, families Heterophlebiidae Handlirsch, 1906 (1, 2) and Oreopteridae Pritykina, 1968 (3): (1, 2) *Erichschmidtia* sp. indet.: (1) specimen PIN, no. 4270/867, (2) specimen PIN, no. 4270/862, (3) Oreopteridae gen. sp. indet., specimen PIN, no. 4270/879.

veins; base of R_3 continuing nodal and subnodal veins; base of IR_3 positioned at middle of distance between N and arc; base of R_{4+5} positioned on boundary between basal one-third of distance between arc and base of IR_3 .

C o m p a r i s o n. The new genus differs from *Euthemis* Pritykina, 1968 in the base of R_{4+5} shifted towards the wing base. It differs from the genus *Proeuthemis* Nel et Jarzembowski, 1996 in the alignment of the base of R_3 with N and sn and in the greater distance between the bases of IR₃ and R_{4+5} . The new genus differs from both previously described genera in the nodus shifted towards the wing base.

Species composition. Type species.

Mongolothemis gobicus sp. nov.

Etymology. From the Gobi Desert.

Holotype. PIN, no. 4270/873, incomplete well-preserved impression of hind wing.

D e s c r i p t i o n (Fig. 68). The number of antenodal veins in both costal and subcostal series is ten in each; the costal—antenodal complex includes two thickened veins in the arculus area. The number of veins between the bases of IR₃ and R_{4+5} is seven to nine. The discoidal space is dilated visibly basally; MA begins to approach CuP at the level of N; the space between R_{4+5} and MA dilates accordingly, and intercalary veins appear in this space.

Measurements, mm. Length of fossil, 26; wing width at level of nodus, 11.

Material. Holotype.

Suborder Calopterigina Selys, 1850 (nom. trans. Pritykina, 1989 (ex Calopterygines Selys, 1850)) (= Zygoptera)

Family Hemiphlebiidae Tillyard, 1926

Representatives of this family probably belong to the ecological group of small ambush predators, weak fliers with a "fluttering" flight. Extant odonates of similar ecology are strongly associated with coastal or semiaquatic vegetation. The family is represented by one monotypic genus in the recent fauna of Australia and two extinct genera (from the Lower Cretaceous of England and Transbaikalia); two genera from the Lower Cretaceous of Brazil are assigned to the superfamily Hemiphlebioidea (Bechly, 1998; Jarzembowski et al, 1998; Vasilenko, 2005).

Genus Enteropia gen. nov.

Et y mology. From the planet Enteropia in *The Star Diaries* by Stanisław Lem.

Type species. Enteropia mongolica sp. nov.



Fig. 68. Odonate Mongolothemis gobicus sp. nov. (Heterophlebiina: Euthemistidae), holotype PIN, no. 4270/873.

D i a g n o s i s. Nodus positioned at base of middle one-third of wing; R_2 with rather sharp bend; IR_2 straight; A_1 weakly zigzagging to level of base of R_{4+5} and zigzagging more distally; supporting vein of pterostigma (br) continuing internal side of Pt; base of IR_2 positioned at level of proximal side of pterostigma; base of R_{4+5} positioned in distal one-third of distance between discoidal cell and nodus; base of R_3 lying slightly proximal to middle of distance between Pt and N.

Comparison. The new genus differs from *Hemiphlebia* and *Mersituria* in the presence of a sharp

bend of R_2 . It differs from *Parahemiphlebia* and *Hemiphlebia* in the zigzagging shape of IR_2 . It differs from *Cretarchistigma* and *Mersituria* in the zigzagging shape of A beginning from the level of the bifurcation of RS.

Species composition. Type species.

Enteropia mongolica sp. nov.

Etymology. From Mongolia.

H o l o t y p e. PIN, no. 4270/884, incomplete hind wing impression.

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Fig. 69. Odonate Enteropia mongolica sp. nov. (Calopterigina: Hemiphlebiidae), holotype PIN, no. 4270/884.

D e s c r i p t i o n (Fig. 69). The base of IR_3 is weakened, not connected to adjacent veins, and probably positioned markedly proximal to sn; IR₃ is straight to the level of the proximal margin of Pt and zigzagging more distally; MA reaches the wing margin at the level of the base of the distal one-third of the distance between N and Pt; the apex of CuP lies in the proximal one-third of the same segment; the apex of A_1 lies slightly distal to the level of N; the bases of crossveins RS are rarely aligned; the number of postnodal veins is six; the number of postsubnodal veins is three; the second wing space is markedly wider than the first; the space between R_2 and R_3 up to the base of IR_2 contains three cells: five cells of irregular shape are present between the apices of MA and CuP; three cells are present between the apices of CuP and A₁; A is connected to the wing margin with a shortened vein diverging from the subdiscoidal cell visibly proximal to its distal margin; the outline of the pterostigma is strongly compressed and thickened; the posterior side of the pterostigma is more convex than the anterior side.

M e a s u r e m e n t s, mm. Length of fossil, 9; wing width at level of nodus, 2.

Material. Holotype.

3.2. Heteroptera

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The overwhelming majority (more than 170 specimens) of adult and nymphal heteropteran specimens collected in Shar Teg are aquatic and amphibious true bugs (Nepomorpha and Gerromorpha) of the families Corixidae, Naucoridae, Veliidae, and Mesoveliidae, absolutely dominated by water boatmen of the family Corixidae (about 98%). This parameter of corixid abundance, especially considering the greater proportion of nymphs (almost twice as great as the proportion of adults) rather obviously demonstrates that corixids were autochthonous; they developed and fossilized in the same lake. Similar abundance of aquatic true bugs is found in the Late Jurassic Karatau locality (southern Kazakhstan), where the overwhelming majority of these insects is represented by a single corixid species, Karataviella brachyptera Becker-Migdisova (Popov, 1968). The Corixidae of Shar Teg belong to the Mesozoic subfamily Velocorixinae, widespread in the Late Jurassic and Early Cretaceous of Siberia, Mongolia, and China (Popov, 1985, 1986, 1988, 1990; Zhang, 1997, 2010; Yao et al. 2004; Yao et al. 2010; etc.). The total absence of the corixid subfamily Diapherininae, abundant in Lower Cretaceous localities of Mongolia (Anda-Khuduk and Shin-Khuduk) and Transbaikalia (Baisa) also supports the conclusion about the Late Jurassic age of Shar Teg deposits. It is surprising that representatives of the typical Late Jurassic genus Karataviella, which is widespread, in addition to the type locality, in Middle Jurassic localities of Siberia (Popov, 1985) and northeastern China (Lin, 1976, 1980; Zhang, 1985, 1986, 2010; Huang et al., 2006), are completely absent in Shar Teg, but this is probably explained by the ecology of these insects.

Corixids live mostly in rather shallow, well-heated standing water bodies with abundant vegetation. The overwhelming majority of species prefer fresh water bodies, but some euryhaline species can live in brackish waters or even in very salty waters of inland water bodies (Scudder, 1976, 1983); I repeatedly observed this in the Gobi part of Mongolia in Sigara (Vermicorixa) lateralis Leach. According to the data on the effects of nonlethal low concentrations of dissolved oxygen in water on the frequency of coming to the surface in Corixidae, the decreased competitive ability and abundance of species at lower concentrations of oxygen can be more important ecologically than lethally low oxygen levels (Macan, 1974: Malcolm, 1980). Therefore, it is not surprising that these insects were abundant and taxonomically diverse in oxygendeficient large lakes of the warm climate zone in the Jurassic, considering also the similarity between Late Jurassic aquatic heteropteran faunas of Mongolia and China. The main data on the biology of extant Corixidae are summarized in monographs devoted to this group (e.g., Hungerford, 1948; Andersen and Weir, 2004; Kanyukova, 2006).

The main direction of biological evolution of corixids was the shift from zoophagy via mixed feeding to mostly phytophagy and facultative zoophagy (Puchkova, 1969). This shift resulted in the emergence of a special filtering apparatus (Parsons, 1966). Cannibalism is also sometimes observed in corixids (Poisson, 1957). The feeding of Corixidae was classified in detail by Popham et al. (1984), who recognized four feeding types: predaceous, detritophagous, phytophagous, and polyphagous; the latter group was considered to dominate the corixid assemblage. Popham et al. (1984) also hypothesized that the predaceous mode of life was initial for corixids. As noted earlier (Jansson and Scudder, 1972), corixids should not be treated as predominantly phytophagous. It was hypothesized that their polyphagy was an adaptation for colonizing temporary water bodies (Bakonyi, 1978). Evolutionary changes in food specialization of corixids during the Mesozoic are outlined in my earlier publications (Popov, 1971, 1986).

Plant mats, widespread in the Late Mesozoic and typical of lakes of that period (Ponomarenko, 1996, 2007, 2010), were an important factor in corixid ecology. Both phytophagous corixids and predaceous saldoid Enicocorinae (or Enicocoridae) of the Late Mesozoic were strongly associated with these mats (Ryzhkova, 2012).

Creeping water bugs (Naucoridae), another abundant group of aquatic heteropterans found in the Shar Teg locality, was also widespread in the Middle and Late Mesozoic of Asia. The abundance of Naucoridae in Shar Teg is relatively low (barely more than 20 specimens, three of which are nymphs); they are represented by three species of the new genera Jurategia gen. nov. and Shartegonaucoris gen. nov. These naucorids are especially similar to those from the Upper Jurassic Karatau locality (Karabastau Formation) of southern Kazakhstan (see Comparison below), characterized by a relatively high generic diversity (three monotypic genera, excluding those remaining undescribed). Late Jurassic naucorids from Shar Teg are similar in the small scutellum, long claval commissure (commissura clavale), and small size to naucorids from the Lower to Middle Jurassic of Eastern Siberia (Irkutsk Basin) (Popov, 1971, 1985). At the same time, abundant Late Mesozoic naucorids recently described from Liaoning Province, northeastern China (Upper Jurassic-Lower Cretaceous, Yixian Formation) (Zhang et al. 2011) are not similar to any other known Jurassic-Cretaceous naucorids.

The relatively scarce amphibious Gerromorpha, which according to the latest data include about 1500 species (Andersen, 1998), are represented in Shar Teg by two extant families: Mesoveliidae (one specimen; Fig. 70.1) and Veliidae (two hemelytra; Fig. 70.2). Mesoveliids, already known from the Mesozoic, are of special interest. They are especially similar to the Late Jurassic mesoveliid Karanabis kiritshenkoi B.-M. (Becker-Migdisova, 1962; Becker-Migdisova and Popov, 1963) from the Karabastau Formation in southern Kazakhstan and to species of the genus Sinovelia described from a Late Mesozoic locality (Upper Jurassic–Lower Cretaceous, Yixian Formation) in the Liaoning Province (Yao et al., 2011). They also show some similarity to Duncanovelia extensa Jell et Duncan (1986) from the Lower Cretaceous (Aptian) of southern Australia (Koonwarra, Victoria). The earliest records of mesoveliids are probably abundant *Engynabis tenuis* Bode from the Lower Jurassic of Lower Saxony, Germany (Bode, 1953), although the assignment of this species to the family Mesoveliidae was doubted by Andersen (1998), who treated it as Gerromorpha inc. sed.

Almost no published data are available on Mesozoic Veliidae; Cretaceous nymphs from Koonwarra assigned to this family are probably early stages of the mesoveliid *Duncanovelia extensa* known from the



Fig. 70. Heteropterans: (1) Mesoveliidae, specimen PIN, no. 4270/548, habitus in lateral view; (2) Veliidae, specimen PIN, no. 4270/549, elytra; (3) Nabidae (Velocipedinae), specimen PIN, no. 4270/609, elytron; (4) Cimicomorpha (? Nabidae s. l.), PIN, no. 4270/589, elytron. Scale bar, 1 mm.

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same period and locality. However, judging from the material collected in Jurassic and Cretaceous deposits, this group of amphibious heteropterans was not so rare in the Mesozoic and awaits description. The only reliably known extinct veliid, *Halovelia electrodominica*, was described from Miocene Dominican amber (Andersen and Poinar, 1998). This veliid should be considered the earliest recorded fossil that doubtlessly belongs to the subfamily Veliinae; it is especially similar in hemelytral venation to the extant subgenus *Plesiovelia*, widespread in the Western Palearctic.

Preliminary analysis of the fauna of aquatic and amphibious Heteroptera of Shar Teg clearly shows the Late Jurassic character of this fauna and specific ecological situation of the locality reflected in these fossils.

The composition of terrestrial heteropterans of Shar Teg is rather peculiar; it has almost nothing in common with Early Cretaceous localities of Siberia, Mongolia, and northeastern China and only some similarity to other Jurassic localities of these territories. The most conspicuous feature of the Shar Teg fauna of terrestrial Heteroptera is almost complete absence (only one hemelytron has been found) of the lygaeoid family Pachymeridiidae, which is rather common in almost all Jurassic or Early Cretaceous localities of Europe and Asia, and of anthocoroid bugs represented by only two impressions of bodies (Fig. 71.1). The two impressions are quite similar to the abundant Late Jurassic anthocoroids of northeastern China, assigned to a separate family, Vetanthocoridae (Yao et al., 2006a). There is also some similarity (strongly elongate preocular part of the head, shape of pronotum, and small scutellum) between these bugs and Hebeicoris luanpingensis Hong (Hong, 1983) from the Middle Jurassic of northeastern China (Jiulongshan Formation, Hebei Province).

Rather scarce, but relatively abundant cimicomorph bugs have been collected in Shar Teg, represented by the peculiar subfamily Velocipedinae of the paraphyletic family Nabidae (s. l.), which is widespread in Jurassic and Early Cretaceous localities of Asia (Eastern Siberia, Kyrgyzstan, Mongolia, and northeastern China), as recently shown (Shcherbakov, 2007). One hemelytron from Shar Teg (Fig. 70.3) is similar in the presence of "dead" cells at the base of the membrane and in the venation pattern of the membrane only to the Early Cretaceous Izinabis kerzhneri Shcherbakov from the Lower Cretaceous Khutel-Khara locality, Mongolia (Shcherbakov, 2007). Two other impressions of incomplete hemelytra are similar in the typical "nabid" membrane venation, which bears numerous short veins in the distal part (Fig. 70.4), to the hemelytra of Medocostinae, another extant subfamily of Nabidae (s. l.). In addition, a well-preserved cimicomorph hemelytron has been found, provisionally assigned to a special new family (Fig. 71.2); the venation of the coriaceous part of this hemelytron is rather similar to that of extant Medocostinae (Nabidae). Moreover, a similar, almost indistinguishable hemelytron, which remains undescribed, is known from the Middle Jurassic Kubekovo locality near Krasnoyarsk, Eastern Siberia.

A significant place in the fauna of terrestrial heteropterans of Shar Teg is occupied by rather scarce, but taxonomically diverse coreoid bugs (eight impressions), represented, according to a preliminary estimate, by four monotypic genera (Figs. 71.3, 71.4). All of them are similar in general morphological characters, especially hemelytral venation, to the genus *Originicorizus* from the Middle Jurassic (Jiulongshan Formation) of Inner Mongolia, China (Yao et al., 2006b).

The composition of the examined heteropterans from the Shar Teg sequence suggests the Late Jurassic age of the assemblage, a conclusion well confirmed by the presence of the Jurassic leptopodomorph family Archegocimicidae. Two new genera and five new species of this family have been described from Shar Teg (Ryzhkova, 2011), the only heteropterans described from this locality to date.

I dedicate this study to my friends and colleagues, the noted Chinese paleoentomologists Zhang Junfeng, Ren Dong, Yao Yunzhi, and Zhang Weiting, who contributed considerably to the study of Mesozoic insects of northern and northeastern China, a fauna similar in many respects to the Late Mesozoic fauna of Mongolia and Siberia.

Infraorder Nepomorpha Popov, 1968 Family Corixidae Leach, 1815

The family Corixidae is the most diverse extant group of aquatic heteropterans (comprising about 40 genera and over 600 species and subspecies), currently globally distributed (Jansson, 1995). Remarkably, of all aquatic heteropterans, corixids are the most similar to terrestrial forms. For instance, they have welldeveloped and functional abdominal scent glands in both nymphs and adults. Primitive New Zealand and Australian corixids of the genus Diaprepocoris Kirk. have preserved the ocelli. In addition, corixids are distinguished from the other families of Heteroptera, both aquatic and terrestrial, in the structure of the abdominal apex; in male and female corixids, it is formed by the eighth segment, split medially into two halves. Corixids are probably especially similar in abdominal structure to the nepomorph family Ochteridae. Corixids are distinguished from all other heteropterans in the structure of the strongly modified forelegs: the one-segmented protarsus is often fused with the tibia and, in males, usually transformed into the pala, equipped with strong setae and small stridulatory denticles used for food filtration, stridulation, and fixation of the female during mating.

In his classical monograph on the classification of this family, Hungerford (1948) divided all extant corixids into six subfamilies: Corixinae, Micronectinae, Diaprepocorinae, Stenocorixinae, Cymatiainae, and Heterocorixinae; this division was subsequently



Fig. 71. Heteropterans: (1) Vetanthocoridae, specimen PIN, no. 4270/600, habitus; (2) Cimicomorpha, specimen PIN, no. 4270/159, elytron; (3) Coreoidea, specimen PIN, no. 4270/576, elytron; (4) Coreoidea, specimen PIN, no. 4270/622, habitus. Scale bar, 1 mm.

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	Coryphocorixa zhangi			Yanliao-	Jiulongsha-	Daohugo-	Haenbea		Bakharia	
	holotype	464	496	corixa chinensis	nocorixa genuine	corixa vulcanica	holotype	2036	holotype	2600
Head (W)	2.1	2.0	2.2	2.2	1.9	1.8	2.3	2.4	3.0	3.0 mm
Head (L)	1.3	1.2	1.2	0.6	0.8	0.6	0.8	0.8	1.0	1.0 mm
Pronotum (W)	2.2	2.1	2.3	2.2	1.9	1.8	2.5	2.7	3.0	3.0 mm
Pronotum (L)	0.8	0.8	0.8	0.8	0.7	0.7	0.8	0.8	1.0	1.0 mm
Scutellum (L)	0.7	0.8	0.8	1.3	0.7	0.8	0.5	0.5	1.5	1.5 mm
Hemelytron (L)	5.4	?	?	5.7	4.7	4.4	5.2	5.3	6.8	6.8 mm
Commissura cl.	1.8	1.8	1.8	1.6	1.7	1.5	1.8	1.8	2.0	2.0 mm
Body (L)	8.5	8.0	8.5	7.8	6.4	6.1	6.6	7.0	10.0	10.0 mm
Body (W)	2.6	2.5	2.6	2.8	2.0	2.1	2.8	3.2	3.6	3.6 mm
Head/Pronotum	1.6	1.5	1.5	0.75	0.87	0.85	1.0	1.0	1.0	1.0
Scutellum/Pronot.	1.0	1.0	1.0	1.6	1.0	1.0	0.6	0.6	1.5	1.4
Commiss./Pronot.	2.5	2.3	2.3	2	2.4	2.1	2.25	2.25	2	2
Commiss./Scutell.	2.5	2.3	2.3	1.23	2.4	1.9	3.6	3.6	1.3	1.4
Body (L/W)	3.2	3.2	3.2	2.78	3.2	2.9	2.3	2.2	2.7	2.7
Pronotum (W/L)	2.75	2.62	2.78	2.75	2.71	2.57	3.1	3.3	3.0	3.0

 Table 3. Measurements (in mm) and ratios of main body parts in species of Mesozoic genera of the subfamily Velocorixinae of Mongolia and China: (W) width and (L) length

universally accepted. However, in my opinion, this classification does not comply with the phylogeny of Corixidae as we know it. Corixids comprise a single family clearly distinguished from other families of aquatic Heteroptera and should be divided into only three extant subfamilies: Diaprepocorinae, Micronectinae, and Corixinae. Each of these subfamilies represents a peculiar direction of adaptation. The subfamily Diaprepocorinae is more plesiomorphic than the other two subfamilies, which is well confirmed by many Mesozoic and Cenozoic fossils. The subfamily Corixinae, in turn, should be divided into three tribes: Cymatiini, Stenocorixini, and Corixini. The subfamily Heterocorixinae and the tribes Glaenocorisini, Graptocorixini, and Agraptocorixini should be included in the tribe Corixini.

Subfamily Velocorixinae Popov, 1986

D i a g n o s i s. Rather small (6-7 mm) to relatively large (9-11 mm) insects, with more or less convex elongate body. Head usually at least twice as wide as long. Pronotum strongly transverse, usually three times as wide as long, leaving scutellum entirely open; pronotum and often also scutellum with longitudinal carinae. Scutellum usually strongly developed, transverse, more than 1.5 times as wide as long. Hemelytra considerably sclerotized, except apically; venation usually weakly pronounced, often indistinct on corium and clavus; embolium rather wide, weakly pronounced; costal fracture also weakly pronounced; claval commissure relatively long. Male genital segments symmetrical.

Composition. The new genus and four other genera (*Velocorixa*, *Cristocorixa*, *Bumbacorixa*, and *Corixalia*) from the Lower Cretaceous of western Mongolia, two genera (*Haenbea* and *Bakharia*) from

the Upper Jurassic of central Mongolia, and three genera (*Yanliaocorixa, Jiulongshanocorixa*, and *Daochugocorixa*) from the Middle–Upper Jurassic of northern and northeastern China. It is possible that some of abundant corixids known from the Lower Cretaceous of southern China, such as *Linicorixa* (Lin, 1980), also belong to this family.

Genus Coryphocorixa Popov, gen. nov.

Et y m o l o g y. From the latinized Greek *coryphe* (head) and the corixid generic name *Corixa* Geoffr.

Type species. C. zhangi sp. nov.

Diagnosis. Medium-sized insects (8-9 mm long). Body strongly elongate, at least three times as long as wide. Head very large, strongly convex, 1.5 times as long as pronotum, slightly more than 1.5 times as wide as long; eyes rather large; eye width also slightly more than 1.5 times as great as distance between eyes in occipital area. Pronotum convex, especially in anterior one-third, forming callous elevation there and short median carina at base, nearly three times as wide as long. Scutellum smooth, medium-sized, nearly as long as pronotum, transverse: 1.7–1.8 times as long as wide. Hemelytra moderately sclerotized; embolium undeveloped; membrane barely pronounced; costal fracture probably absent; claval commissure 2.5 times as long as scutellum. Male genital segments symmetrical.

Species composition. Type species.

C o m p a r i s o n. The new genus is similar in the presence of distinct longitudinal median carina on pronotum to the Late Jurassic genera *Haenbea* and *Bakharia;* it is similar in the ratio of lengths of the claval commissure and pronotum (Table 3) to Haenbea and especially Jiulongshanocorixa from the Middle Jurassic of northeastern China (Jiulongshang Forma-



Fig. 72. Heteropteran *Coryphocorixa zhangi* gen. et sp. nov.: (a) holotype PIN, no. 4270/510, habitus, dorsal view; (b) paratype PIN, no. 4270/504, habitus, lateral view; (c) nymph, paratype, PIN, no. 4270/458), habitus. Scale bar, 1 mm.

tion, Hebei Province). The new genus is distinguished from all genera of the subfamily by the strongly elongate head, which is 1.5 times as long as the pronotum.

Coryphocorixa zhangi Popov, sp. nov.

Etymology. In honor of the noted Chinese paleoentomologist Zhang Junfeng, in recognition of his work on Mesozoic corixids of China.

Holotype. PIN, no. 4270/510, direct impression of almost complete body without preserved legs; Mongolia, Shar Teg locality, section 443/1; Upper Jurassic.

Description (Figs. 72, 73). The same as diagnosis of the genus.

Measurements. See Table 3.

Fifth-instar nymphs (Fig. 72.3). Body length, 5.0– 5.5 mm; body width, 1.8–2.0 mm. The body is elongate oval, more than 2.5 times as long as wide. The head is weakly transverse, at least 1.7 times as wide as long; the eyes are rather large; the eye width is at least 1.7 times as great as the distance between the eyes in the occipital area. The pronotum is strongly transverse, 3.5 times as wide as long; the anterior and posterior margins of the pronotum are almost straight; the lateral margins are slightly convex; the wing cases of the third tergite reach the second abdominal segment. The metanotum measured medially is 1.5 times as long as the mesonotum; the posterior margin is arcuately convex. All three abdominal glands are well developed.

M a t e r i a l. In addition to the holotype, paratypes nos. 4270/426+, 464+(-), 496+(-), 504+(-), and completely preserved nymphs nos. 4270/426+, 458+, and 462+, a total of 60 adult specimens and over 100 nymphs of different instars have been collected in section 443/1. In addition, some specimens come from sections 422/4 (one adult), 423/11 (four nymphs), 423/6 (two adults), 441/4 (one hemelytron), and 442 (five adults and seven nymphs).

Identification key to Jurassic genera of the subfamily Velocorixinae of Mongolia and northeastern China

- 1(2) Head at least 1.5 times as long as pronotum; pronotum basally with distinct median carina; body three times as long as wide......*Coryphocorixa* gen. nov.
- 2(1) Head slightly shorter than, or equal in length to, pronotum; body slightly less than thrice as long as wide.
- 3(6) Pronotum with distinct longitudinal median carinae; head and pronotum equal in length; pronotum at least thrice as wide as long.
- 4(5) Pronotum with one longitudinal carina, at least thrice as long as wide; scutellum very small, slightly



Fig. 73. Heteropteran *Coryphocorixa zhangi* gen. et sp. nov.: (a) holotype PIN, no. 4270/510, habitus, dorsal view, (b) paratype PIN, no. 4270/504, habitus, lateral view, (c) paratype, PIN, no. 4270/458, nymph, habitus. Scale bar, 1 mm.

- 5(4) Pronotum with two longitudinal carinae; scutellum much larger, 1.5 times as long as pronotum; claval commissure considerably shorter, only 1.3– 1.4 times as long as scutellum; body very large (10 mm long)......Bakharia Popov
- 6(3) Pronotum with weakly pronounced longitudinal median carinae; head slightly shorter than pronotum (ratio is 0.75–0.87).
- 7(8) Scutellum 1.5 times as long as pronotum and only slightly shorter than claval commissure (1.2 times as long as scutellum); head relatively short (Table 3)..... Janliaocorixa Zhang
- 8(7) Scutellum equal in length to pronotum and at most half as long as claval commissure; head relatively long (Table 3).

Mongolia (Popov, 1986). Such a great abundance of

naucorids is probably accounted for by the ecological

situation. Unfortunately, the incomplete preservation of the overwhelming majority of naucorid impressions

prevents the determination of their taxonomic posi-

Two new genera, Jurategia and Shartegonaucoris, are described below. Jurategia is very similar to the majority of Mesozoic naucorids (strongly transverse pronotum, long claval commissure, and rather small size) and to Leipolygaeus similis Lin from the Middle Jurassic locality near the village of Pengzhuang, Hanshan Formation, erroneously assigned by the author of the species to the terrestrial family Lygaeidae (Lin, 1985), but actually, judging from the photograph, a naucorid. It should be noted that the same characters are observed in Potamocoridae, the only extant Neotropical plesiomorphic naucoroid family. Jurategia and Shartegonaucoris are especially similar to naucorids from the Upper Jurassic Karatau locality (Karabastau Formation), southern Kazakhstan (see Comparison below), which shows a relatively high generic diversity (three monotypic genera, excluding undescribed forms). Late Jurassic naucorids of Shar Teg are similar in the small scutellum, long claval commissure, and small size to naucorids from the Lower-Middle Jurassic of Eastern Siberia (Irkutsk Basin) (Popov, 1971, 1985). At the same time, abundant Late Mesozoic naucorids recently described for the first time from Liaoning Province, northeastern China (Upper Jurassic-Lower Cretaceous, Yixian Formation) (Zhang et al., 2011) are not similar to previously known Jurassic-Cretaceous naucorids. Because of the mediocre preservation of the material and insufficient quality of drawings, which poorly represent the morphology of these bugs, it is impossible to determine their actual taxonomic position. Their only peculiar feature that can be noted with certainty is the exceptionally large size (14-17 mm), atypical of Jurassic naucorids. The assignment of two paratypes (CNU-HE-LB 2006665 and CNU-HE-LB 2006664) to Naucoridae is also questionable. Their narrow bodies and position of the "raised" hind legs are typical of Notonectidae. Naucorids (Mongonecta indistincta Popov) collected in Lower Cretaceous localities of Myangade are unusually abundant (166 specimens), and Gurvan-Ereni-Nuru (33 specimens), western

Family Naucoridae Fallen, 1814

- 9(10) Claval commissure almost 2.5 times as long as scutellum.....Juilongshanocorixa Zhang
- 10(9) Claval commissure only twice or slightly less than twice as long as scutellum.....

UPPER JURASSIC LAGERSTÄTTE SHAR TEG, SOUTHWESTERN MONGOLIA

......Dauhugocorixa Zhang

Genus Jurategia Popov, gen. nov.

Etymology. From the Jurassic and the Shar Teg locality.

Type species. Jurategia laticlavalis sp. nov.

Diagnosis. Medium-sized insects (6-7 mm long). Body wide, oval, at most 1.5 times as long (without head) as wide. Scutellum small. Pronotum strongly transverse. Hemelytra strongly chitinized, without veins, except for clavus, twice as long as wide; clavus wide, at least thrice as long as wide, with anal vein; claval commissure rather long, at most twice as long as scutellum; costal fracture absent. Large pale spot distinct in basal part of costal margin of hemelytra.

Species composition. J. laticlavalis sp. nov. and J. yaoi sp. nov.

Comparison. The pronotum in *Jurategia* is as strongly transverse as in Aidium and Nectonaucoris from the Late Jurassic of Karatau (southern Kazakhstan) and possibly in Leipolygaeus from the Middle Jurassic of southern China (Anhui Province, Hanshan Formation); the new genus is distinguished from these genera mainly by the small scutellum. The strongly transverse pronotum and small scutellum are also found in the naucorid Miroculus laticephalus from the Late Jurassic to Early Cretaceous (Yixian Formation) of eastern China. Less transverse pronotum and even smaller scutellum, but equally long claval commissure are found in *Ijanecta angarica* (Ijanectinae) from the Early Jurassic of Eastern Siberia (Popov, 1971, 1985).

R e m a r k s. Considering the differences in shape and configuration (sometimes not preserved) of the pronotum and position of the scutellum between specimens assigned to the new genus, it is not improbable that the genus is composite.

Jurategia laticlavalis Popov, sp. nov.

Etymology. From the Latin *latus* (wide) and *clavus* (part of hemelytron).

Holotype. PIN, no. 4270/580, adult, sex unknown, direct body impression; head, pronotum, and legs missing; Mongolia, Shar Teg locality, outcrop 443/1, Upper Jurassic.

Description (Figs. 74.1, 75.1). The body is broadly oval, 1.2 times as long (without head) as wide; the scutellum is 1.7 times as wide as long; the hemelytron is 2.2–2.3 times as long as wide; the claval commissure is 1.7 times as long as the scutellum.

Measurements, mm. Body length (without head and pronotum), 5.5; body width, 4.5; mesoscutum. 2.8: scutellum: length, 0.7: width, 1.2: hemelytron: length, 5.2; width, 2.3; clavus: length, 2.8; width 0.9; claval commissure, 1.4.

Remarks. Judging from the position of the scutellum, the pronotum in J. laticlavalis was probably strongly transverse and shorter than in *I. yaoi*.



Fig. 74. Heteropterans: (1) *Jurategia laticlavalis* gen. et sp. nov., holotype PIN, no. 4270/580, habitus; (2) *Jurategia yaoi* sp. nov., holotype PIN, no. 4270/565, habitus; (3) *Shartegonaucoris weitingae* gen. et sp. nov., holotype PIN, no. 4270/572, habitus. Scale bar, 1 mm.

M a t e r i a l. In addition to the holotype and paratype PIN, no. 4270/582, provisionally identified remains of adult body (no. 4270/557) and hemelytra from section 443/1 and specimens nos. 4270/ 567, 578, and 593, identical to holotype in size and proportions of clavus and corium; remains of nymphs of different instars, nos. 4270/ 563, 573, 579, 581, 583, 587, and 591.

Jurategia yaoi Popov, sp. nov.

Etymology. In honor of the noted Chinese paleoentomologist Yao Yunzhi, who contributed considerably to the study of the Mesozoic entomofauna of China.

Holotype. PIN, no. 4270/565, adult male, direct impression of body; head, pronotum, and legs missing; Shar Teg, outcrop 443/1; Upper Jurassic.

Description (Figs. 74.2, 75.2). The body is elongate oval, 1.5 times as long (without head and pronotum) as wide; the scutellum is 1.57 times as wide as long; the hemelytra are 2.4 times as long as wide; the claval commissure is twice as long as the scutellum; the weakly pronounced and short costal fracture is traceable in the middle of the anterior margin of the hemelytron; the genital segments are shown in Fig. 74.2.

M e a s u r e m e n t s, mm. Body length (without head and pronotum), 7.5; body width, 5.0; scutellum: length, 0.7; width, 1.1; hemelytron: length, 6.0; width, 2.5; clavus: length, 3.0; width, 1.0; claval commissure, 1.4.

C o m p a r i s o n. J. yaoi differs from J. laticlavalis in the larger size and narrower body as well as in the longer claval suture and the slightly narrower elytra, almost 2.5 times as long as wide.

R e m a r k s. Judging from the position of the scutellum, the pronotum in *I. yaoi* was probably strongly transverse and shorter than in *J. laticlavalis*

Material. Holotype.

Genus Shartegonaucoris Popov, gen. nov.

E t y m o l o g y. From the Shar Teg locality and the name of the Recent naucorid genus *Naucoris*.

Type species. *Shartegonaucoris weitingae* sp. nov.



Fig. 75. Heteropterans: (1) *Jurategia laticlavalis* gen. et sp. nov., holotype PIN, no. 4270/580, habitus; (2) *Jurategia yaoi* sp. nov., holotype PIN, no. 4270/565, habitus; (3a, 3b) *Shartegonaucoris weitingae* gen. et sp. nov., holotype PIN, no. 4270/572, (3a) habitus, dorsal view; (3b) habitus, ventral view. Scale bar, 1 mm.

D i a g n o s i s. Body elongate oval, almost twice as long as wide. Pronotum strongly transverse, four times as wide as long, with slightly convex (almost straight) lateral margins and straight posterior margin. Scutellum very large, elongate, almost twice as long as wide. Hemelytra strongly chitinized, without veins; clavus more or less wide, four times as long as wide; costal fracture absent; rather large pale spots clearly pronounced; membrane weakly pronounced. Tibiae and tarsi densely covered with swimming setae. Species composition. Type species.

C o m p a r i s o n. The genus *Shartegonaucoris* strongly differs from *Jurategia* in the very large scutellum, almost twice as long as the pronotum and almost equal in length to the claval commissure, in the spotted elytra, and in the small body size. It is especially similar to the Jurassic genus *Aidium* (in the strongly transverse pronotum and very large scutellum) from the Late Jurassic of Karatau (southern Kazakhstan) and differs from it in the narrower body (slightly more than half as long) and the smaller body size.

Shartegonaucoris weitingae Popov, sp. nov.

Etymology. In honor of the noted Chinese paleoentomologist Zhang Weiting, who has considerably contributed to the study of the Mesozoic heteropteran fauna of China over the last few decades.

Holotype. PIN, no. 4270/572, adult, sex unknown; part and counterpart; head missing; Mon-golia, Shar Teg, outcrop 443/1; Upper Jurassic.

Description (Figs. 74.3, 75.3a, 75.3b). Pale spots are especially clearly pronounced in the basal and distal parts of the corium. The metatibia is almost 1.5 times as long as the metafemur; the two-segmented tarsi are almost equal in length to the tibiae; the tarsomeres are subequal in length.

M e a s u r e m e n t s, mm. Body length (without head), 4.8; body width, 2.5; pronotum: length, 0.5; width, 2.0; scutellum: length, 0.7; width, ? 1.8; heme-lytron: length, 4.0; clavus: length, 2.0; width, 0.5; claval commissure, 0.8; hind leg length: femur, 0.9; tibia, 1.3; tarsus, 1.5 (0.8 + 0.7).

M a t e r i a l. In addition to holotype, remains of nymphs of different instars PIN, nos. 4270/566. 571, 574, 575, 590, 592, and 597 from outcrop 443/1.

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3.3. Coleoptera

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ARCHOSTEMATA

S u p e r f a m i l y Cupedoidea Laporte, 1836

Family Cupedidae Laporte, 1836

Cupedids are treated here as one family, without recognizing Ommatidae as a separate family, because the presence of extinct Notocupedini and Mesocupedini makes the hiatus between Cupedidae and Ommatidae too small to consider these taxa as separate families. Cupedids are rather scarce in Shar Teg (11 specimens) and none of fossils are sufficiently complete. The specimens treated below are assigned to this family based on the characteristic cellular structure of elytra and tuberculate integument. Representatives of the genus *Notocupes* are dominant, as usual in Mesozoic localities. The second genus, *Anaglyphites*, is among dominants only in the Karatau locality.

Subfamily Ommatinae Sharp et Muir, 1912

Tr i b e Notocupedini Ponomarenko, 1966

Genus Notocupes Ponomarenko, 1964

Notocupes brachycephalus Ponomarenko, 1994

Notocupes brachicephalus: Ponomarenko, 1994, p. 87.

The species was described from the Jurassic Bakhar locality, central Mongolia, Bakhar sequence. Two incomplete specimens from the Shar Teg locality were tentatively assigned to this species in the original description: dismembered beetle (PIN, no. 2470/888 from outcrop 441, Bed 4) and isolated elytron (PIN, no. 2470/45 from outcrop 434, Bed 2). PIN, nos. 2470/891, an incomplete elytron, possibly also belongs to this species. Since the first of the abovelisted specimens seems quite different from the holotype, it is described below (Figs. 26.1a, 26.1b).

Two incomplete elytra, abdomen, two incomplete legs, and crumpled wing with almost indiscernible venation are present. In the left elytron, the lateral spaces, crushed during the shrinkage of the sediment, are not visible, so that the elytron looks very narrow. In the right elytron, the apical portion is missing, but the lateral spaces and rather wide epipleural rim, which bears cells, are partly preserved, so that it is seen that the elytron is rather wide, only three times as long as wide. Tubercles on elytral veins are not visible. The abdomen is narrowed beginning from the base of the fourth visible ventrite; the anterior part of each ventrite is narrow, sharply raised; punctation on the raised and remaining parts of the ventrite is quite similar, rather coarse.

M e a s u r e m e n t s, mm. Body length, about 9.5; elytron length, 6.5; length of abdomen, about 3.

Notocupes exiguus Ponomarenko, 1994

Notocupes exiguus: Ponomarenko, 1994, p. 88.

The species was described from the Jurassic Bakhar locality, central Mongolia, Bakhar sequence. PIN, no. 2470/892, an isolated elytron from outcrop 443, Bed 1 (Fig. 26.2), lacks substantial differences from the elytra of this species.

Measurements, mm. Elytron length, 3.1; width, 1.4.

Genus Zygadenia Handlirsch, 1906

The genus was introduced by Handlirsch for Curculionites tuberculatus Giebel, 1856 from the Lower Purbeck of southern England and originally was not assigned to any suprageneric taxon. Ponomarenko (2000), describing cupedids from the Semen locality in eastern Transbaikalia, synonymized Zygadenia with *Notocupes* based on the similarity in elytron structure and, subsequently (Ponomarenko, 2006), having examined the holotype, demonstrated that the genus Zygadenia belonged to the family Cupedidae and synonymized with this genus several genera described either from more or less complete specimens or from isolated elytra. Those synonymies seemed reasonable then, because only one rather justified genus (Notocupes) had been described from the Jurassic or Cretaceous and it had the same elvtron structure as Zygadenia. However, to date, the genus Amblomma Tan, Ren et Liu, 2005 has been described from the Lower Cretaceous of China and has not been synonymized with Notocupes, although it also has a similar elytron structure. Therefore, it is reasonable to use the name Zygadenia only as a formal taxon for isolated elvtra that cannot be assigned to any species of a natural genus. The genus Zygadenia is known from the Middle Triassic to Early Paleocene, whereas Notocupes is only known from the Carnian to Turonian.

Zygadenia giebeli Ponomarenko, sp. nov.

Etymology. In honor of C. Giebel, who described the first species of the genus.

H o l o t y p e. PIN, no. 2470/46, direct impression of right elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 434, Bed 2.

Description (Fig. 26.3). Elytron of a rather large beetle. The elytron base is not preserved; the sides are parallel from the base to the preapical quarter. The apex is symmetrical, pointed; the "tail" is absent. The main veins are slightly zigzagging, rather similar to intermediate veins. The epipleural rim is rather narrow; the cells of the rim are hardly discernible; spines or indentations in the anterior part of the elytron are absent. The cells are large, longitudinally oval; each row contains about 20 cells.

M e a s u r e m e n t s, mm. Body length, about 18; elytron length, 12; width, 3.4.

C o m p a r i s o n. The new species is especially similar in size and shape of the elytron and type of cells to *Zygadenia tuberculata* (Giebel, 1856) from the Lower Cretaceous of England and differs from it in the narrower epipleural rim and less prominent, somewhat zigzagging main veins.

Material. Holotype.

Zygadenia handlirschi Ponomarenko, sp. nov.

Etymology. In honor of A. Handlirsch, who described the genus.

H o l o t y p e. PIN, no. 2470/886, direct impression of left elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 434, Bed 2.

D e s c r i p t i o n (Fig. 26.4). Elytron of a mediumsized beetle. The elytron base is straight; the sides are parallel from the base to the preapical quarter. The apex is symmetrical, pointed, weakly protruding as a short "tail." The main veins are rather similar to intermediate veins. The epipleural rim is broad, preapically dilated, with two cell rows throughout its extent; spines or indentation in the anterior part of the elytron are absent. The cells are large, longitudinally oval; each row contains about 25 cells.

M e a s u r e m e n t s, mm. Body length, about 13; elytron length, 9.5; width, 3.0

C o m p a r i s o n. The new species is similar in size and shape of the elytron and broad preapically dilated epipleural rim to the elytron of *Amblomma porrecta* Tan, Ren et Shih, 2006 from the Upper Jurassic to Lower Cretaceous of China and differs from it in the elytron apex protruding as a "tail" and in the distinctly more elongate cells.

Material. Holotype.

Subfamily Cupedinae Laporte, 1836

Tribe Mesocupedini Ponomarenko, 1969

Genus Anaglyphites Ponomarenko, 1964

A small beetle without head, prothorax, and legs, assigned to this genus based on the size, wide body, short metaventrite, broad metepimere, flat abdominal ventrites with raised sutures between them, abundant small cells of the elytra, and short, wide, and rounded apical abdominal segment. It is similar to *Liassocupes parvus* Zeuner, 1962 from the Lower Jurassic of England and differs from it in the shape of the apical abdominal ventrite, which is subtriangular and longer in *Liassocupes*. Another, very small beetle is also assigned to this genus based on the same characters as in the above-discussed specimen. Many important characters of this beetle are indiscernible because of its size.

Anaglyphites crassipygus Ponomarenko, sp. nov.

E t y m o l o g y. From the Latin *crassus* (thick) and the latinized Greek *pyge* (rump).

H o l o t y p e. PIN, no. 2470/885, beetle without head, prothorax, and legs; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 424, Bed 2.

Description (Fig. 27.1). A rather small beetle with a wide flattened body, weakly narrowing posteriad. The mesoventrite is rather long and has a longitudinal suture. The mesepimera are oblique, only slightly laterally dilated. The mesocoxae are large, rounded. The metaventrite is almost thrice as wide at the posterior margin as long. The metepimeron is wide, approximately half as wide anteriorly as long. The abdomen is barely longer than the mesothorax and metathorax taken together, narrowed from the base of the preapical ventrite; the preapical ventrite is somewhat shorter than the apical ventrite; the apical ventrite is almost thrice as wide basally as long.

M e a s u r e m e n t s, mm. Estimated body length, about 5; elytron length, 3.3; width, 1.9.

C o m p a r i s o n. The new species is more similar in the shape and size of the body to relatively large representatives of the genus, while in the size and in the short apical abdominal ventrite, which is only slightly longer than the preapical ventrite, it is especially close to *A. paulus* Ponomarenko, 1964. It differs from all congeners in the rounded apical ventrite.

Material. Holotype.

Anaglyphites minutissimus Ponomarenko, sp. nov.

Etymology. From the Latin *minutissimus* (smallest).

H o l o t y p e. PIN, no. 2470/1014, beetle without most of antennae and legs; Shar Teg; Upper Jurassic, Shar Teg sequence, section 423/6.

Description (Fig. 27.2). Small beetle with a flattened body weakly narrowing posteriad. The head is slightly shorter than wide at the base, widest near the weakly protruding eyes, and more strongly narrowing anteriad than posteriad. A necklike constriction is absent. The antennae are attached in front of the eyes; the basal half of the antenna is filiform; the proximal antennomeres are slightly thickened. The pronotum is 1.5 times as wide as the head and 1.5 times as wide as long; the sides of the pronotum are rounded; the anterior margin is slightly wider than the posterior margin. The elytra at the shoulders are wider by one-third than the pronotum base. The mesoventrite is rather long. The mesocoxae are rather small, rounded. The metaventrite is 1.5 times as wide at the posterior margin as long. The metepimeron is narrow, approximately half as wide anteriorly as long. The abdomen is markedly longer than the mesothorax and metathorax taken together, narrowed from the base of the preapical ventrite; the apical ventrite is 1.5 times as long as the preapical ventrite; the apical ventrite is 2.5 times as wide basally as long. The elytron is rather wide, weakly narrowed from the base almost to the apex; the elytron base is oblique; the sutural margin is almost straight; the external margin is weakly convex. The two elytral veins closest to the suture join near the apex. The cells are small; each row contains about 30 cells.

M e a s u r e m e n t s, mm. Body length, about 1.9; elytron length, 1.2; width, 0.4.

C o m p a r i s o n. The new species is the smallest representative of the genus and the whole family. It is especially similar in body shape and size to *A. paulus* Ponomarenko, 1964, which is twice as large. The new species is distinguished from all congeners by the wide and rounded apical ventrite. It is also distinguished by

the longer head, the pronotum less strongly narrowed posteriad, and the longer metaventrite.

Material. In addition to the holotype, PIN, no. 2470/889, an isolated elytron.

S u p e r f a m i l y Asiocoleoidea Rohdendorf, 1961

Family Asiocoleidae Rohdendorf, 1961

The family was originally introduced for a monotypic Permian genus. Several other genera were subsequently described in this family; as a result, the hiatus between this family and the Late Triassic family Tricoleidae Ponomarenko, 1969 became incomparable to the differences between other related families and it was proposed to treat the family Tricoleidae Ponomarenko, 1969 as a junior synonym of the family Asiocoleidae Rohdendorf, 1961. Until recently, all taxa of this family were described based exclusively on isolated elvtra. The genus *Loculitricoleus Tan*, Huang et Ren, 2009 was described from the famous Jurassic Daohugou locality, China. The genus was originally established to include two species, probably synonymous, and was assigned to the family Tricoleidae. As a result, the family Asiocoleidae currently includes one more or less natural genus (Loculitricoleus) and up to ten formal genera described based on isolated elytra.

One of the isolated elytra collected in Shar Teg proved to belong to a beetle of this family. It is quite similar in the position of veins and cells to the elytron of *Loculitricoleus* and can be assigned to this genus. At the same time, the structure of this elytron complies with the diagnosis of the formal genus *Tetracoleus* Ponomarenko, 2009, species of which are distributed from the Middle Permian to Middle Triassic. Description of a new species in this genus would have considerably broadened the time range of its distribution; therefore, it is preferred to describe it in the genus *Loculitricoleus*.

Genus Loculitricoleus Tan et Ren, 2009

Loculitricoleus mongolicus Ponomarenko, sp. nov.

H o l o t y p e. PIN, no. 2470/898, part and counterpart of left elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 443, Bed 1.

Description (Fig. 28). The elytron is rather broad, 3.5 times as long as wide; the apex is shifted towards the sutural margin; the sutural margin is weakly convex, rimmed. Each row contains over 40 cells; the cells are rounded. All main veins are free. The external space and adjacent space contain three cell rows each; the next space is strongly dilated basally and contains up to seven cell rows basally, six cell rows medially, and four cell rows distally; the sutural space contains four cell rows and weakly dilates basally. The elytral cells do hot form regular transverse rows.

M e a s u r e m e n t s, mm. Estimated body length, about 6; elytron length, over 4; elytron width, 1.3.

C o m p a r i s o n. The new species differs from the elytra of *Loculitricoleus tenuatus* Tan et Ren, 2009 and *L. flatus* Tan et Ren, 2009 in the smaller number of cell rows in the two external spaces; it differs from the elytra described in the formal genus *Tetracoleus* Ponomarenko, 2009 as follows: from *T. borealis* Ponomarenko, 2009, in the smaller number of cell rows in two external spaces; from *T. sennikovi* Ponomarenko, 2011 and *T. orenburgensis* Ponomarenko, 2012 in the greater number of cell rows in the sutural space; from *T. meyeni* Ponomarenko, 2012, in the smaller number of cell rows in the second space from the external margin; from *T. tricoleoides* Ponomarenko, 2012, in the smaller number of cell rows in the second space from the sutural margin.

M a t e r i a l. In addition to the holotype, paratype PIN, no. 2470/896.

S u p e r f a m i l y Schizophoroidea Ponomarenko, 1968

Family Schizophoridae Ponomarenko, 1968

Representatives of the family Schizophoridae are rather scarce in Shar Teg (ten specimens), and none of them are more or less completely preserved; most of the specimens are isolated elytra; only two are incomplete bodies of beetles. One of these beetles can be assigned to the widespread Late Mesozoic genus Tersus based on the characteristic punctation of the metaventrite; the other is described below in a new genus. Judging from the size, shape, and structure, these isolated elvtra belonged to beetles of five or six species. They could represent species of the natural genera Tersus Martynov, 1926, Tersoides Ponomarenko, 1969, Vago Hong, 1982, Menopraesagus Tan, Ren et Shih, 2007, or Homocatabrycus Tan, Ren et Shih, 2007. Genera of the family Schizophoridae usually cannot be distinguished by the elytral structure; the differences in the structure of elytra, which depend on preservation, are usually greater than differences between taxa. Many isolated elvtra of this type were described as natural taxa, but these taxa are usually impossible to identify in new material. The family Schizocoleidae was described for such isolated elytra and it was proposed to use it as formal. However, a huge amount of work is needed to revise the composition of this family and establish a formal system.

Genus Tersus Martynov, 1926

The beetle is assigned to this genus based on the characteristic punctation of the metaventrite, transverse suture shifted anteriad along the median line on the metaventrite, and wide pronotum, not narrower at the base than the elytra at the shoulders.

Tersus minor Ponomarenko, sp. nov.

Etymology. From the Latin *minor* (smaller).

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H o l o t y p e. PIN, no. 2470/899, part and counterpart of beetle without most of legs; the tucked head makes it impossible to examine its details or details of the prosternum; the beetle was positioned obliquely in the burial, so that the right and left halves of the impression are asymmetrical; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 443, Bed 1.

Description (Fig. 29.1). Rather small, oval, flattened beetle. The pronotum is large; the base of the pronotum is not narrower than the elytra at the shoulders; the pronotum is narrowed weakly anteriad, half as long as wide. The mesoventrite is short, with two large notches anteriorly. The mesocoxae are large, rounded, their diameter is only slightly smaller than the distance between them and the posterior margin of the mesoventrite. The metepisternum is rather wide. dilating in the anterior quarter to twice as wide as more posteriorly. The metaventrite is short; lateral to the coxae, it is less than half as long as wide at the posterior margin. The paracoxal suture is shifted strongly anteriad. The surface of the metaventrite is densely covered with large punctures fused into transverse impressions behind the mesocoxae. The metacoxae are slightly oblique, short, much wider than long. The abdomen is approximately equal in length to the thorax, narrowed from the base of the third ventrite. The base of the abdomen is 1.5 times as wide as the base of the apical ventrite; the apical ventrite is twice as long as the preapical ventrite. The elytron is moderately narrow, three times as long as wide, the elytron base is oblique; the external margin is convex; the greatest width is behind the middle: the sutural margin is almost straight; the apex is shifted towards the sutural margin. The mesofemur is weakly thickened; the metafemur is visibly thickened; the tibiae are linear, slightly curved.

M e a s u r e m e n t s, mm. Estimated body length, about 6; elytron length, 4.5; elytron width, 1.5.

C o m p a r i s o n. The new species is the smallest species of the genus. It is especially similar in the oval body and sculpture of the metaventrite to *Tersus* (*Vago*) oblongus (Hong, 1982) and differs from it in the smaller size, larger and more widely set mesocoxae, shorter metaventrite, and the abdomen narrowed less strongly posteriad.

R e m a r k s. None of available isolated elytra fit beetles of this genus.

Material. Holotype.

Genus Sodovia Ponomarenko, gen. nov.

Type species. S. sharotegica sp. nov., by monotypy.

Diagnosis. Medium-sized beetle, rather narrow, flattened. Mesocoxae almost contiguous. Metepisternum dilated strongly anteriad. Sutures of metaventrite smoothed out. Apical abdominal ventrite wide and short, not longer than preapical ventrite. Elytron narrow; impression on lateral margin of elytron opposite "schiza" absent. Composition. Type species.

C o m p a r i s o n. The new genus differs from all genera of the family in the wide and short apical abdominal ventrite and in the nearly contiguous mesocoxae; it differs from the majority of Jurassic to Lower Cretaceous genera in the absence of a depression or notch in the lateral margin of the elytron. It is especially similar in the elytral structure to *Malmelater priscus* (Oppenheim, 1888) from the Upper Jurassic of Solnhofen.

Sodovia sharotegica Ponomarenko, sp. nov.

Etymology. From the Shar Teg locality.

Holotype. PIN, no. 2470/95, beetle without head, prothorax, and legs; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 441, Bed 4.

Description (Fig. 29.2). The body is wide, narrowed weakly posteriad. The mesoventrite is rather short. The scutellum is trapezoid, narrowed posteriad. The mesocoxae are large, rounded, slightly longer than wide. The metaventrite is half as long and half as wide at the anterior margin as wide at the posterior margin. The metepimeron is wide, approximately 1.5 as long as wide anteriorly. The metaventrite is roundly narrowed anteriad, half as wide at the anterior margin and half as long as wide at the posterior margin. The metaventrite punctation is fine. A row of densely set punctures, which are much larger than the punctures on the remaining part of the body, extends along the poorly visible transverse suture on the metaventrite. The metacoxae are shortened strongly laterally, less than twice as wide as long along the medial body line. The abdomen is 1.7 times as long as the mesothorax and metathorax taken together and narrowed from the base of the third ventrite; the preapical ventrite is slightly longer than the apical ventrite, which is three times as wide at the base as long; the abdominal apex is rounded. The elytron is narrow, 3.4 times as long as wide; the elytron base is rounded, slightly oblique; the margins of the elytron in the basal two-thirds are almost straight, then narrowing towards the symmetrical apex.

M e a s u r e m e n t s, mm. Estimated body length, about 10; elytron length, 8.5; width, 2.5.

R e m a r k s. None of available isolated elytra fit beetles of this species.

Material. Holotype.

ADEPHAGA

Superfamily Gyrinoidea Latreille, 1810

Family Gyrinidae Latreille, 1810

Genus Mesogyrus Ponomarenko, 1973

Isolated Mesozoic elytra with characteristic loops of elytral grooves are described in the genus *Mesogyrus*, although it cannot be proved with certainty that they actually belong to beetles of this genus. The genus is known from the Jurassic and basal horizons of the Lower Cretaceous.

Mesogyrus elongates Ponomarenko, sp. nov.

Etymology. From the Latin *elongatus* (elon-gate).

H o l o t y p e. PIN, no. 2470/47, direct impression of elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 434, Bed 2.

Description (Fig. 30). Rather small, convex, elongate elytron, narrowed slightly posteriad.

M e a s u r e m e n t s, mm. Estimated body length, about 9; elytron length, about 6; length of preserved part, 5.5; elytron width, 2.3.

C o m p a r i s o n. The new species is especially similar in shape and size of the elytron to *M antiquus* Ponomarenko, 1973 from the Upper Jurassic of Karatau and differs from it in the very weak posteriad narrowing. The elytron of the new species is the narrowest of all species of this genus and much larger than the elytron of other known Jurassic representative of the genus, *M. sibiricus* Ponomarenko, 1985 from the Abasheva Formation of the Kuznetsk Basin. By contrast, Early Cretaceous members of the genus are larger than the new species.

Material. Holotype.

S u p e r f a m i l y Dytiscoidea Leach, 1815 Family Coptoclavidae Ponomarenko, 1961 Subfamily Coptoclaviscinae Soriano, Ponomarenko et Delclos, 2007 Genus *Coptoclavella* Ponomarenko, 1980

The beetle described below is assigned to the family Coptoclavidae based on the eyes completely divided into the upper and lower halves, to the subfamily Coptopclaviscinae, based on the nonswimming legs, and to the genus *Coptoclavella*, based on the transverse head. The genus is known from the basal Cretaceous of Mongolia and England and from the Barremian of Spain.

Coptoclavella jurassica Ponomarenko, sp. nov.

Etymology. From the Jurassic Period.

Holotype. PIN, no. 2470/1007, counter impression of beetle without most part of legs; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 443, Bed 1.

Description (Fig. 31.1). Rather small, elongate, flattened beetle. The head is transverse, 1.5 times as wide at the base as long, widest near the strongly protruding upper eyes, narrowed anteriad more strongly than posteriad. The genae are short; the temples are slightly shorter than the eyes. The labrum is protruding, rounded. The lower eyes are approximately of the same size as the upper eyes, rounded, located at the head margin. The antennae are short, filiform, attached anterior to the eyes. The head is 1.3 times as wide as the pronotum and equal in width to the pronotum; the pronotum is 2.2 times as wide as long; the sides of the pronotum are rounded; the anterior margin is roundly notched, narrower by one-third than the posterior margin. The elytra at the shoulders are slightly wider than the pronotum base. The mesoventrite is short. The mesocoxae are large, rounded, widely set. The scutellum is semicircular. The metaventrite is short; the distance between the mesocoxae and paracoxal suture is slightly greater than the diameter of the coxae. The longitudinal suture is distinct. The metepisternum does not reach the mesocoxae. The metacoxae are transverse; the femoral plate of the metacoxae is small, reaching the middle of the metacoxae. The metacoxa, including the femoral plate, is half as long as wide. The elytron is rather narrow, thrice as long as wide, narrowed behind the middle, with oblique base; the external margin is convex, and the sutural margin is almost straight. The disc of the elytron has fine grooves; no punctures are visible in these grooves; the sutural grooves are curved along the sutural margin towards the external margin. The legs are short. The mesofemur and metafemur are weakly and evenly thickened; the tibiae and tarsi are linear.

M e a s u r e m e n t s, mm. Body length, about 7.0; width, 3.0; elytron length, 5.0.

C o m p a r i s o n. The new species is similar in the grooved elytra and short metacoxae to small femoral plates to *C. striata* Ponomarenko, 1986 from the basal Cretaceous of western Mongolia and differs from it in the anteriorly notched pronotum and in the large and widely set mesocoxae.

Material. Holotype.

Subfamily Timarchopsinae Wang, Ponomarenko et Zhang, 2009 Genus *Timarchopsis* Brauer, Redtenbacher

et Ganglbauer, 1889

Timarchopsis longus Ponomarenko, sp. nov.

Et y m o l o g y. From the Latin *longus* (long).

H o l o t y p e. PIN, no. 2470/947, part and counterpart of beetle without head and prothorax; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

D e s c r i p t i o n (Fig. 31.2). Medium-sided, elongate, flattened beetle. The mesothorax is rather long; the scutellum is rounded. The mesepimera are rather narrow, slightly dilated anteriad, oriented almost longitudinally. The mesocoxae are large, rounded. The metaventrite is short; the distance between the mesocoxae and paracoxal suture is at most as great as the diameter of the mesocoxae. The longitudinal suture is distinct. The anterior metaventral process is triangular. The metepisternum is weakly dilated anteriad, not reaching the mesocoxae. The metacoxae are long, slightly oblique; the femoral plates of the metacoxae are large, almost reaching the lateral margins of the coxae. The metacoxa, including the femoral plate, is only slightly wider than long. The abdomen is narrowed from the base of the fourth ventrite. The suture between the second and third ventrites is complete. The first three ventrites are subequal in length; two succeeding ventrites are slightly shorter; the preapical ventrite is 2.5 times as long as the apical ventrite. The junctions between ventrites are mobile; the ventrites strongly overlap. The base width of the apical ventrite is only slightly smaller than the base width of the preapical ventrite. The elytron is smooth.

M e a s u r e m e n t s, mm. Estimated body length, about 15; width, 5; elytron length, 10.

C o m p a r i s o n. The new species is similar in the body shape to *T. latus* (Ponomarenko, 1977) from the Jurassic of Central Asia (Sagul locality) and differs from it in the femoral plates without lateral notches; it is similar in the shape of the femoral plates to *T. sainshandensis* Ponomarenko, 1977 from the Jurassic of eastern Mongolia and differs from it in the elongate body and much larger mesocoxae.

M a t e r i a l. Holotype. This species may also be represented by incomplete isolated elytra (PIN, nos. 2470/936 and 2470/982). The elytra are smooth, with a weakly convex sutural margin and the apex shifted towards the sutural margin, i.e., the beetle was flattened. The estimated elytron length is about 10 mm; the width is about 4 mm.

In addition to the above-described specimens, fragmentary fossils that belong to one or two larger coptoclavid species have been collected in Shar Teg. These include an isolated elytron (PIN, no. 2470/74), smooth, with an almost straight sutural margin and the apex shifted towards the sutural margin; two-thirds of the external margin are also almost straight; more distally, the elytron roundly narrows; the elytron is 13.9 mm long and about 4.2 mm wide. Two abdominal fragments (PIN, nos. 2470/80 and 2470/903) are typical in structure of Adephaga and belong to a wider beetle, about 10 mm wide and estimated as about 20 mm long; only the basal parts of the abdomen are preserved; the suture between the second and third ventrites is less distinct than the suture between the first and second ventrites.

S u p e r f a m i l y Caraboidea Latreille, 1802

The ground beetle specimens collected in Shar Teg are rather few and all of them are fragmentary. Specimen PIN, no. 4270/946 is the posterior one-third of a rather large beetle. Judging from the shape of the femoral plates and position of the coxae, the beetle probably belongs to Trachypachydae–Eodromeinae, although this cannot be strictly proved. Another indirect evidence of this assignment is the fact that the beetle has elytra without punctate grooves, while all large Carabidae–Protorabinae have elytra with punctate grooves. If the assignment is correct, the beetle should belong to the group of the largest Mesozoic ground beetles, which had relatively short flattened bodies, long legs, protruding non-falcate mandibles with short teeth, elytra without punctate grooves, and coarse granulate sculpture of the integument (*Procalosoma, Evertus, Karatoma*, and *Dundorabus*). The beetle in question differs from all the above-listed genera, except *Procalosoma* and *Evertus notatus* Ponomarenko, 1986, in the wide and blunt apical abdominal ventrite and differs from *E. notatus* in the shape of the femoral plates of the metacoxae. Therefore, the specimen is assigned to the genus *Procalosoma*.

PIN, no. 4270/949, an isolated elytron, has characteristic punctate grooves and almost certainly belongs to the family Carabidae and subfamily Protorabinae, since it is the only subfamily of Carabidae known in the Jurassic. PIN, no. 4270/948, a leg, apparently belongs to a small ground beetle.

Family Trachypachydae Leconte, 1861 Subfamily Eodromeinae Ponomarenko, 1977

Genus ?Procalosoma Handlirsch, 1906

Procalosoma: Handlirsch, 1906, p. 548; Ponomarenko, 1985, pp. 137, 140, 141.

Type species. *Procalosoma minor* Handlirsch, 1906 from the Tithonian of Solnhofen, Germany, by monotypy.

D i a g n o s i s. Large flattened beetle. Head long, narrowed anteriad; antennae extending beyond prothorax base. Metaventrite wide; abdomen short. Femoral plate of metacoxa large, subquadrate, approximately as long as wide. Elytra with irregular rows of tubercles, without punctate grooves. Legs long; femora protruding far beyond body outline; tibiae slender, almost not dilated apically.

Species composition. Type species and possibly the new species described below.

C o m p a r i s o n. The new genus is distinguished by the slender tibiae and the wide subquadrate femoral plates of the metacoxae.

Procalosoma incertum Ponomarenko, sp. nov.

Etymology. From the Latin *incertus* (uncertain).

H o l o t y p e. PIN, no. 2470/946, counter impression of hind legs and abdomen; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423/6

D e s c r i p t i o n (Fig. 33.1). The body is flattened; the abdomen is short and wide, narrowed from the base. The metacoxa, including the femoral plate, is half as long as wide; the femoral plate is wider than long. The suture between the second and third abdominal ventrites is complete, but very weakly pronounced. The first three ventrites are subequal in length; the last three ventrites are shorter by one-third than the first three. The base of the apical ventrite is narrower than the preapical ventrite base by only onethird. The metatrochanter is large; the metafemur is only 2.5 times as long as the metatrochanter. The femur is dilated preapically. The tibia is slender, almost slightly apically dilated, and slightly shorter than the femur. The tibia is thrice as long as the first metatar-somere. The ventrites are densely punctate.

M e a s u r e m e n t s, mm. Estimated body length, about 13; width, 7; abdomen length, 5.7.

C o m p a r i s o n. The new species is distinguished by the wider femoral plates, the tibia shorter than the femur, and the wider and shorter apical abdominal ventrite.

M a t e r i a l. Holotype. A somewhat larger isolated elytron (PIN, no. 4270/981: Fig. 33.2) may also belong to this species. The elytron has an albescent spot extending along the external margin; such spots are sometimes found in beetles of this group; the elytron was probably weakly sclerotized in this area. The elytron surface has many, about 20, rows of small punctures; wider intervals divide the rows into several groups. The elytron is 11 mm long and 4.3 mm wide.

POLYPHAGA

S u p e r f a m i l y Hydrophiloidea Latreille, 1802

Family Helophoridae Leach, 1815

Genus Helophorus Fabricius, 1775

Subgenus Mesosperchus Ponomarenko, 1977

Helophorus costalis Ponomarenko, sp. nov.

Etymology. From the Latin *costalis* (ribbed).

Holotype. PIN, no. 2470/997, beetle without head and legs; only dorsum preserved; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 443, Bed 1.

Description (Fig. 36.2). Small beetle with a convex body narrowed anteriad. The pronotum is twice as wide as long; the sides of the pronotum are almost straight; the anterior margin is not notched; the posterior margin is 1.7 times as wide as the anterior margin. The disc of the pronotum has three longitudinal grooves and short diagonal longitudinal depressions diverging from the base of the median groove towards the lateral grooves. The entire pronotum surface is covered with large rounded dense granules and smaller sparse granules between them. The posterior margin of the pronotum is crenate. The elytra are only slightly wider at the shoulders than the pronotum base. The elytron has ten deep finely punctate grooves and lacks a scutellar row; it is rather narrow, evenly narrowing in the apical one-third; the elytron base is straight; the apex is shifted slightly towards the suture. All intervals of the elytra are raised, and covered with large granules, similar to that of the pronotum and barely varying in size. The epipleural rim is narrow. Isolated elytra are strongly convex, narrowing almost from the base. Six sutural grooves reach the external margin of the elytron in the apical one-third.

M e a s u r e m e n t s, mm. Body length, about 3.0; elytron length, 1.8-2.0; width, 0.6.

C o m p a r i s o n. The new species is assigned to the genus *Helophorus* based on the granulate pronotum with longitudinal grooves. It differs from known representatives of the Mesozoic subgenera *Mesohelophorus* and *Mesosperchus* in the presence of additional diagonal depressions, in the absence of the scutellar row of punctures, and in the raised granulate intervals of the elytra. In contrast to representatives of the subgenus *Mesohelophorus*, the granules of *H. costalis* probably lack setae, because punctures marking the attachment sites of such setae are indiscernible in the apical parts of the granules (however, this difference could have resulted from differences in fossilization).

M a t e r i a l. In addition to the holotype, isolated elytra (PIN, nos. 2470/988, 990) from outcrop 423/6. Considerably larger elytra of similar structure have also been collected in Shar Teg, 2.8–2.9 mm long and even more convex: PIN, nos. 2470/1003, 1004 from outcrop 443/1 and PIN, no. 2470/989 from outcrop 423/6. Perhaps, they belong to a different, closely related species.

Polyphaga incertae sedis

Genus Polysitum Dunstan, 1924

The genus was originally described as natural from the Upper Triassic of Australia and later treated as formal for beetles from the Middle Jurassic of Siberia (Ponomarenko, 1983) and basal Cretaceous of Mongolia (Ponomarenko, 1986). The new species described below is assigned to this genus based on the body structure typical of Mesozoic hydrophiloids and smooth elytra (the polysitum morphotype).

Polysitum sharategense Ponomarenko, sp. nov.

Etymology. From the Shar Teg locality.

H o l o t y p e. PIN, no. 2470/1005, beetle without head, pronotum, and legs; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 443, Bed 1.

Description (Fig. 37.1). Small beetle with a flattened body, narrowed weakly posteriad. The elytron is smooth, rather narrow, twice as long as wide, evenly narrowed almost from the base; the base is straight; the apex is symmetrical. The epipleural rim is absent. The mesoventrite is short; the mesepimeron is rectangular. The mesocoxae are large, rounded, contiguous. The metaventrite is half as long as wide at the posterior margin; the posterior margin of the metaventrite is 1.5 times as wide as the anterior margin. The metepimeron is wide, only slightly wider anteriorly than posteriorly. The abdomen is slightly longer than the mesothorax and metathorax taken together, narrowed from the base of the third ventrite; the apical ventrite is half as wide as the abdominal base, 1.5 times as long as the preapical ventrite, and 2.5 times as wide at the base as long.

M e a s u r e m e n t s, mm. Body length, about 3.5; elytron length, 2.7; width, 0.9.

C o m p a r i s o n. The new species differs from *P. punctatum* Dunstan, 1924 in the larger mesocoxae, the elytron narrowed almost from the base, the wide metepisternum, and the longer apical abdominal ventrite; it differs from *P. elongatum* Ponomarenko, 1983 in the wider body, larger mesocoxae, the elytron narrowed almost from the base, and the wider and longer apical abdominal ventrite; it differs from *P. rugosum* Ponomarenko, 1986 and *P. hosbayari* Ponomarenko, 1986 in the larger mesocoxae and in the metepisternum dilated weakly anteriad.

Material. Holotype.

Genus Hydrobiites Heer, 1865

Hydrobiites: Heer, 1865, pp. 91, 95; Handlirsch, 1906, p. 456; Ponomarenko, 1985, p. 64; 1990, p. 50; Ponomarenko, 2011, p. 415.

The genus was described as a formal taxon for isolated elytra with either punctate or impunctate grooves or with regular puncture rows. The grooves of the sutural part of the elytron curve along a rather strongly convex sutural margin, run almost parallel, without converging, and reach the external margin of the elytron near the apex.

Among extant beetles, such elytra are found in the genus *Hydrobia* (Hydrophilidae). Isolated elytra of this structure appeared in the terminal Permian (Vyazniki, Babii Kamen', and other localities). Most Mesozoic hydrophiloids, including those described from Shar Teg, have elytra of this type. Isolated elytra that could not belong to beetles of described species because of their structure (rather shallow poorly visible grooves) and size are described below as new species.

Hydrobiites mongolicus Ponomarenko, sp. nov.

Etymology. From Mongolia.

Holotype. PIN, no. 2470/1002, isolated left elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 443, Bed 1.

Description (Figs. 37.2a-37.2d). The elytron is weakly convex, rather narrow, 2.6 times as long as wide; the base is straight; the external margin is roundly curved towards the sutural margin in the apical one-third and meets it almost at a right angle; the apex is asymmetrical, shifted towards the sutural margin; the sutural margin is almost straight basally and weakly curved towards the external margin behind the middle. The epipleural rim is narrow. The elvtral grooves are narrow and rather shallow; the punctures in these grooves are rather large; the distances between the punctures are wider than the punctures; the spaces between the grooves are flat. In some spaces, usually in the basal part of the elytron, isolated punctures are visible. The sutural margin is sometimes bordered by a dense row of small punctures. The grooves run towards the apical part of the external margin of the elytron independently and almost parallel; only the external groove can curve along the external margin of the elytron near the apex. The scutellar groove is absent.

M e a s u r e m e n t s, mm. Elytron length, 3.0-4.3 (holotype 4.04); width, 1.5.

C o m p a r i s o n. The new species is similar in size and rather shallow grooves to *H. bellus* (Geinitz, 1884) and differs from it in the asymmetrical apex of the elytron and the larger and more distinct punctures.

M a t e r i a l. Holotype and paratypes PIN, nos. 2470/984 (outcrop 423/6), 996 (outcrop 424-II/5), 998 (outcrop 443/1), 1314 (outcrop 423/6).

Hydrobiites minor Ponomarenko, sp. nov.

Etymology. From the Latin *minor* (smaller).

Holotype. PIN, no. 2470/986, isolated left elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

Description (Figs. 37.2e, 37.2f). The elytron is weakly convex, rather narrow, 2.6 times as long as wide; the elytron base is convex; the apex is almost symmetrical, blunt; the external margin is weakly roundly dilated towards the middle of the elytron and curved towards the sutural margin more distally; the sutural margin is almost straight at the base, curved towards the external margin behind the middle. The epipleural rim is narrow. The elytral grooves are narrow and rather shallow, almost indiscernible; the punctures in the grooves are rather large; the distances between punctures are wider than the punctures; the spaces between the grooves are flat. In some spaces, isolated punctures are visible. The grooves are weakly undulate; they run towards the apical part of the external margin of the elytron independently and almost parallel; only the external groove can curve along the external margin of the elvtron near the apex. The scutellar groove is present, long.

Measurements, mm. Elytron length, 2.0; width, 1.8.

C o m p a r i s o n. The new species is similar to the above-described species and differs from it in the smaller size and symmetrical apex of the elytron.

Material. Holotype and paratypes PIN, nos. 2470/985, 987 (outcrop 423/6).

Coleoptera incertae sedis

Form family Permosynidae Tillyard, 1924

Formgenus Dzeregia Ponomarenko, 1985

D i a g n o s i s. Second groove from sutural margin shortened, ending blindly behind middle of elytron.

C o m p a r i s o n. The formgenus is similar to *Permosyne* Tillyard, 1924, but in the type species of *Permosyne*, the shortened groove ends on the sutural groove.

Dzeregia platis Ponomarenko, sp. nov.

Etymology. From the Greek *platys* (wide, broad).

H o l o t y p e. PIN, no. 2470/1324, isolated right elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

Description (Fig. 76.1). The elytron is weakly convex, rather wide, 2.1–2.2 times as long as wide; the base is convex; the apex is almost symmetrical, blunt; the external margin protrudes roundly towards the middle of the elytron and curves towards the sutural margin more distally; the sutural margin roundly protrudes towards the middle of the elytron and curves towards the external margin behind the middle. The epipleural rim is narrow. The elvtral grooves are narrow and rather shallow, almost indiscernible; the punctures in the grooves are rather large; the distances between punctures are much wider than the punctures; the spaces between the grooves are flat. In some spaces, isolated punctures are visible. The sutural groove is curved along the sutural margin, reaching the apical quarter; the next groove reaches the middle of the elytron; the next three grooves almost reach the apex, running along the sutural margin; the external groove curves along the external margin and reaches the apical quarter. The scutellar groove is absent.

M e a s u r e m e n t s, mm. Elytron length, 5.2-5.7 (holotype 5.7); width, 2.5-2.7 (holotype 2.7).

C o m p a r i s o n. The new species is similar in the shape and size of the elytron to *D. lata* Ponomarenko, 1985 and differs from it in the slightly larger size and in the shortened groove not passing into the apical half of the elytron.

Material. Holotype and paratype PIN, no. 2470/993 (outcrop 423/6).

Formgenus Artematopodites Ponomarenko, 1990

The elytra are more frequently medium-sized and large, relatively narrow, and convex, or, less frequently, small and wider. The disc has from eight to ten punctate grooves; the second and third grooves from the sutural margin are shortened, blindly ending behind the middle of the elytron.

C o m p a r i s o n. The formgenus is similar to the genus *Permosyne* Tillyard, 1924, but in the type species of *Permosyne*, the shortened groove ends at the sutural groove. The elytra of the formgenus *Artematopodites* could belong mostly to beetles of the family Lasiosynidae.

Artematopodites latissimus Ponomarenko, sp. nov.

Etymology. From the Latin *latissimus* (widest, broadest).

Holotype. PIN, no. 2470/992, isolated left elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

Description (Fig. 76.2). The elytron is wide, 2.5 times as long as wide, flattened, weakly convex; the



Fig. 76. Beetles Polyphaga inc. sed.: (1a, 1b) *Dzeregia platis* Ponomarenko, sp. nov., holotype PIN, no. 2470/1324, photograph and habitus; (2a, 2b) *Artematopodites latissimus* Ponomarenko, sp. nov., holotype PIN, no. 2470/992, photograph and habitus.

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base is convex; the apex is almost symmetrical, blunt; the external margin is mostly almost straight, curved in the distal quarter towards the apex and truncated almost straightly; the sutural margin is almost straight in the basal half of the elytron and roundly protruding in the apical one-third. The epipleural rim is narrow. The elytral grooves are narrow and rather shallow, almost indiscernible: the punctures in the grooves are very small, inconspicuous; the distances between them are much wider than punctures; the spaces between the grooves are flat. The sutural groove curves along the sutural margin, reaching the apical quarter; the groove anterior to it extends slightly farther than the middle of the elytron; the third groove from the sutural margin is slightly longer than it; the next three grooves closely approach the apex running along the sutural margin; the external groove curves slightly along the external margin and reaches the apical quarter. The scutellar groove is absent.

Measurements, mm. Elytron length, 5.2; width, 2.1.

C o m p a r i s o n. The widest and one of the smallest species of the genus, distinguished by the markedly narrowed sutural groove. It differs from elytra of the family Lasiosynidae and from isolated elytra that could be associated with beetles of this family.

Material. Holotype.

Formgenus Platycrossos Dunstan, 1924

Diagnosis. Elytra medium-sized or small, wide, and convex. Disc with six to eight punctate grooves or few puncture rows. Epipleural rim very broad, usually more than twice as wide as intervals between grooves.

C o m p a r i s o n. The genus is distinguished by the very broad epipleural rim.

Platycrossos mongolicus Ponomarenko, sp. nov.

Etymology. From Mongolia.

H o l o t y p e. PIN, no. 2470/1323, isolated right elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

D e s c r i p t i o n (Fig. 77.1). The elytron is convex, rather wide, widest in the basal quarter and almost symmetrically narrowed more distally, 1.8 times as long as wide; the elytron base is straight; the apex is shifted towards the external margin, blunt; the sutural margin is almost straight in the basal half of the elytron and roundly protruding in the apical one-third. The epipleural rim is twice as wide as the intervals between

the grooves, weakly narrowed posteriad, separated from the disc by a deep groove. The elytral disc has eight grooves; the grooves are narrow and rather shallow, almost indiscernible; the punctures in the grooves are fine, inconspicuous; the distances between the punctures are much wider than punctures; the spaces between the grooves are flat. The sutural groove curves along the sutural margin, reaching the apical quarter. The basal internal corner of the elytron, which usually contains the scutellar groove, is occupied by a short, strongly cut oblique groove without punctures, followed by a short row of punctures identical to those found in the basal part of the sutural groove.

Measurements, mm. Elytron length, 2.50; width, 1.35.

C o m p a r i s o n. The new species is similar in the convex elytron with clearly visible grooves to *P. tumidus* (Tillyard, 1916) and *P. subtumidus* Dunstan, 1924 and differs from them in the presence of a short strong oblique groove in the basal internal corner of the elytron; it additionally differs from the former species in the smaller size and from the latter species in the epipleural rim narrowed weakly posteriad.

Material. Holotype.

Plarycrossos latus Ponomarenko, sp. nov.

Etymology. From the Latin *latus* (wide, broad).

H o l o t y p e. PIN, no. 2470/1320, isolated right elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

Description (Fig. 77.2). The elytron is convex, rather wide, widest in the basal half, twice as long as wide; the elytron base is straight; the apex is shifted towards the external margin, blunt; the external margin is mostly almost straight, but curved towards the apex in the distal one-third, where it is truncated in an almost straight line; the sutural margin roundly protrudes. The epipleural rim is twice as wide as the intervals between the grooves, narrowed weakly posteriad up to the apical one-third, and more strongly narrowed distally, separated from the disc by a deep groove. The elytral disc has eight grooves; the grooves are narrow and rather shallow, almost indiscernible; the punctures in the grooves are fine, inconspicuous; the distances between the punctures are much wider than punctures: the spaces between the grooves are flat. The basal half of the elytron has a strongly cut impunctate groove running close to the sutural groove and parallel to it.

Fig. 77. Beetles Polyphaga inc. sed.. Genus *Platycrossos*: (1a, 1b) *Platycrossos mongolicus* Ponomarenko, sp. nov., holotype PIN, no. 2470/1323, photograph and habitus; (2a, 2b) *Plarycrossos latus* Ponomarenko, sp. nov., holotype PIN, nos. 2470/1320, photograph and habitus; (3a, 3b) *Plarycrossos loxonicus* Ponomarenko, sp. nov. PIN, no. 2470/1334, photograph and habitus; (4a, 4b) *Plarycrossos ovum* Ponomarenko, sp. nov., holotype PIN, no. 2470/1321, photograph and habitus; (5a, 5b) *Plarycrossos longus* Ponomarenko, sp. nov., holotype PIN, no. 2470/1321, photograph and habitus; (5c, 5b) *Plarycrossos longus* Ponomarenko, sp. nov., holotype PIN, no. 2470/1321, photograph and habitus; (5c, 5b) *Plarycrossos longus*, specimen PIN, no. 4270/1326, photograph.



Measurements, mm. Elytron length, 3.52; width, 1.76.

C o m p a r i s o n. The new species is similar in the convex elytron and clearly visible grooves to *P. tumidus* (Tillyard, 1916), *P. subtumidus* Dunstan, 1924 and the above-described species and differs from them in the presence of the strong groove in the sutural part of the elytron and in the shape of the epipleural rim, almost not narrowing up to the apical one-third of the elytron.

Material. Holotype.

Plarycrossos loxonicus Ponomarenko, sp. nov.

Etymology. From the Greek *loxos* (slanting).

Holotype. PIN, no. 2470/1334, isolated left elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

Description (Fig. 77.3). The elvtron is convex. rather wide, widest at the base, 1.9 times as long as wide; the elytron base is straight, broadly rimmed; the apex is shifted towards the external margin, blunt; the external margin is mostly almost straight, but convex curving towards the apex in the distal quarter; the sutural margin roundly protrudes, bordered by a deep impunctate groove. The epipleural rim is widest at the elytron base, gradually narrowing posteriad to the apical one-third, and separated from the disc by a deep groove. The grooves on the disc run slanting from the base to the sutural margin; they are narrow and rather shallow, almost indiscernible; the punctures in the grooves are rather large; the distances between the punctures are much wider than punctures; the spaces between the grooves are flat. The basal half of the elvtron has a strongly cut impunctate groove running parallel and close to the sutural groove.

Measurements, mm. Elytron length, 2.64; width, 1.35.

C o m p a r i s o n. The new species differs from species similar to *P. tumidus* (Tillyard, 1916) (*P. subtumidus* Dunstan, 1924 and the above-described congeners) in the slanting orientation of grooves on the elytral disc and in the rimmed elytral base, which makes the elytral disc entirely surrounded by the rim.

Plarycrossos ovum Ponomarenko, sp. nov.

Etymology. From the Lain ovum (egg).

Holotype. PIN, no. 2470/1321, isolated left elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

Description. (Fig. 77.4). The elytron is convex, wide, almost regular ovate, widest in the basal one-third, 1.9 times as long as wide; the elytron base is convex, rimmed; the apex is acute, slightly shifted towards the sutural margin; the external and sutural

margins are almost symmetrically convex; the sutural margin is bordered by a deep impunctate rim. The epipleural rim is widest at the basal one-third of the elytron, gradually narrowing towards the base and towards the apex, and separated from the disc by a deep groove. The grooves on the disc run slanting from the base to the sutural margin; they are narrow and rather shallow, almost indiscernible; the punctures in the grooves are rather large; the distances between the punctures are much wider than punctures; the spaces between the grooves are flat.

Measurements, mm. Elytron length, 5.3; width, 1.35.

C o m p a r i s o n. The new species differs from species similar to *P. tumidus* (Tillyard, 1916) (*P. subtumidus* Dunstan, 1924 and the above-described congeners, except *P. loxonicus* sp. nov.) in the slanting orientation of grooves on the elytral disc and in the rimmed elytral base, which makes the elytral disc entirely surrounded by the rim; among species with such characters, the new species is especially similar in the wide ovate elytron to *P. petalus* Ponomarenko, 1985 and differs from it in the small and almost indiscernible punctures, more conspicuous grooves on the elytral disc, and the apex shifted towards the sutural margin.

Material. Holotype.

Plarycrossos longus Ponomarenko, sp. nov.

Etymology. From the Latin *longus* (long).

H o l o t y p e. PIN, no. 2470/1331, isolated right elytron; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 423, Bed 6.

Description (Figs. 77.5a, 77.5b). The elvtron is convex, rather narrow, almost regular ovate, widest in the middle, 2.3 times as long as wide; the elytron base is convex, rimmed; the apex is acute, slightly shifted towards the external margin; the humeral angle of the elytron is a right angle; the external and sutural margins are almost symmetrically convex and bordered by a deep impunctate groove. The epipleural rim is widest at the base of the elytron, gradually narrowing towards the middle, but not narrowing more distally, separated from the disc by a deep groove. The grooves on the disc are almost indiscernible; the punctures in the grooves are rather small; the distances between the punctures are much wider than punctures; the spaces between the grooves are flat. The puncture rows run almost parallel to the axis of the elytron.

Measurements, mm. Elytron length, 3.39; width, 1.59.

C o m p a r i s o n. The new species is distinguished by the rather narrow, almost symmetrical elytron with a rimmed base, which makes the disc entirely surrounded by the rim, and by the almost indiscernible grooves, so that only the puncture rows are visible. UPPER JURASSIC LAGERSTÄTTE SHAR TEG, SOUTHWESTERN MONGOLIA

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M at erial. Holotype. It is possible that this spe-

cies is also represented by specimen PIN,

no. 2470/1321 (Fig. 77c) from the same outcrop; it is

similar in size and shape of the elytron and in the rim,

3.4. Coleoptera

but puncture rows on the disc are not visible at all.

Family Jurodidae Ponomarenko, 1985 = Sikhotealiniidae Lafer, 1996

The new species is assigned to the family Jurodidae based on the presence of tubercles behind the eyes (in J. shartegiensis, the tubercles are fused into a single transverse convexity and only the posterior margin of this convexity is notched weakly medially), elvtra with many longitudinal rows of large punctures, large scutellum, and three visible abdominal sternites.

Genus Jurodes Ponomarenko, 1985

The species is assigned to the genus Jurodes based on the median elevation on the head, constriction of the head behind the eyes, and maximum width of the abdomen in the middle.

Jurodes shartegiensis Yan sp. nov.

E t y m o l o g y. From the Shar Teg locality.

Holotype. PIN, no. 2470/1010, counter impression of complete beetle, head damaged, legs missing; Shar Teg; Upper Jurassic, Shar Teg sequence, outcrop 443/1.

Description (Fig. 34). The pronotum is almost twice as wide as the head, transversely rectangular, with two broad oblique depressions on the sides; the median part of the pronotum is also convex; the scutellum has a broad rounded apex; the base of the elytron is at most 3.5 times as wide as the scutellum.

M e a s u r e m e n t s, mm. Body length, about 2.5; width, 1.2; pronotum length, 0.4; width, 0.7; elytron length, 1.8; width, 0.6.

Comparison. The new species differs from all congeners in the wide pronotum.

R e m a r k s. The new species differs from Sikhotealinia in the wide pronotum. The holotype and paratype partly retain metanotum fragments; they are shown in the drawing.

Material. Holotype and paratype PIN, no. 4270/1006, male from the same locality.

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A total of 35 specimens of Neuroptera have been collected in Shar Teg. Only 11 of them are identified to family; others are wing fragments varying in size from small (estimated complete length is 6-7 mm, the size class of Prohemerobius minor Khramov, 2011) to large (estimated complete length is 20 mm and more). Some fragments of large wings with a broad costal space and branching subcostal veinlets in this space probably belong to Osmylopsychopidae or families with similar venation.

Six genera are known in the locality (Khramov, 2010, 2011, 2014). Only two of them, Dimidiosmylus gen. nov. and Frustumopsychops gen. nov., are probably endemic to Shar Teg, with a reservation for the current level of knowledge on fossil Neuroptera. Two other genera can be regarded as typical of the Middle and Upper Jurassic of the Asian region; for instance, in addition to Shar Teg, the genus Leptolingia Ren, 2002 (Grammolingiidae) has been recorded in Daohugou (China; Middle Jurassic: Ren, 2002) and in two other localities of Mongolia, Bakhar (Middle-Upper Jurassic) and Khoutiyn Khotgor (Upper Jurassic: Khramov, 2012); and Jurakempynus Wang et al., 2011 (Osmylidae) has also been found in Daohugou and Karatau (Kazakhstan, Upper Jurassic). Finally, two other genera link Shar Teg to earlier, Lower Jurassic localities: Prohemerobius Handlirsch, 1906 (Prohemerobiidae) also occurs in the Upper Lias of Germany and England, and Sogjuta O. Martynova, 1958 (Osmylidae) has also been recorded in Sogyuty (Kyrgyzstan, Lower Jurassic).

It should be noted, however, that Prohemerobius minor Khramov, 2011 described from Shar Teg may have nothing to do with the European Prohemerobiidae. There is a possibility that it belongs to primitive Berothidae, which had a pectinate CuA in the forewing and appeared in the second half of the Jurassic. Such berothids have been recorded in Daohugou (genus Sinosmylites Makarkin et al., 2011), Karatau, and Khoutiyn Khotgor. If this is the case, the Shar Teg assemblage lacks neuropteran genera known in European localities.

The family Kalligrammatidae is typical of Middle Jurassic to Lower Cretaceous localities of Asia and Europe, and Shar Teg, in which three small fragments of kalligrammatid wings have been recorded, is no exception. The record of a representative of the family Grammolingiidae (Leptolingia shartegica Khramov, 2010, text-fig. 3), known only from the Jurassic of Asia, puts Shar Teg in line with such Asian localities as Sai-Sagul (Kyrgyzstan, terminal Lower Jurassic and

basal Middle Jurassic), Khoutiyn Khotgor, and Karatau (Khramov, 2012), Daohugou (Ren, 2002; Liu et al., 2011; Shi et al., 2011, 2012, 2013), and Bakhar (original unpublished data), in which grammolingiids are also present.

Incerta familia

Genus Dimidiosmylus Khramov, gen. nov.

Etymology. From the Latin dimidium (half) and the generic name *Osmylus;* masculine gender.

Type species. D. ramosus sp. nov.

Diagnosis. Veins in costal space of forewing simple, usually without branching; crossveins abundant in proximal half of wing, distributed chaotically; veins of Rs dichotomizing close to base; MP2 deeply forked; cubital and anal veins pectinate; CuP considerably more intensely branching than CuA.

Species composition. Type species.

Comparison. *Dimidiosmylus* is similar to representatives of the family Osmylidae in the simple veins in the costal space and pectinate cubital and anal veins in the forewing. At the same time, Dimidiosmylus differs from the overwhelming majority of osmylids in the structure of MP; in the forewings of osmylids, MP is usually two-branched (in the majority of representatives), simple (in Stenosmylinae), or branched close to the wing margin (Porisminae and Eidoporisminae). However, MP divided into more branches rarely occurs in some osmylids; in some undescribed members of the subfamily Kempyninae collected in Daohugou, MP2 in the forewing is deeply divided, as in Dimidiosmylus. Therefore, the structure of MP does not contradict the possibility of assignment of Dimidiosmylus to Osmylidae. Nevertheless, branches of Rs dichotomizing close to the base, found in *Dimidiosmy*lus, are atypical of Osmylidae. Therefore, taking into account the fact that the specimen is fragmentary, at present Dimidiosmylus cannot be assigned with certainty to any family. *Dimidiosmylus* is distinguished from all other neuropteran genera by the two-branched MP2 and by the intensely branching radial sector combined with the characters typical of Osmylidae.

Dimidiosmylus ramosus Khramov, sp. nov.

Etymology. From the Latin *ramosus* (having many branches).

H o l o t y p e. PIN, no. 4270/1494, impression of proximal half of forewing; Mongolia, Gobi–Altai Province, Shar Teg locality; Upper Jurassic, Shar Teg sequence.

Description (Fig. 78). The first and second branches of Rs bifurcate twice close to the base; MP dichotomizes at the level of the base of the first branch of Rs; MP2 dichotomizes at the level of the base of the second branch of Rs; CuA has five branches; CuP has 15 branches; A1 and A2 occupy approximately the equal areas and have five branches each; A3 has three branches. M e a s u r e m e n t s, mm. Length of fragment, 12; width, 7; estimated total forewing length, 20–21. M a t e r i a l. Holotype.

Family Polystoechotidae Handlirsch, 1906

Genus Frustumopsychops Khramov, gen. nov.

Etymology. From the Latin *frustum* (crumb, piece) and the generic name *Psychopsis;* masculine gender.

Type species. F. pectinatus sp. nov.

D i a g n o s i s. Costal space broad, with short row of crossveins joining distinct humeral vein (hv); MP two-branched; MP2, CuA, CuP, and A1 pectinate.

Species composition. Type species.

Comparison and remarks. Frustumopsychops is similar in general venation pattern and wing shape to representatives of the families Osmylopsychopidae, Brongniartiellidae, and Psychopsidae, but it is especially close to Palaeopsychops Andersen, 2001, which includes ten species known from the Eocene of Denmark, Canada, and the United States (Archibald and Makarkin, 2006). Based on the pectinate branching pattern of single MP, Makarkin and Archibald (2003) proposed to assign *Palaeopsychops* to Polystoechotidae rather than to any of the above-listed families. Considering the similarity of *Frustumopsychops* to Palaeopsychops, I describe it in this family, although it is not improbable that, in the future, the family assignment of the two genera will be reviewed. Frustumopsychops is readily distinguished from Palaeopsychops by the two-branched MP as well as by the smaller size (in species of *Palaeopsychops*, except *P. angustifascia*tus Andersen, 2001, the wing is at least 40 mm long) and by the pectinate CuP and A1.

Frustumopsychops pectinatus Khramov, sp. nov.

Etymology. From the Latin *pectinatus* (pectinate).

H o l o t y p e. PIN, no. 4270/1503, impression of proximal half of forewing; Mongolia, Gobi–Altai Province, Shar Teg locality; Upper Jurassic, Shar Teg sequence.

D e s c r i p t i o n (Fig. 79). The veins in the costal space of the forewing abundantly branch; the row of crossveins in the costal space is short and positioned close to Sc (at the level of the humeral vein). Some crossveins are present in the radial sector; they are denser between MP2, CuA, and CuP; in the proximal part of the wing, crossveins are not arranged in regular rows. MP2 has at least five branches; CuA, CuP, and A1 have ten, seven, and six branches, respectively. A2 has four pectinately diverging branches.

M e a s u r e m e n t s, mm. Length of fragment, 14; width, 8; estimated total forewing length, 27–28.

Material. Holotype.



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Fig. 78. Neuropteran *Dimidiosmylus ramosus* gen. et sp. nov., holotype PIN, no. 4270/1494: (a, b) forewing. Scale bar, 2 mm.





CONCLUSIONS

A total of 297 species of 161 families, including more than 140 species of 132 families of insects, have been recorded in Shar Teg, including 31 insect species newly described here.

Based on the above, it is evident that the Shar Teg biota was rather diverse, although it was considerably less diverse than of modern ecosystems. In the family Mesocinetidae (Coleoptera) represented in the Shar Teg assemblage by the greatest number of specimens. 30 specimens identified to species represent nine species and almost two-thirds of the specimens belong to one species. This situation dramatically differs from that of the Neogene; Neogene species are very rarely represented by more than one specimen. Moreover, it should be noted that the Shar Teg biota existed under conditions of a frost-free equable climate. The diversity found in other Mesozoic Lagerstätten is also relatively low. In the modern frost-free zones, the diversity of the biota is much higher than in cold zones. The high diversity of the Recent biota could be associated with the high diversity of angiosperms, but angiosperms became widespread from the middle of the Cretaceous, whereas the diversity of the biota of Eocene localities that existed in paratropical equable climate was also rather low.

This raises the question, Why the continental nature of the Mesozoic did not support high diversity.

Beginning from the terminal Triassic, fossil remains of aquatic insects, especially mayfly and stonefly larvae, are dominant in oryctocoenoses of Mesozoic localities and usually represented by many species. However, in the terminal Jurassic, stonefly larvae almost disappear (even though stoneflies are common extant insects!) and, in Lower Cretaceous localities, aquatic insects are often only represented by odonate larvae of one species and coptoclavids, the most typical Mesozoic water beetles.

Which properties of Mesozoic water bodies caused these changes?

There are several groups of insects found in localities clearly concentrated around the Jurassic–Cretaceous boundary. Furthermore, insects of these groups are often abundant in such localities and recorded in different facies. No single ecological explanation can be found for concentration of these groups, e.g., Mesocinetidae and Velocorixinae.

What could be the cause of such concentration?

The Shar Teg oryctocoenosis shows certain features that usually characterize water bodies with unusual conditions (salinity, high water temperature, etc.); however, such features have not been recognized in enclosing deposits of this locality.

What is the cause of this contradiction?

Wings of large dragonflies, neuropterans, and orthopterans are found in the deposits as fragments with straight margins, as if cut with scissors. These fragments do not look like results of fragmentation by water currents.

What was the cause of this fragmentation?

The list of such questions could be continued, but it is more important to suggest why in spite of the rather detailed and versatile analysis of the biota such questions nevertheless remain. There are three main reasons: (1) rich localities of similar age are too few and ecologically dissimilar; (2) there are too few experts capable of analyzing the fauna at a sufficient level; even the community of Russian paleontologists, the largest in the world, could not treat the fauna of Shar Teg in its entirety; and (3) paleontologists do not pay sufficient attention to "routine" work on descriptions: only about half of the fauna has been described. and discussions of undescribed materials can result in many mistakes. Unfortunately, a sufficient level of work cannot be provided without rather broad international collaboration, and the number of such international projects decreases instead of increasing.

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