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## Jurassic Cladocera (Crustacea, Branchiopoda) with a description of an extinct Mesozoic order

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*(Accepted 11 December 2006)*

### Abstract

This paper describes extinct Jurassic Cladocera (Crustacea: Branchiopoda) from four well-known palaeontological sites. *Leptodorosida zherikhini* sp. nov., gen. nov. from Ust'-Baley (Lower Jurassic) belongs to an extinct family, Leptodorosididae fam. nov., and a new order, the Cryptopoda ordo nov. This order differs from the Haplopoda and the Onychopoda in having serially-similar filtering limbs with valves completely covering the post-cephalic body. Cryptopoda differs from the Anomopoda and Ctenopoda in having antennae II with both exopod and endopod possessing four segments. Segments 2–4 of the exopod (and perhaps the endopod) possess numerous setae. A second cryptopod, *Leposida ponomarenkoi* sp. nov., gen. nov., was found in Chalunikhka and Unda (Uppermost Jurassic). So, the extinct Cryptopoda existed for at least 25 million years during the Jurassic. Our finding of an extinct order possessing characters intermediate between recent cladoceran orders provides fossil evidence for cladoceran monophyly. I also describe a new ctenopod, *Smirnovidaphnia smirnovi* sp. nov., gen. nov. from Ust'-Baley as a member of the family Sididae. It belongs to the tribe Sidini of the subfamily Sidinae, but differs from recent genera of this tribe in having numerous setae on the second exopod segment. *Archedaphnia testacea* Smirnov, 1971, previously described from Novospasskoye (Lower-Middle Jurassic), is apparently a ctenopod, and, most probably, a member of *Smirnovidaphnia* gen. nov. Finally, I found claws, presumably belonging to unknown cladocerans, from the Ust'-Baley and four other localities from the Lower to Upper Jurassic. I conclude that cladocerans were present and common in Mesozoic waters.

**Keywords:** *Branchiopoda, Crustacea, Ctenopoda, fossil, Mesozoic, new order, systematics, taxonomy*

### Introduction

Recent fossil discoveries have necessitated a rethinking of the age of cladocerans. Fryer (1991), Smirnov (1992), and Kotov and Korovchinsky (2006) described cladocerans from the Cretaceous and the Jurassic/Cretaceous boundary.

For many years, *Archedaphnia testacea* Smirnov, 1971 was the sole cladoceran taxon described from the Jurassic. Zherikhin (1985) represented photographs of several impressions of "crustaceans of unclear taxonomic status" from Ust'-Baley, a Lower Jurassic locality in Siberia well known to palaeontologists since the 19th century

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(Oppenheim 1885; Brauer et al. 1889). A re-examination of this material herein led to the conclusion that the numerous and well-preserved specimens from Ust'-Baley belong to two different cladoceran species, both from extinct genera. My subsequent efforts resulted in the finding of fossil cladocerans in some other Mesozoic localities, also well studied by palaeontologists (Rasnitsyn and Quicke 2002).

This communication continues the description of Jurassic cladocerans in the collection of the Palaeontological Institute of the Russian Academy of Sciences (PIN) (Kotov and Korovchinsky 2006).

## Methods

Numerous rock fragments with undetermined microcrustaceans from eight Jurassic localities (see below) were examined under stereo- and compound microscopes, and only fragments with comparatively complete and distinct impressions were selected for further work. The fossil specimens from Chalunikha and Unda were covered by a thin layer of rock matrix, and were made more clearly visible by adding a drop of alcohol on the surface of the rock fragment (Rasnitsyn and Quicke 2002).

Micrographs were predominantly taken by scanning electron microscope (CAMSCAN MB2300) after coating specimens with gold. Some photographs were obtained with a digital camera (Nikon CoolPix 950) attached to an optical microscope (Zeiss Axiolab).

I followed the geological time-scale of Gradstein et al. (2005).

The following abbreviation is used: AII, antenna II with setae, the number of which is described as an "antennal formula".

## Localities

### *Localities with unambiguous cladocerans*

*Ust'-Baley.* Right bank of the Angara River downstream of village of Ust'-Baley at the mouth of Baley Creek, Olonkovsky District, Irkutsk Area, Asian Russia.

The Ust'-Baley palaeocenosis is a well-described Mesozoic "hypotrophic" lake (Zherikhin and Kalugina 1985), of type "B" according to Sinitshenkova and Zherikhin (1996). It was a small, shallow, permanent lake in a large river valley (but completely isolated from the river), with a low primary production and high oxygen concentration, closely surrounded by a forest of Ginkgopsida and Czekanowskiales, fallen leaves of which were antibiotically active and with greatly depressed microbial activity. Littoral vegetation was poorly developed, a liverwort *Isoetites angustifolius* and a horsetail *Equisetites sibiricus* were restricted to the water's edge. *Baleiichtys gracillosus* Rohon, 1890 (Rholidophorida), a planktivorous fish (Zherikhin and Kalugina 1985), and insects also populated the lake.

Age: lower subformation of Tcheremkhovo Formation, Toarcian age (about 183–176 Mya), uppermost Lower Jurassic (Kirichkova and Travina 2000; Rasnitsyn and Quicke 2002).

Fauna: *Leptodorosida zherikhini* sp. nov., *Smirnovidaphnia smirnovi* sp. nov., and undetermined claws possibly belonging to a cladoceran.

*Novospasskoe.* West (2 km) of village of Novospasskoye, 4 km N of Lake Tsagan-Nur in the Tugnuy Depression, Mukhor-Shibir' District, Buryat Autonomous Republic, Asian Russia.

Novospasskoe was a typical Mesozoic lake of type "A" according to Sinitshenkova and Zherikhin (1996), a deep mountain lake formed when a river valley was naturally dammed.

It was a cold oligotrophic water body with low primary production and ample oxygen. Liverworts and horsetails occurred rarely, and were restricted to the water's edge. Cladocerans were numerous, and likely the main primary consumers (Zherikhin and Kalugina 1985). It is interesting that chaoborids (i.e. *Praechaoborus tungunicus* Kalgina, 1985), whose larvae are strong predators of cladocerans today, were also common.

Age: Ichetyu Formation, Toarcian to Aalenian age (about 183–172 Mya), from uppermost Lower to lowermost Middle Jurassic (Rasnitsyn and Quicke 2002). However, the deposits involved may be of somewhat different age (Ponomarenko 1993).

Fauna: *Smirnovidaphnia testacea* (Smirnov 1971).

*Chalunikha*. South slope of Chalunikha Mountain, right bank of River Unda 500 m from the cemetery of village of Zhidka, Baley District, Chita Area, Asian Russia.

Age: Chalunikha Formation, probably Tithonian age (151–146 Mya), uppermost Upper Jurassic (Rasnitsyn 1990).

Fauna: *Leposida ponomarenkoi* gen. nov., sp. nov.

*Unda*. Right bank of the Unda River downstream of village of Zhidka, Baley District, Chita Area, Asian Russia. It was a typical lake of type "A" (see above) according to Sinitshenkova and Zherikhin (1996).

Age: Glushkov Formation, Tithonian age (151–146 Mya), uppermost Upper Jurassic (Rasnitsyn 1990), with age very close to the previous locality (Chalunikha).

Fauna: *Leposida ponomarenkoi* gen. nov., sp. nov.

*Localities with undetermined claw-like impressions, probably belonging to cladocerans*

*Sogyuty*. South shore of Issyk-Kul Lake near Kadzhi-Say village, Ton District, Kirghizia.

Age: Dzhil Formation, Hettangian-Sinemurian age (about 200–190 Mya), Lower Jurassic (A. G. Ponomarenko, personal communication).

*Sagul (Shurab III)*. Southwest (20 km) of Samarcandek village, Batken district, Osh Area, Kirghizia.

Age: Sagul Formation, Lower-Middle Jurassic (Rasnitsyn and Quicke 2002).

*Kubekovo*. Left bank of the Yenisey River near Kubekovo village, downstream of the town of Krasnoyarsk, Emelyanovsk District, Krasnoyarsk Area, Russia.

Age: upper subformation of Itat Formation, Aalenian–Bathonian age (about 176–165 Mya), Middle Jurassic (Rasnitsyn and Quicke 2002).

*Tushilga (=Tushleg)*. North slope of Tushilga mountain, 10 km SW of Sain-Shand, East Gobi Aymag, SE Mongolia.

Age: Khamar-Khuburin Formation, probably Aalenian age (about 176–172 Mya), Middle Jurassic (A. G. Ponomarenko, personal communication).

## Results

**Class BRANCHIOPODA** Latreille, 1817 *sensu* Calman, 1909

**Superorder DIPLOSTRACA** Gerstaecker, 1866

**Order CRYPTOPODA** ord. nov.

*Type (sole) family*. Leptodorosididae fam. nov.

*Etymology*

The name of the order is derived from Greek  $\chi\rho\upsilon\pi\tau\tau\varsigma$  (hidden, secret) and  $\pi\omicron\delta\varsigma$  (leg), keeping in mind that limbs of these animals were hidden under valves, and details of the limbs are unknown now.

*Diagnosis*

Head massive, covered with a head shield. Post-cephalic body enclosed in valves of carapace. AII with both exopod and endopod four-segmented, segments 2–4 of exopod armed with numerous setae. Limbs filtratory, serially similar.

*Differential diagnosis*

The new order differs from the gymnomeran cladocerans (orders Onychopoda Sars, 1865 and Haplopoda Sars, 1865) in having serially similar filtratory limbs and post-cephalic body enclosed in valves, and from the “calyptomeran” cladocerans (orders Anomopoda Sars, 1865 and Ctenopoda Sars, 1865) in AII with both exopod and endopod four-segmented. Also, it differs from the Ctenopoda in having massive head covered with a head shield, and from Anomopoda in having serially similar limbs and numerous setae on segments 2–4 of the exopod.

*Age*

There is direct fossil evidence that the order existed at least from the uppermost Lower Jurassic to the uppermost Upper Jurassic, at least from 175 to 151 Mya.

**LEPTODOROSIDIDAE** fam. nov.

*Type (sole) genus.* *Leptodorosida* gen. nov.

*Etymology*

The family is named after its type genus.

*Diagnosis and differential diagnosis*

As for the order Cryptopoda ord. nov.

***Leptodorosida*** gen. nov.

*Type species.* *Leptodorosida zherikhini* sp. nov.

*Etymology*

*Leptodora* Lilljeborg, 1861 is the type (single) genus of the family Leptodoridae Lilljeborg, 1861 of the gymnomeran order Haplopoda; *Sida* Straus, 1820 is the type genus of the family Sididae, Baird 1850 of the “calyptomeran” order Ctenopoda. Among all cladocerans, AII of *Leptodorosida* gen. nov. is maximally similar with one of *Leptodora*, while general body shape is similar with sidids.

*Diagnosis*

Body elongated with expressed postero-dorsal angle. Distal extremity of head protruding anteriorly, posterior portion of head inflated. AII with proximal segment of endopod long and proximal segment of exopod of moderate length, second segment of exopod shorter than 3 + 4 segments. Each of segments 3–4 of endopod with a series of setae.

*Differential diagnosis*

*Leptodorosida* gen. nov. differs from the second known genus from the order Cryptopoda ord. nov., *Leposida* gen. nov., in elongated body and large proximal segments of antennal branches.

***Leptodorosida zherikhini* sp. nov.**

(Figures 1, 2A–C)

*Etymology*

This species is dedicated to the outstanding palaeontologist, Professor V. V. Zherikhin, who published images of Ust'-Baley cladocerans as "crustaceans of unclear taxonomic status" (Zherikhin 1985, Plate 7), and participated greatly in the reconstruction of Jurassic palaeocenoses (Zherikhin 1985; Zherikhin and Kalugina 1985; Sinitshenkova and Zherikhin 1996). His untimely death in December 2001 was a great loss to Russian palaeontology.

*Type locality*

Ust'-Baley.

*Material studied*

Holotype: complete body in lateral position, with distinct head, valves and AII, PIN 1873/106 (Figure 1A). Paratypes: AII, PIN 1873/27; complete body with AII (0)-(7)-(?)-(?)/(0)-(6)-(4?)-(?), PIN 1873/31; complete impression with AII (0)-(?)-(?)-(?)/(0)-(8)-(4)-(?), PIN 1873/32; unclear impression with AII (0)-(7)-(4)-(?)/(0)-(8)-(?)-(?), PIN 1873/50; AII (0)-(>6)-(4)-(8)/(?)-(6)-(5)-(5), PIN 1873/57; AII (0)-(7)-(?)-(?)/(0)-(≥7)-(?)-(?), PIN 1873/65; AII (0)-?(/0)-(>5)-(4)-(?), PIN 1873/67; AII (0)-(>7)-(5)-(6)/(0)-(7)-(4)-(5), PIN 1873/69; AII, PIN 1873/70; AII (0)-(8)-(4)-(7)/(0)-(7)-(?)-(?), PIN 1873/76; AII (0)-(7)-(5)-(6)/(0)-(7)-(?)-(?), PIN 1873/78; complete body with AII (0)-(>5)-(5)-(?)/(0)-(8)-(?)-(?), PIN 1873/79; AII (0)-(6)-(5)-(?)/(0)-(7)-(4)-(>3), PIN 1873/80; complete body with distinct head, mandibles and unclear AII, PIN 1873/81; complete body with distinct head, mandibles and unclear AII, PIN 1873/82; AII (0)-(>5)-(4)-(6)/(0)-(>6)-(4)-(?), PIN 1873/83; unclear body contour with mandibles, AII (0)-(?)-(?)-(?)/(0)-(>6)-(?)-(?), PIN 1873/85; head, unclear valves, AII (0)-(6)-(>5)-(?)/(0)-(>4)-(4)-(>3), PIN 1873/86; AII (0)-(7)-(6)-(>6)/(0)-(6)-(4)-(>3), PIN 1873/87; AII (0)-(7)-(6)-(>8)/(0)-(8)-(4)-(5), PIN 1873/88; complete body with distinct head and valves, PIN 1873/89; complete body with unclear head and valves, PIN 1873/90; complete body with distinct head, mandibles, AII (0)-(>5)-(6)-(?)/(0)-(≥6)-(?)-(?), PIN 1873/91; complete body, 1873/94; complete

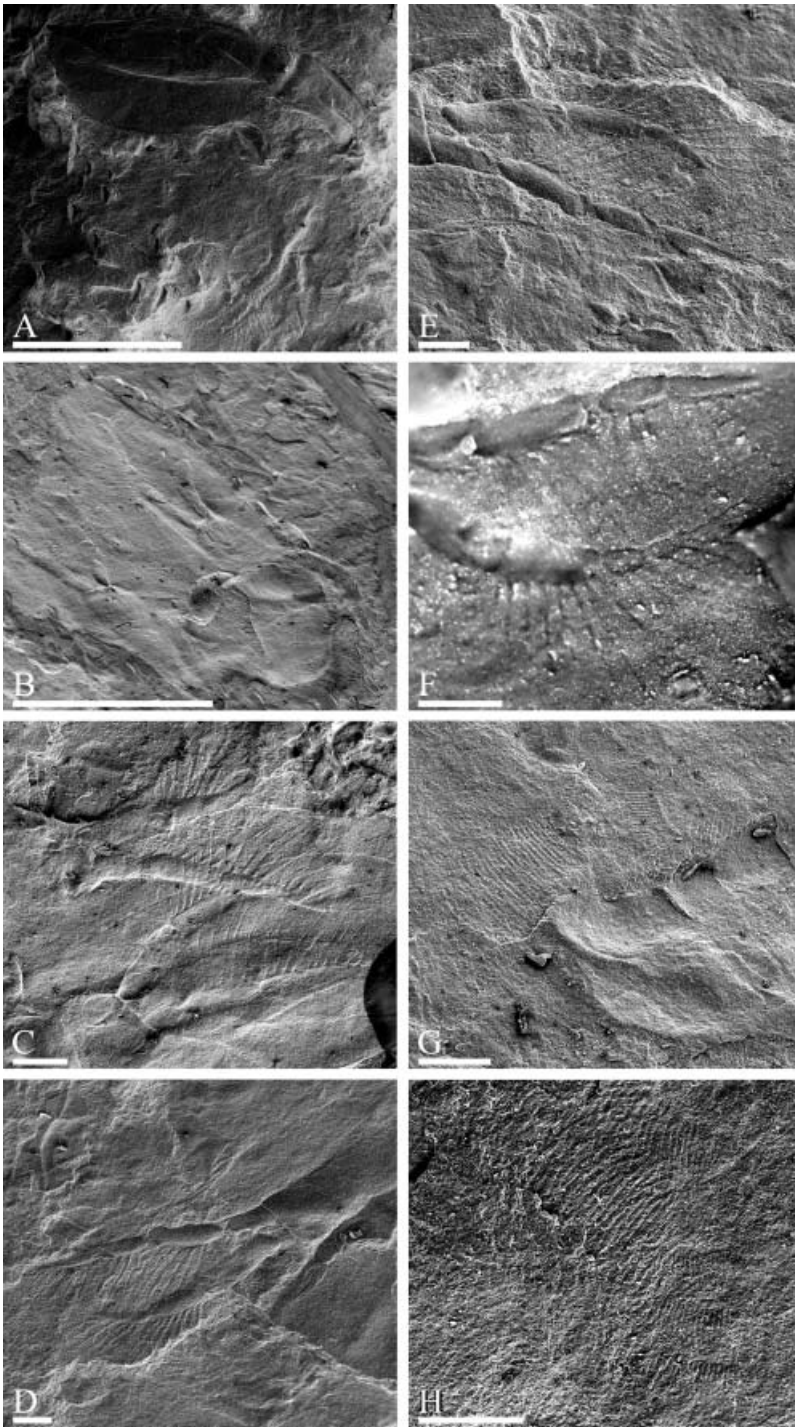


Figure 1. SEM (A–E, G, H) and optical (F) micrographs of *Leptodorosida zherikhini* gen. nov., sp. nov., Ust'-Baley, Asian Russia. (A) Holotype, PIN 1873/106; (B) paratype, general view, PIN 1873/102; (C) antenna II, PIN 1873/101; (D, E) antenna II, PIN 1873/115; (F) antenna II, PIN 1873/123; (G) head and thoracic limbs, PIN 1873/107; (H) thoracic limbs, PIN 1873/116. Scale bars: 1 mm (A, B); 0.1 mm (C–H).

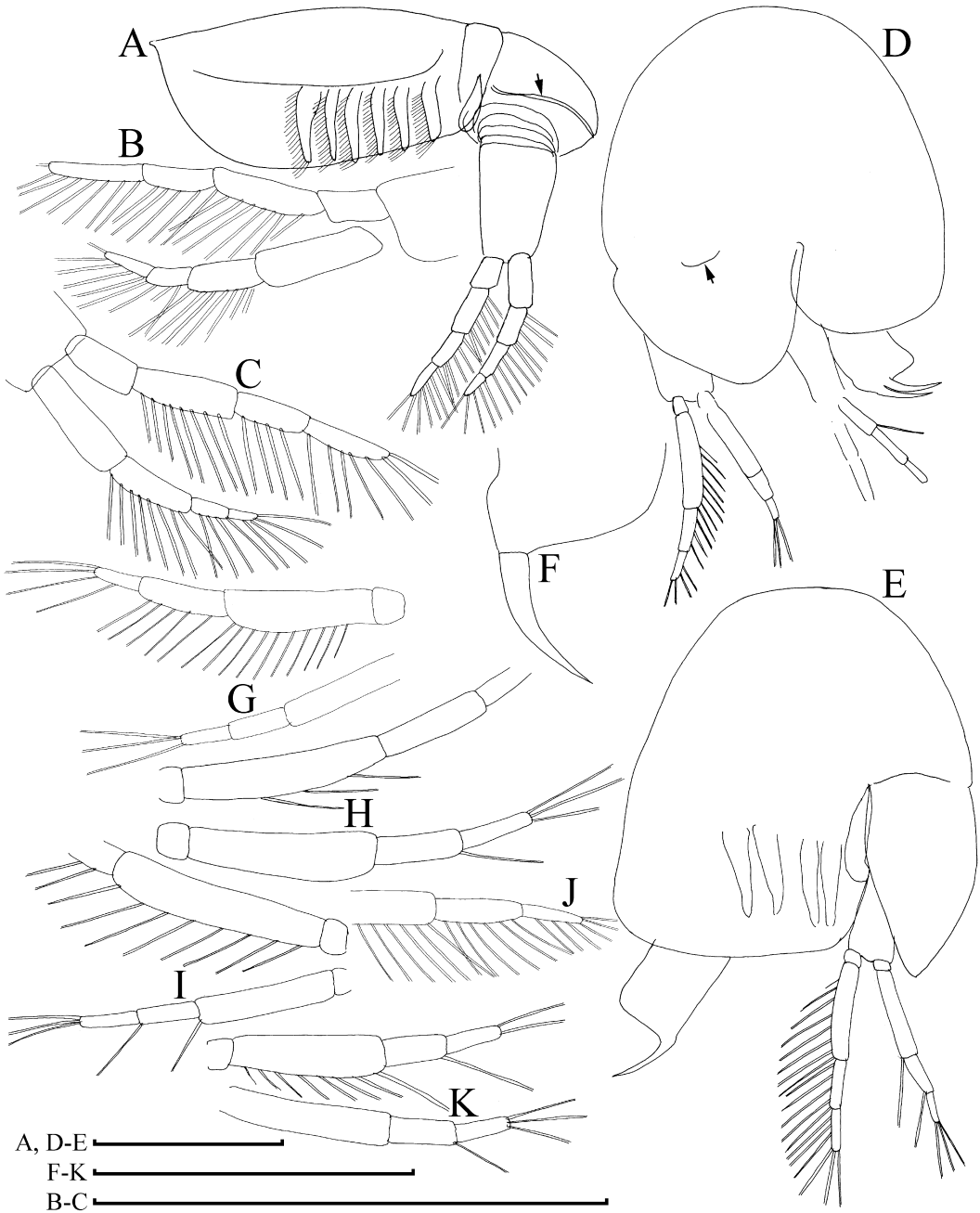


Figure 2. Mesozoic Cryptopoda ord. nov. (A) *Leptodorosida zherikhini* gen. nov., sp. nov. from Ust'-Baley, reconstruction based on several impressions; (B, C) antenna II, PIN 1873/115 and 1873/121; (D) *Leposida ponomarenkoi* gen. nov., sp. nov. from Chalunikha, general view of holotype, PIN 4042/60, see also Figure 3A; (E) reconstruction based on several impressions; (F) postabdomen, PIN 4042/65; (G-I) antenna II, PIN 4042/60 (holotype), 4042/61, and 4042/62; (J, K) *Leposida ponomarenkoi* gen. nov., sp. nov. from Unda, antenna II, PIN 3015/2415 and 3015/2421. Scale bars: 1 mm.



body, PIN 1873/95; AII, PIN 1873/96; complete body, AII (0)-( > 5 )-( 5 )-( > 4 )/( 0 )-( ? )-( 4 )-( ? ), AII ( 0 )-( ≥ 7 )-( ≥ 6 )-( ? )/( 0 )-( 6 )-( ? )-( ? ), PIN 1873/101; complete body, PIN 1873/102; complete body with distinct head and traces of limbs, PIN 1873/107; AII, PIN 1873/110; AII, PIN 1873/113; AII ( 0 )-( ≥ 8 )-( ≥ 4 )-( > 7 )/( 0 )-( 7 )-( 4 )-( ≥ 4 ), PIN 1873/115; AII, mandibles and limbs, PIN 1873/116; AII, PIN 1873/117; AII ( 0 )-( ≥ 7 )-( 4 )-( 7 )/( 0 )-( 8 )-( 4 )-( 4 ), PIN 1873/123.

### Diagnosis

As for the genus.

### Description

Body elongated (height/length = about 0.3–0.4), subovoid (Figures 1A, B, 2A), with slightly convex dorsal margin and distinct postero-dorsal angle, postero-ventral angle absent. Head massive, 0.3–0.4 body length, strongly chitinized, forming a head shield, with its distalmost extremity protruding anteriorly. Posterior portion of head slightly inflated (most probably, powerful mandibular muscles were attached here), posterior head margin as a shallow incision. A distinct fold (fornix) on lateral surface of head (Figure 2A, arrow), covering coxal portion of AII. Valve firm, probably thick-walled, oval-elongated, without marginal setae.

Antenna I not found. AII strong and long, length from base to tip of exopod more than half of body length. Basal segment strong, thick. Both antennal branches long, thin, four-segmented (Figures 1C–F, 2B, C). Exopod longer than endopod. First segment of exopod of moderate size, lacking setae, second to fourth segments elongated, each with a series of setae, length of second segment less than that of third plus fourth segments. Endopod with long first segment, lacking setae, second segment large, with a series of setae, third and fourth segments small, each with a series of setae. Antennal formula (0)-(5–8)-(4–>6)-(6–>8)/(0)-(6–8)-(4–5)-(4–5). No spines were found on any segments and on the basal segment of AII. Mandibles asymmetrical, large, strongly chitinized, with molar surfaces of primitive, triturating type, lacking any large projections. Thoracic limbs were not distinct in the majority of specimens, probably hidden in most under strong valves, but two impressions of *Leptodorosida* were associated with uniform limbs of filtering type (Figure 1G, H), although their number and details remain unclear. Eggs were not found.

Size 1.8–2.2 mm. Apparently, specimens had strong cuticle and were weakly deformed.

Specimens with postabdominal claws were absent. Thin paired claws 0.5–0.8 mm long, lacking denticles, were found on many fragments without clear association with body parts of other specimens, but they are too large to belong to *Leptodorosida*.

### Comments

In the Jurassic lake Ust'-Baley, *L. zherikhini* sp. nov. co-occurred with *Smirnovidaphnia smirnovi* sp. nov. (see below). But on rock fragments the former can be easily differentiated from the latter in having a strongly chitinized head and AII with numerous setae on the endopod.

***Leposida*** gen. nov.

*Type (sole) species.* *Leposida ponomarenkoi* sp. nov.

*Etymology*

The name of the new genus is a consequent series of bi-letter initial fragments of names of the families from four Recent orders of the cladocerans: *le*—Leptodoridae (Haplopoda), *po*—Polyphemidae (Onychopoda), *si*—Sididae (Ctenopoda), *da*—Daphniidae (Anomopoda).

*Diagnosis*

Body high, without postero-dorsal angle. Distal extremity of head protruding ventrally. AII with proximal segments of endopod and exopod short, length of second segment of exopod more than that of third plus fourth segments.

*Differential diagnosis*

See section on *Leptodorosida* gen. nov.

***Leposida ponomarenkoi*** sp. nov.

(Figures 2D–K, 3)

*Etymology*

This species is dedicated to Dr A. G. Ponomarenko, leader of the expedition of PIN to Unda, where this animal was collected. He participated greatly in forming the crustacean collection of PIN and consulted me on many issues of palaeontology.

*Type locality*

Clalunikha.

*Material studied*

Holotype: a specimen in antero-lateral position, 1.9 mm length, PIN 4042/60 (Figures 2D, 3A, B). Paratypes: eight specimens on six rock fragments, PIN 4042/61–69.

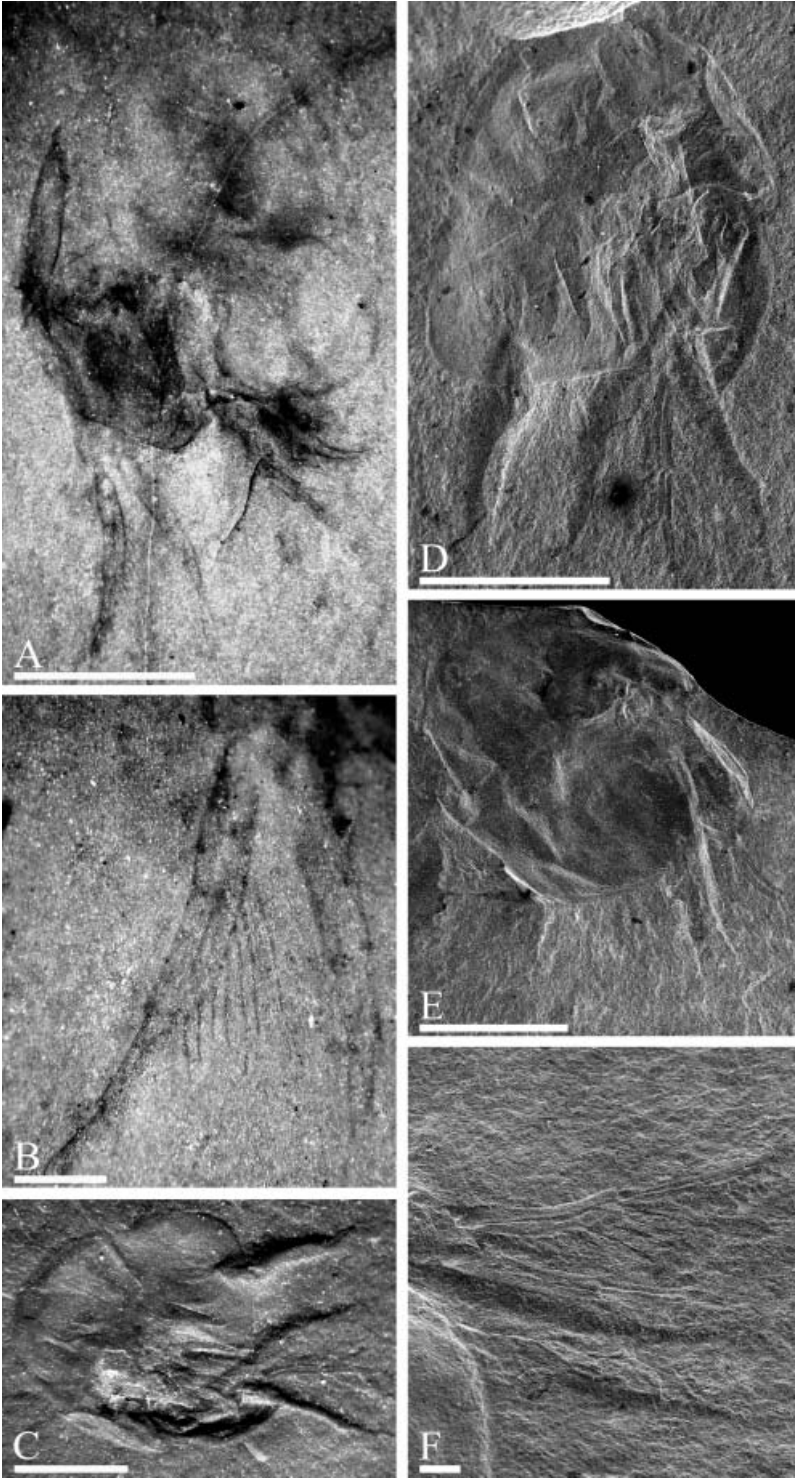
*Other material studied.* Unda: 10 specimens, PIN 3015/2415–2424.

*Diagnosis*

As for the genus.

*Description*

Body very high, height/length = about 0.9–1.1, rounded (the animal was likely sub-globular), with strongly convex dorsal margin, without postero-dorsal angle,



postero-ventral angle widely rounded (Figures 2E, 3C–E). Head massive, about 0.4 body length, with a head shield, its distalmost extremity protruding ventrally. On some impressions there is a line seeming to be a posterior head border (Figure 3D). In the holotype, there is an indistinct spot in the posterior portion of the head which may be the trace of a large, subovoid dorsal organ (Figure 2D, arrow). Head shield wide (with width more than length), its lateral portion covering basis of AII. Valve without marginal setae. Postabdomen massive (Figure 2E, F), with well-defined distal margin as in some recent anomopods, i.e. *Bosmina* or alonine *Nicsmirnovius* (Kotov 1996; Van Damme et al. 2003; Kotov and Sanoamuang 2004). Postabdominal claw thin, regularly bent.

Antenna I not found. AII thin and long, length from base to tip of exopod slightly less than body length. Basal segment strong, thick. Both antennal branches long, thin, four-segmented, exopod longer than endopod. Exopod (Figures 2G–K, 3B) with first segment small, lacking setae, second to fourth segments elongated, each with a series of setae (but bad preservation does not allow their number to be counted in the majority of specimens), length of second segment more than that of third plus fourth segments. Endopod with small first segment, lacking setae, second segment large, third and fourth segments smaller. I saw only a distal seta on the second segment, a distal seta on the third segment, and three apical setae on the fourth endopod segment, but there is a chance that the animal possessed more setae, which were lost. So, approximate antennal formula (0)-(≤10)-(≤6)-(≤6)/(0)-(1?)-(1?)-(3?). No spines were found on any segments. Mandibles small. In some impressions, unclear outlines of serially similar thoracic limbs (≥5) can be observed (Figure 3C, D), but no setae were seen. Eggs were not found.

Size 1.8–2.4 mm.

#### Comments

Unfortunately, preservation of fossils from Chalunikha and Unda is weak compared to those from Ust'-Baley. I did not find any evidence of the presence of more than one species in each locality. Also, I did not find any differences between specimens from the two localities, so I placed cladocerans from Unda in the same species, although I did not include them in the type series of *L. ponomarenkoi* sp. nov.

Due to moderate preservation of the specimens from Chalunikha and Unda, I have doubts that *Leposida* gen. nov. really lacked lateral setae on segments 2–4 of endopod, the latter was less preserved than the exopod in all specimens. It is possible that the endopod of *Leposida* gen. nov., sp. nov. was of the *Leptodorosida*-type.

**Order CTENOPODA** Sars, 1865

**Family SIDIDAE** Baird, 1850

**Subfamily SIDINAE** Baird, 1850

**Tribe SIDINI** Baird, 1850

***Smirnovidaphnia*** gen. nov.

*Type species. Smirnovidaphnia smirnovi* sp. nov.

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Figure 3. Optical (A–C) and SEM (D–F) micrographs of *Leposida ponomarenkoi* gen. nov., sp. nov., Chalunikha (A, B) and Unda (C–F), Asian Russia. (A, B) Holotype PIN 4042/60, general view and antenna II; (C–E) lateral view, PIN 3015/2415, 3015/2424, and 3015/2423; (F) antenna II, PIN 3015/2423. Scale bars: 1 mm (A, C–E); 0.1 mm (B, F).

*Etymology*

This genus is dedicated to the outstanding investigator of Recent and fossil cladocerans, Professor Nikolai Nikolaevich Smirnov. Most probably, the first representative of this genus was described under the name *Archedaphnia testacea* Smirnov, 1971 from Novospasskoye as a member of the family Daphniidae Straus, 1820. The second part of the new genus name refers to the genus *Daphnia* O. F. Müller, 1785, the type genus of the family Daphniidae, into which *Smirnovidaphnia testacea* was initially placed. But it is *S. smirnovi* sp. nov. from Ust'-Baley which is selected here as the type species of the genus due to a significantly better preservation of specimens.

*Diagnosis*

Antennal exopod three-segmented, its second and third segments with numerous setae. All setae of endopod uniform, unspecialized. Spines on all segments except apical endopod segment, absent (or very small and due to this were not preserved in fossils). Endites on inner-distal portions of limbs not fused.

*Differential diagnosis*

The most spectacular difference of *Smirnovidaphnia* from all Recent ctenopods is the presence of projecting unfused endites on inner-distal portions of thoracic limbs. Among eight valid Recent and fossil genera of the Sidinae described previously (Korovchinsky 2004; Kotov and Korovchinsky 2006), only two genera (*Sida* and *Limnosida*) have a three-segmented exopod of AII. They were placed by Korovchinsky (1986) in the tribe Sidini Baird, 1850, but this grouping must be checked (because it was based on symplesiomorphies). In any case, *Smirnovidaphnia* gen. nov. has numerous (up to 12) lateral setae on the second segment of the exopod of AII, which distinguishes it from the Recent genera *Sida* and *Limnosida* with three to four setae there. Probably, the third segment of AII in *Smirnovidaphnia* also has more setae than *Sida* or *Limnosida*, but their number cannot be counted in *S. testacea*.

*Age*

Lower-Middle Jurassic.

***Smirnovidaphnia smirnovi* sp. nov.**  
(Figures 4, 5A–C)

*Type locality*

Ust'-Baley.

*Etymology*

This species is also dedicated to Professor N. N. Smirnov.

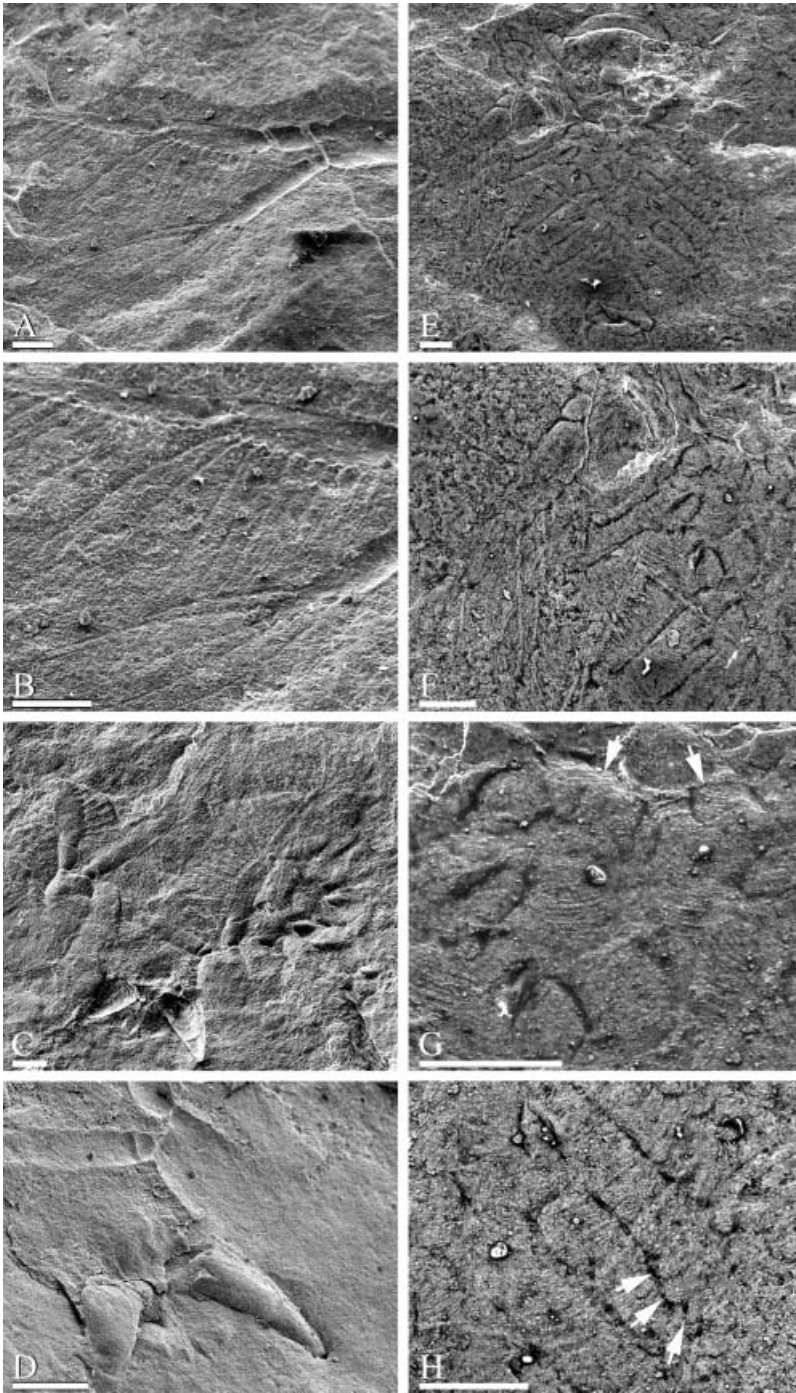
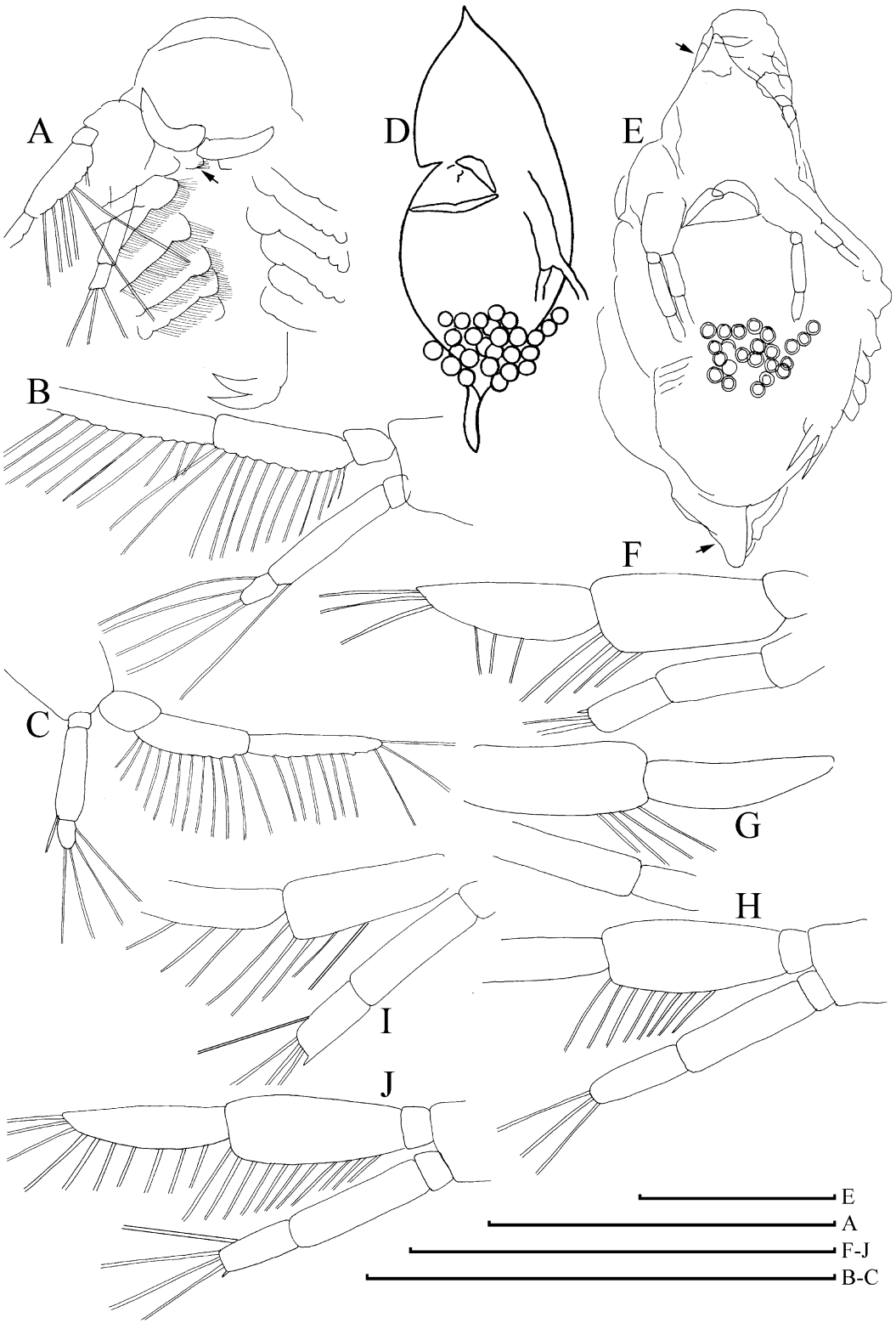


Figure 4. SEM micrographs of *Smirnovidaphnia smirnovi* gen. nov., sp. nov., Ust'-Baley, Asian Russia. (A, B) Holotype, antenna II, PIN 1873/100; (C, D) paratype, PIN 1873/105, two antennae II and mandibles; (E-H) paratype, PIN 1873/92, general view, and details of morphology. Scale bars: 0.1 mm.



*Material studied*

Holotype: indistinct body with AII (0)-(≥11)-(>10)/(0)-(1)-(4), PIN 1873/100 (Figure 4A, B). Paratypes: indistinct body with postabdominal claws and AII (0)-(>8)-(?)/(0)-(1)-(4), PIN 1873/29; indistinct body with AII (0)-(>8)-(12)/(0)-(0)-(?), PIN 1873/33; AII (0)-(10)-(12)/(0)-(?)-(4), PIN 1873/56; AII (0)-(9)-(?)/(0)-(?)-(4), PIN 1873/59; AII ?/(0)-(1)-(4), PIN 1873/63; AII (0)-(≥12)-(>10)/(0)-(1)-(4), PIN 1873/68; AII (0)-(>9)-(?)/(0)-(?)-(4), PIN 1873/72; AII (0)-(8)-(?)/(0)-(?)-(?), PIN 1873/75; AII (0)-(>6)-(?)/(0)-(?)-(?), PIN 1873/77; body with distinct head, valves, mandibles, and thoracic limbs, PIN 1873/92; body with less distinct limbs, PIN 1873/93; AII (0)-(>10)-(>13)/(0)-(1)-(4), PIN 1873/103; AII (0)-(?)-(?)/(0)-(1)-(4), PIN 1873/104; a body with AII (0)-(>7)-(?)/(0)-(?)-(4), AII (0)-(12)-(13)/(0)-(0)-(?), PIN 1873/105; AII ?/(0)-(1)-(4), PIN 1873/111; AII (0)-(>6)-(>6)/(0)-(?)-(>3), PIN 1873/112; AII ?/(0)-(1)-(4), PIN 1873/114; AII (0)-(11)-(>9)/(0)-(?)-(?)/, PIN 1873/118; AII ?/(0)-(1)-(4), PIN 1873/119; AII (0)-(12)-(>11)/(0)-(1)-(4), PIN 1873/122.

*Description*

Body oval, elongated. Head small, about 25% of body length, without head shield. Valves thin-walled, delicate, suboval, lacking marginal setae. Postabdominal claws short, massive, lacking denticles (Figure 4E).

AII with basal segment thick, massive (Figure 4C). Exopod significantly longer than endopod, three-segmented, first segment of moderate size, second segment large, thin, with numerous (up to 12) setae, third (apical) segment longer than second segment, thin, with numerous (more than 13) setae (Figures 4A, B, 5B, C). Endopod approximately as long as basal segment, three-segmented, its first (proximal) segment small, without setae, second segment long, with a single seta near its distal end, third (apical) segment small, with three apical setae and a single lateral seta, all endopod setae uniform, unspecialized. Antennal formula (0)-(8-12)-(9->13)/(0)-(1)-(4). No spines were found on any of the antenna segments. Mandibles small, strongly chitinized (Figure 4D). Maxilla I as a small body with numerous (at least 10) setae (Figures 4G, 5A, arrow). Six limbs of similar structure, each limb with well-developed gnathobase supplied with numerous (more than 10) setae, large basal endite and three unfused distal endites (Figure 4H, arrows), exopods were not preserved. No eggs were found.

Size 0.92–1.30 mm (from anteriormost extremity to tip of postabdominal claw, because posterior margin of valves was indistinct in majority of specimens).

*Differential diagnosis*

It differs from *S. testacea* in its small size and in having thinner segments of antennal branches, especially of the second segment of the exopod.

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Figure 5. Jurassic Ctenopoda. (A) *Smirnovidaphnia smirnovi* gen. nov., sp. nov. from Ust'-Baley, ventral view, PIN 1873/92; (B, C) antenna II, PIN 1873/68 and 1873/122; (D, E) *S. testacea* from Novospasskoe, reconstruction of holotype, PIN 3000/40 by Smirnov (1971) and my reconstruction; (F–I) antenna II, PIN 3000/1, 3000/19, 3000/36, and 3000/46; (J) reconstruction of antenna II based on all fragments. Scale bars: 1 mm.



*Comments*

There were several exceptionally well-preserved specimens of *S. smirnovi* with thoracic limbs (Figures 4E–H, 5A) (note that *S. smirnovi* sp. nov. in any state of preservation can be easily differentiated from *L. zherikhini* sp. nov. from the same locality in structure of AII and absence of head shield). Obviously, *S. smirnovi* sp. nov. has six serially similar filtratory limbs, so it belongs to the Ctenopoda. In addition, the specimens from Ust'-Baley have AII with endopod strongly shorter than exopod, with armature of both branches similar to Recent sidid ctenopods. These specimens are therefore attributed to the family Sididae, namely to the tribe Sidini of the subfamily Sidinae.

***Smirnovidaphnia testacea* (Smirnov, 1971)**

(Figures 5D–J, 6)

*Archedaphnia testacea* Smirnov 1971, p 120–121, Figures 1, 2; Zherikhin 1985, p 100, Plate 7, Figures 10–12.

*Type locality*

Novospasskoe.

*Material studied*

Holotype: PIN 3000/40.

*Other material studied.* Fifty specimens, PIN 3000/1–22, 24–39, 41, 42, 45, 46, 59–66.

*Redescription*

Body moderately elongated (Figure 6A, G). Head large, about third of body length, without a head shield. Valves suboval, lacking marginal setae. Postabdominal claws relatively short, massive, lacking denticles (Figure 6E).

Mandibles small, strongly chitinized, left and right asymmetrical (Figures 5E, 6C, D). AII relatively small, basal segment massive. Exopod significantly longer than exopod, three-segmented, first segment small, second segment large, thick, with numerous setae (poor preservation of specimens does not allow their number to be counted) (Figure 6B, F, arrows), third (apical) segment approximately as long as second segment, but thinner, also with numerous setae (their maximum number unknown). Endopod approximately as long as basal segment, three-segmented, its first (proximal) segment small, second segment long, seeming to lack setae, third (apical) segment approximately half of third segment, with three apical setae, a sub-lateral seta, and a small spine. There is a possibility that some setae on AII (specially a latero-distal seta on second endopod segment, as in the majority of ctenopods) were lost. No spines were found on any segments except the distal segment of the endopod, but these may have been lost. Reconstruction of AII based on a series of specimens is represented in Figure 5J. Within brood pouch there are numerous (up to 26) resting eggs, brownish, surrounded with a strong membrane (Figure 6G, H).

Size 2.27–4.32 mm, but edges of impressions are not distinct enough; in addition, specimens were strongly compressed and deformed.

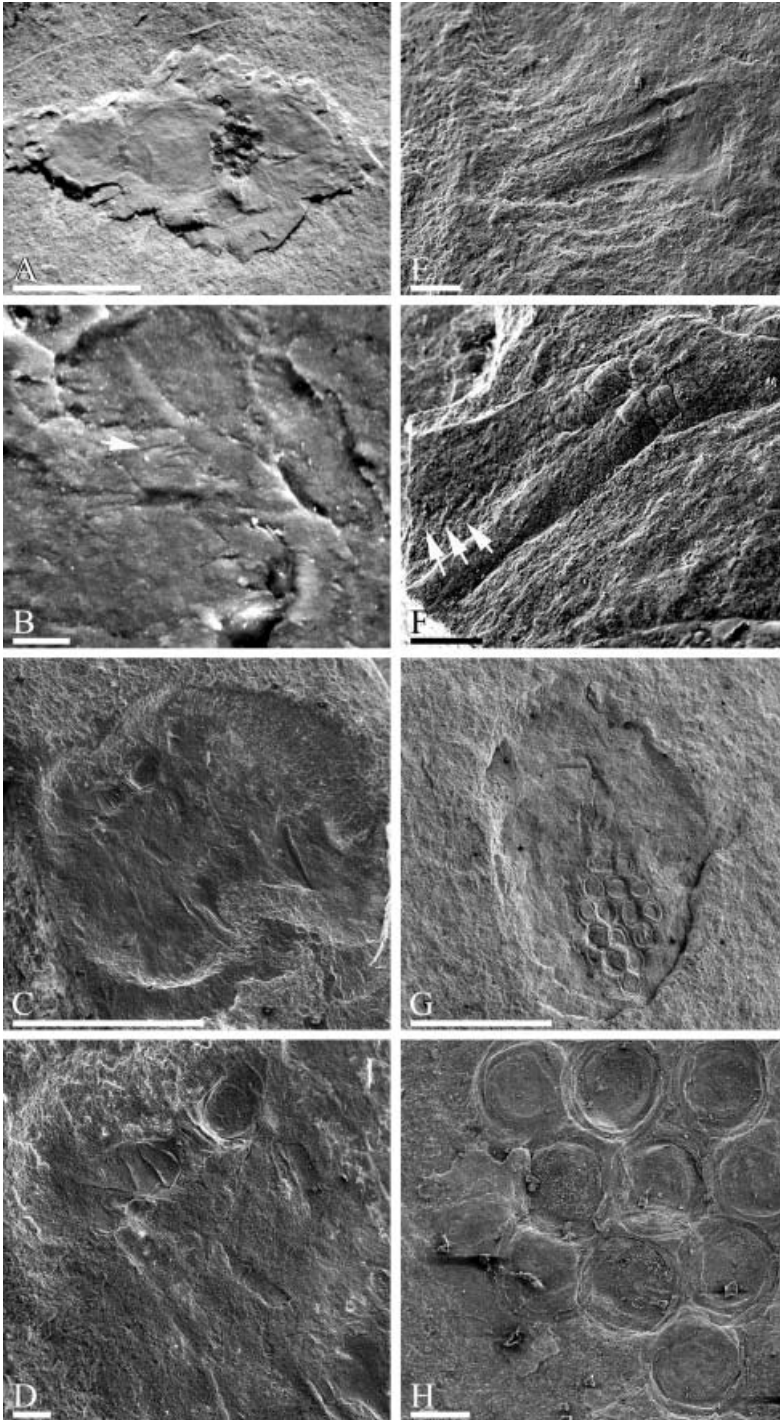


Figure 6. Optical (A, B) and SEM (C–H) micrographs of *Smirnovidaphnia testacea*, Novospasskoe, Asian Russia. (A) Holotype, PIN 3000/40; (B) antenna II, PIN 3000/46; (C) PIN 3000/1, general view; (D) its mandibles and antenna II; (E) its postabdominal claws; (G, H) PIN 3000/015, general view and resting eggs. Scale bars: 1 mm (A, C, G); 0.1 mm (B, D–F, H).

*Comments*

Smirnov (1970) described his genus *Archedaphnia* with four species based on material from mudstones of the Maichat and Ak-Kolka Formations, at the Karaungir River in Saur Range, East Kazakhstan, Upper Changhsigian age, the uppermost Permian. *Archedaphnia kazakhstanica* Smirnov, 1970 was selected as the type species. My re-examination of Smirnov's Permian specimens led to the conclusion that they are not cladocerans, and, most probably, not arthropods: not one segmented appendage was found. So, the generic name *Archedaphnia* is not applicable to "*Archedaphnia*" *testacea* Smirnov, 1971, which is an apparent cladoceran.

Smirnov (1971) placed *A. testacea* in the family Daphniidae (Anomopoda). But this determination was erroneous, based on the details of the holotype. Smirnov himself (Smirnov 1971, p 120) noted strong membranes of the eggs in fossil specimens. I have no doubts that these eggs (Figure 6G, H) were resting eggs. But any traces of an ephippium, a most characteristic trait of the anomopods, are absent in specimens from Novospasskoye. So, the taxon does not belong to the Anomopoda. Both the "helmet" on the head and the "caudal needle" on the posterior portion in Smirnov's (1971) reconstruction (reproduced here as Figure 5D), appeared due to deformation of the specimen marked as the holotype (Figure 6A). My reconstruction of the holotype's appearance is represented in Figure 5E, regions of the "helmet" and the "caudal needle" marked by arrows. Other studied specimens have no projection on the anteriormost and posteriormost extremities of the body.

AII is poorly preserved in the holotype, but is relatively more clear in some other specimens. Reconstruction of AII (Figure 5J), based on a series of better preserved specimens (Figure 5F–I), led me to the conclusion that "*Archedaphnia*" *testacea* is a ctenopod from the tribe Sidini of the subfamily Sidinae, like the animal from Ust'-Basley. The generic status of "*Archedaphnia*" *testacea* is not fully resolved due to relatively poor preservation of all available specimens. Most probably, it belongs to the genus *Smirnovidaphnia* gen. nov., like *S. smirnovi* from Ust'-Baley. The seta on the second endopod segment, the absence of which "distinguishes" *S. testacea* from *S. smirnovi*, was most probably lost in all studied specimens of the former, which are significantly more poorly preserved as compared with the latter.

*Differential diagnosis*

See section on *S. smirnovi*.

**Undetermined claws of type 1***Localities and material*

Ust'-Baley: PIN 1873/37, 39, 40, 44–48, 52, 62, 84, 108, 109, and many others without assigned number. Sogyuty: PIN 2903/732–735. Tushilga: PIN 4024/103, 104. Shurab III: PIN 2345/429–436.

*Description*

Claw remarkably thin, almost straight, lacking any denticles or setules (Figure 7A, B). Size 0.5–0.7 mm.

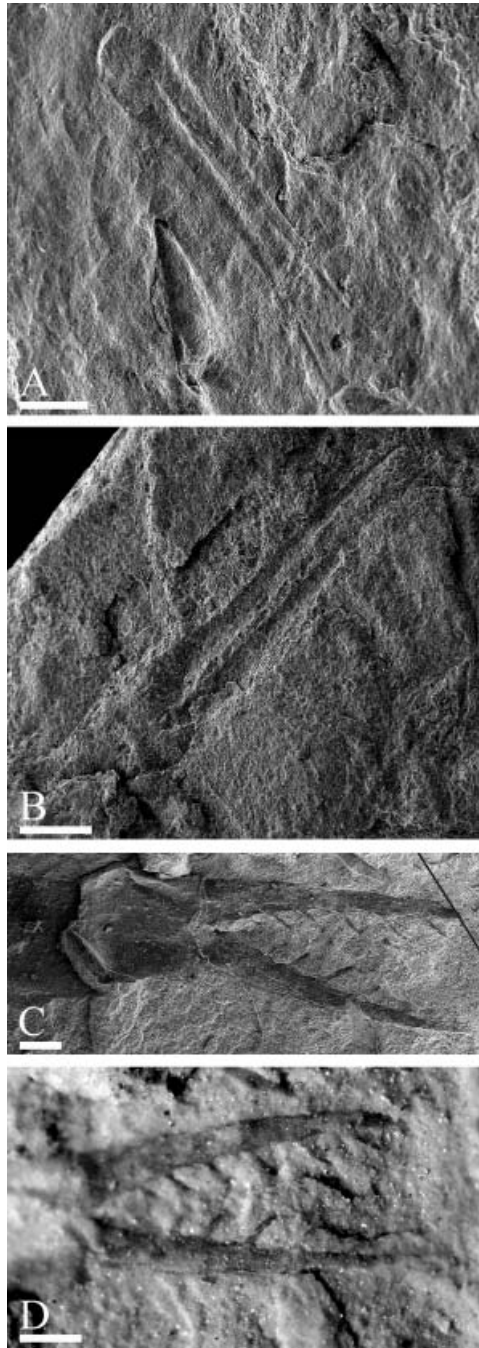


Figure 7. Undetermined claws from possible remains of fossil cladocerans. (A) Type 1 from Ust'-Baley, PIN 1873/108; (B) type 1, Sogyuty, PIN 2903/732; (C, D) type 2, Kubekovo, PIN 1255/1558 and 1255/912. Scale bars: 0.1 mm.

*Comments*

In Ust'-Baley the claws were not associated with any specimen. In other localities only these claws were found, while other microcrustacean fossils were absent. There is a chance that the "owner" of these claws was a cladoceran species. The claws are relatively similar to those in recent haplopod *Leptodora*.

**Undetermined claws of type 2***Locality*

Kubekovo.

*Material studied*

PIN 1255/912, 914, 942, 1558 and numerous un-numbered claws on fragments with insects from this locality.

*Description*

Claw with thick base, regularly narrowing distally up to very sharp tip, slightly curved, four to six thin denticles along inner margin (Figure 7C, D). Size 0.60–0.85 mm.

*Comments*

Only the claws were found. My consultations with palaeontologists did not lead to identification of the claws as parts of any insects. In the same strata, there are numerous conchostracans belonging to eight species (with dominance of *Pseudestheria* sp.), but all of them are small-sized, as was reported by Trusova (1985). I also did not see any single conchostracan specimen longer than 2 mm, the aforementioned claws are too large to be parts of these animals. So, the claws do not belong to any determined fossils from Kubekovo. There is a chance that the "owner" of the claws was a large cladoceran. The largest Recent cladocerans reach sizes of 4–5 mm (though the haplopod *Leptodora* reaches 18 mm!), specimens of this size can possess claws of the necessary length. Among Recent species, ctenopods *Sida* and *Limnosida* have claws maximally similar to those from Kubekovo.

**Discussion***Fifth cladoceran order and its phylogenetic position*

The main problem in erecting the new "calyptomeran" order is to formulate its differences from the orders Anomopoda and, especially, the Ctenopoda (see Table I; Figure 8). Limbs of *Leptodorosida* gen. nov. were of a ctenopod type (filtering and serially similar)—a limb type missing in the Anomopoda. My differentiation of the new order from the ctenopods is based mainly on the characters of AII, which was relatively well preserved.

In ctenopods, the number of segments in both exopod and endopod never exceeds three, with a two-segmented exopod in a majority of genera. The antennal endopod in ctenopods is unique, with a long segment (second one in case of three-segmented endopod and first

Table I. Comparison of four Recent orders of the Cladocera and Cryptopoda ord. nov. (only characters known for the latter are included).

Character	Anomopoda	Ctenopoda	Onychopoda	Haplopoda	Cryptopoda ord. nov.
Thorax and abdomen enclosed in valves	+	+	–	–	+
Antenna II, number of endopod segments	3	0–3	3	4	4
Antenna II, numerous setae on endopod segments 2–4	–	–	–	+	+
Mandibles with strong spines	–	–	+	+	–
Thoracic limbs filtratory	+	+	–	–	+
Morphology of thoracic limbs of different pairs strongly different	+	–	–	–	–

one in case of two-segmented endopod) bearing a single seta, and a small terminal segment with three to four setae (Figure 7F). The single exception is *Holopedium*, females of which possess no endopod. Still, this character state is unique for the family Holopediidae Sars, 1865. Note that the Jurassic *Smirnovidaphnia* gen. nov., the most archaic known sidid, already demonstrates the above-mentioned characteristic “ctenopod” organization of AII.

Among Recent cladocerans, AII with both branches four-segmented is known only for the haplopod *Leptodora*. The Jurassic *Leptodorosida* gen. nov. differs from *Leptodora* in having a large basal segment of the exopod (unique for cladocerans!), and having no setae on the basal segment of the endopod (apparently apomorphic character).

A massive head with a head shield supplied with fornices (as in the Cryptopoda ord. nov.) requires evaluating plesiomorphies of the cladocerans. Fryer (1995, p 59) listed “short head lacked a headshield” as a peculiarity of a pro-anomopod, reconstructed by him. But just a massive head is a characteristic trait of the closest relatives of the cladocerans, “conchostracans”, including *Cyclestheria*, regarded by many authors (Martin and Cash-Clark 1995; Olesen et al. 1996; Negrea et al. 1999; Swain and Taylor 2003) as a sister group of the cladocerans. Although conchostracan investigators never speak about a “head shield” or “head capsule” in the terminology of Dumont and Negrea (2002), the head of conchostracans is basically similar to that in some cladocerans, for example Daphniidae, for which the latter term is used. Also, some conchostracans, i.e. *Lynceus*, have fornices. In contrast to Fryer (1995), I believe the pro-anomopod, as well as a pro-cladoceran (which are, to my mind, quite similar), can be described as an animal with a massive head, possibly covered with a head shield, as in *Leptodorosida* gen. nov. In contrast, a head lacking a head shield in ctenopods, haplopods, and onychopods, as well as in anomopod macrothricids and moinids, is an apomorphic state.

Few authors (Martin and Davis 2001) doubt the necessity of regarding the main cladoceran groups, described by Sars (1865) in a rank of tribes, as separate orders. Instead, the majority of investigators (Martin and Cash-Clark 1995; Dumont and Negrea 2002; Korovchinsky 2004) follow the approach of Fryer (1987), who suggested the rank of order for each of the Anomopoda, Ctenopoda, Haplopoda, and Onychopoda. I have provided evidence here for a new, extinct, lineage, the fifth cladoceran order.

There is no consensus among recent investigators about the phylogenetic relationships among the cladoceran orders. Sars (1865) proposed the Calyptomera (Anomopoda + Ctenopoda) and Gymnomera (Haplopoda + Onychopoda). This point of view was supported recently by De Waard et al. (2006) and Stenderup et al. (2006), but in both cases in reality support of the branch “Calyptomera” was not sufficient for an accurate

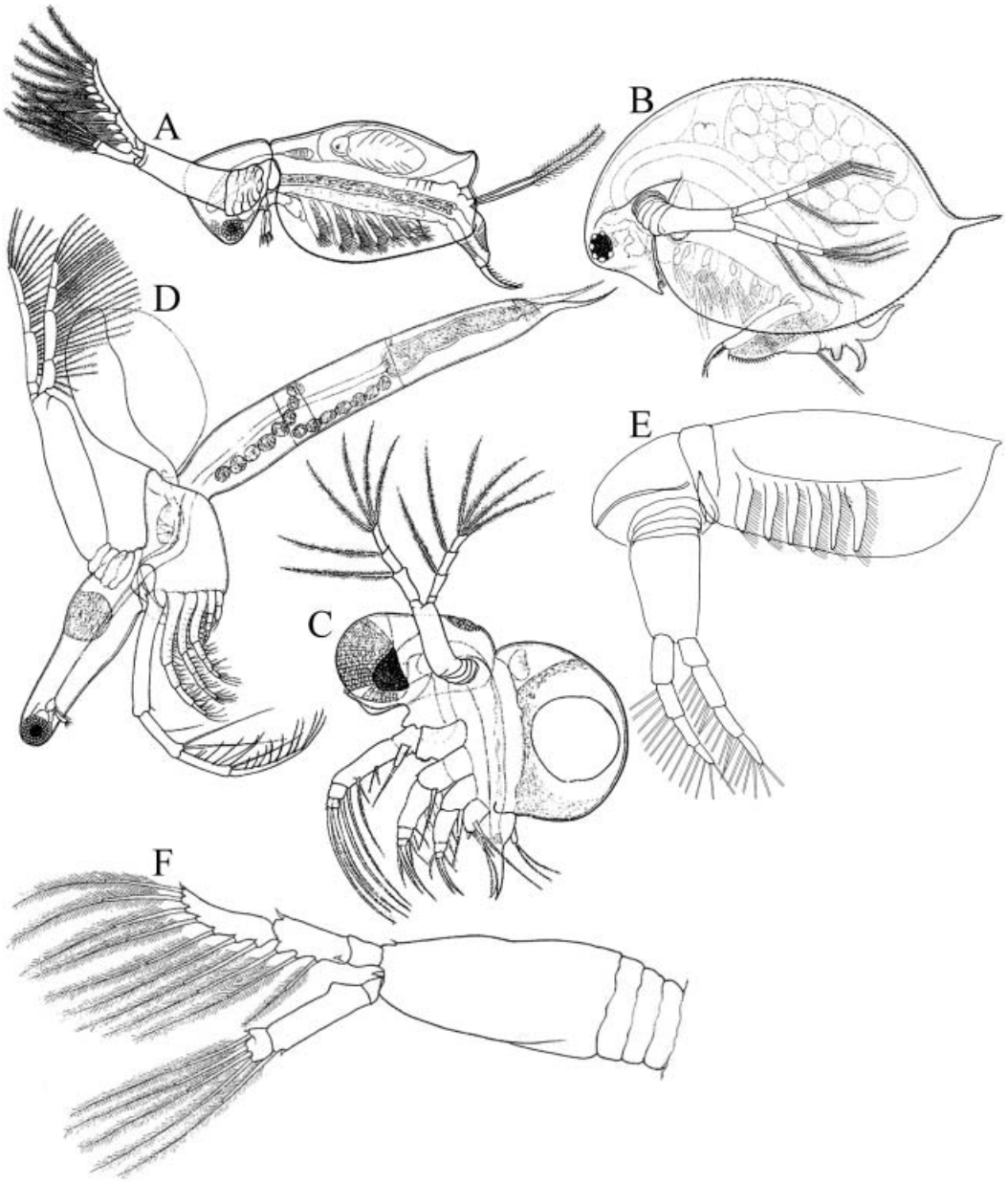


Figure 8. Representatives of Recent (A–D, F) and extinct (E) orders of the Cladocera. (A) *Limnosida frontosa* (Ctenopoda); (B) *Daphnia pulex* (Anomopoda); (C) *Podon leuckarti* (Onychopoda); (D) *Leptodora kindtii* (Haplopoda); (E) *Leptodorosida zherikhini* gen. nov. (Cryptopoda ord. nov.); (F) antenna II of *Limnosida frontosa* (Ctenopoda). (A–D, F) After Lilljeborg (1901).

conclusion. Other recent authors have doubted the monophyly of the first (Swain and Taylor 2003), or the second (Dumont and Negrea 2002) group, or both groups (Olesen 2003). Fryer (1987) suggested a complete polyphyly of the cladocerans, without any grouping, but this point of view has not been accepted by a majority of subsequent authors (Dumont and Negrea 2002; Swain and Taylor 2003; Olesen 2003).

Only a few years ago, Fryer (2002, p88) remarked of the cladocerans that “of their ancestors we have as yet no helpful fossil evidence”. But now this situation has changed, and I think that my finding of Cryptopoda ord. nov, resembling the hypothetical pro-cladocerans, and possessing intermediate characters between the “Calyptomera” and Gymnomera, may be regarded as new evidence of cladoceran monophyly.

Phylogeny of the cladocerans can be a theme of a special expanded discussion, and of a special large article (if not a monograph), not of this short communication. Here I prefer to agree with the tree constructed by Swain and Taylor (2003), well supported by data from different genes, with a basal position of the Anomopoda, paraphyletic “Calyptomera” (Anomopoda plus Ctenopoda) and monophyletic Hymnomera (Haplopoda plus Onychopoda). *Leptodorosida* gen. nov. is apparently the most archaic known cladoceran, but its position on the tree (according to Swain and Taylor 2003 or according to other aforementioned authors) is somewhat ambiguous. The extinct order is “a collection of plesiomorphies”, having no synapomorphies with Recent orders. Most probably, Cryptopoda ord. nov. is a maximally basal taxon of the cladoceran clade (keeping in mind the unique large basal segment of the antennal exopod), but it can be also a relative of the Anomopoda, or even an archaic pro-hymnomeran. My finding does not support any viewpoint on the cladoceran phylogenetic tree within a monophyletic approach. But, better preserved fossil cladocerans could supply us with strong evidence for the correctness of one of the other variants of the phylogenetic tree.

#### *Comments on fossil ctenopods and anomopods*

Surprisingly, the most common fossil cladocerans are ctenopods, now known since Earlier Jurassic. Their bodies are soft, the cuticle is not so thick and firm as in anomopods (especially, chydorids), but their AII is a well-preserved structure. Previously Kotov and Korovchinsky (2006) found a ctenopod *Archelatona* belonging to the tribe Latonini Korovchinsky, 1985 of the subfamily Sidinae from the Lower Cretaceous, similar to Recent advanced sidid genera.

In contrast, *Smirnovidaphnia* gen. nov. is the most archaic known representative of the family Sididae. All its characters of generic rank are plesiomorphies for the family Sididae. At the same time, this extinct Jurassic genus had already a very characteristic AII of the sidid type, slightly differing from that in Recent genera only in a less oligomerized system of the exopod setae. But the endopod of *Smirnovidaphnia* was already indistinguishable from that in recent sidids!

No fossil anomopods have been found at the studied Jurassic localities, although they apparently may have existed at that time (Fryer 1995; Sacherová and Hebert 2003). Both Permian (Smirnov 1970) and Jurassic (Smirnov 1971) records of the anomopods were misidentifications. So, the oldest anomopods known at this moment are from the Jurassic–Cretaceous boundary (locality Khotont; see Smirnov 1992). Ehippia from Khotont can be already attributed to Recent genera *Daphnia*, *Simocephalus*, and *Moina*. Older anomopods will be likely found in the future.

Recently Korovchinsky (2006) concluded that the extant Cladocera is a relict group of “living fossils”, whose taxa were widely distributed in the past. Previously, cladocerans were considered to be rarely preserved in the Mesozoic strata, but my study supports the hypothesis that Jurassic cladoceran rarity is due to investigators overlooking or not actively looking for cladocerans. I found Jurassic cladocerans, including a new order, by analysing



rock fragments in PIN from localities well known to palaeontologists. It is likely that the collections of other museums also contain overlooked cladoceran fossils.

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