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First record of fossil Mesozoic Ctenopoda (Crustacea, Cladocera)

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Pre-Pleistocene representatives of the crustacean order Ctenopoda Sars, 1865 are unknown. Here we describe Mesozoic fossil specimens of ctenopods from two localities in Mongolia: Khotont (Jurassic/Cretaceous boundary, about 145 Mya) and Khutel Khara (Lower Cretaceous, about 129 Mya). All specimens apparently belonged to the tribe Latonini Korovchinsky, 1986 of the subfamily Sidinae Baird, 1850. At the Khotont site, ctenopods were the most numerous microscopic animal fossils. We assigned these cladocerans to a new genus and species ***Archelatona zherikhini* gen. nov., sp. nov.** Our findings support a pre-Cretaceous origin for cladocerans.

ADDITIONAL KEYWORDS: Sididae – Mongolia – systematics.

INTRODUCTION

It is well known that cladoceran body parts (head shields, antennal segments, post-abdominal claws) and hard egg cases (ephippia) are commonly preserved in lacustrine sediments (Frey, 1962, 1964). However, until Smirnov (1970, 1971) described Late Palaeozoic to Mesozoic fossil anomopods, the cladocerans were considered a comparatively young group (Tasch, 1969). Lai Xing-rong & Li Ying-pei (1987) also found older fossilized ephippia (from Eocene and Oligocene deposits). Recently, Anderson, Crighton & Hass (2004) described crustaceans similar to the Cladocera in the Early Devonian Rhynie chert. Nevertheless, all of the known pre-Pleistocene cladocerans likely belong to one order, the Anomopoda Sars, 1865. The missing cladoceran orders (Ctenopoda Sars, 1865, Haplopoda Sars, 1865, and Onychopoda Sars, 1865) apparently form a clade (Swain & Taylor, 2003) and lack the hard egg case (ephippium) that is readily fossilized in the anomopods. Remains older than about 200 000 years are unknown for the non-anomopod cladocerans (Kadota, 1987).

The extensive collection of the Paleontological Institute of the Russian Academy of Sciences (PIN) houses numerous fossils, including those of microcrustaceans, obtained in expeditions to different regions of Northern and Central Asia (Rasnitsyn & Quicke, 2002). The investigation of impressions of this collection resulted in finding the Permian/Jurassic genera *Archedaphnia* Smirnov, 1970 and *Propleuroxus* Smirnov, 1970 (Smirnov, 1970, 1971). Then three species of the Prochydoridae Smirnov, 1992, and the ephippia of different Daphniidae Straus, 1820 from the Jurassic/Cretaceous boundary were described by Smirnov (1992).

Sinitshenkova & Zherikhin (1996) reported cladocerans as common, and sometimes dominating in abundance, for several Mesozoic lakes. Our re-examination of these fossils confirmed their conclusion, revealing numerous cladoceran impressions, which have yet to be investigated. The aim of this publication is to describe Mesozoic cladocerans of the order Ctenopoda Sars, 1865. These are the first pre-Pleistocene fossils from non-ephippial cladocerans.

MATERIAL AND METHODS

The accessible rock fragments from two Mongolian localities (see below) were examined under stereo- and compound microscopes; 21 fragments from Khutel Khara, with comparatively complete and distinct

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impressions, and a single fragment from Khotont were selected. Micrographs were taken using a scanning electron microscope (CAMSCAN MB2300) after coating with gold.

Abbreviations: AII, rami of antenna II with setae, the number of which is described as an 'antennal formula'.

RESULTS

FAMILY SIDIDAE BAIRD, 1850
SUBFAMILY SIDINAE BAIRD, 1850
TRIBE LATONINI KOROVCHINSKY, 1986
ARCHELATONA GEN. NOV.

Type species. *Archelatona zherikhini* sp. nov.

Etymology. The name originates from the Greek ἀρχή meaning origin, and the genus name *Latona*, from which the name of the tribe Latonini was derived.

Diagnosis. Large cladocerans, with body size about 1.8–3.0 mm. Antenna II with two-segmented exopod and three-segmented endopod. Distolateral spines on both basal and distal segments of antennal exopod small. Antennal setae (7–9)–(11–15)/(0)–(≥ 1)–(4), all setae of endopod similar, unspecialized.

Differential diagnosis. *Archelatona* gen. nov. differs from all close (Recent) genera of the tribe (*Latona*, *Latonopsis*, *Sarsilatona*, *Pseudosida*) in having small distolateral spines on both the basal and the distal segments of the antennal exopod and similar, unspecialized setae on the endopod.

ARCHELATONA ZHERIKHINI SP. NOV.

Etymology. This species is dedicated to the outstanding palaeontologist, Professor V. V. Zherikhin, whose many contributions include organizing PIN expeditions, collecting fossils and determining taxonomies of fossils. His untimely death in December 2001 was a great loss to Russian science.

Type locality. Khutel Khara, mudstones 75 km southeast of Sain Shand, East Gobi Aymag, Mongolia. The geological structure of this locality was reported by Verzilin & Kalmykova (1993). The sediments were deposited in a small (but permanent), oligotrophic mountain lake that formed when a volcanic basalt field dammed a valley. More than 3300 impressions of insects from 14 orders and 49 families have been recovered from these sediments (A. G. Ponomarenko, pers. comm.). Ctenopod remains are very common; they appear to have dominated among the group of microscopic animals. Mono-egged daphnid ephippia are also relatively common, but no single adult specimen has been found.

Age. Lower Tsagan Tsab Formation, Lower Cretaceous, 129 ± 9 Mya (Verzilin & Kalmykova, 1993).

Holotype. PIN 3965/3332 (stub sputtered with gold). AII: (7)–(13)/(0)–(1)–(4). There are two antennae II (belonging to different specimens) on the fragment; the holotype is the better preserved one, marked by an arrow. Label of the holotype: '*Archelatona zherikhini* gen. nov., sp. nov., Khutel-Khara, Mongolia, 3965/3332, Holotype'.

Paratypes. (1) PIN 3965/3293. AII: (8)–(> 11)/(0)–(1?)–(4). AII: (8)–(13)/(0)–(1?)–(4). (2) PIN 3965/3295. AII: (9)–(13)/(0)–(?)–(?). AII: (7)–(≥ 10)/?. AII: (7)–(> 8)/?. (3) PIN 3965/3298. AII: incomplete. AII: incomplete. (4) PIN 3965/3299. Unclear body contour, mandibles and AII: (?)–(≥ 10)/?. AII: (7)–(?)/?. (5) PIN 3965/3301 AII: (7)–(≥ 8)/(0)–(1)–(4). (6) PIN 3965/3303. Unclear body contour, mandibles and AII: (8)–(13)/(0)–(?)–(4). (7) PIN 3965/3304. AII: (8)–(15)/(0)–(?)–(?). (8) PIN 3965/3308. AII: incomplete. (9) PIN 3965/3317. Body contour, mandibles and AII: unclear. (10) PIN 3965/3320. AII: (7)–(?)/(0)–(?)–(?). (11) PIN 3965/3321. AII: (8)–(?)/(0)–(2?)–(4). (12) PIN 3965/3323. AII: unclear. (13) PIN 3965/3324. AII: (11)–(8)/(0)–(1)–(4). AII: unclear. (14) PIN 3965/3325. AII: (≥ 7)–(12)/?. AII: unclear. (15) PIN 3965/3326. AII: incomplete. (16) PIN 3965/3332. AII: (?)–(≥ 10)/(0)–(1)–(4) – on the same fragment as the holotype. (17) PIN 3965/3333. AII: (≥ 6)–(≥ 12)/(0)–(1)–(4). Body contour, mandibles, two AII (unclear), limbs. (18) PIN 3965/3334. AII: (6?)–(≥ 12)/0-(1)–(4). (19) PIN 3965/3335. AII incomplete. (20) PIN 3965/3337. Many mandibles. (21) PIN 3965/3338. Many mandibles.

Diagnosis. As for the genus.

Description. Mostly rami of swimming antennae are preserved, sometimes accompanied by body contours, mandibles and filtering setae of thoracic limbs (Fig. 1A–C). Accordingly, the morphological features of these cladocerans may be reconstructed as follows. Body is probably widely ovoid. Antenna II long and massive, with two-segmented exopod and three-segmented endopod (Figs 1D–F, 2A–D). In exopod, the proximal segment relatively short and wide, with a small distolateral spine (Fig. 2B), whereas distal segment is relatively long, also having a small distolateral spine (Fig. 2C,D). Number of setae of the inner margin of the exopod somewhat variable, ranging from seven to nine on the proximal segment and from 11 to 15 on the distal segment. Endopod seems to be always armed with five setae. Antennal formula (7–9)–(11–15)/(0)–(1)–(4). Each seta of exopod sits on a conspicuous basal prominence. Length of exopod 0.63–0.95 mm. Endopod composed of a short basal segment, a long middle segment with an apical seta, and a short, rounded distal segment bearing a single lateral seta and three apical seta. In some specimens (i.e. 3965/3321), it seems that

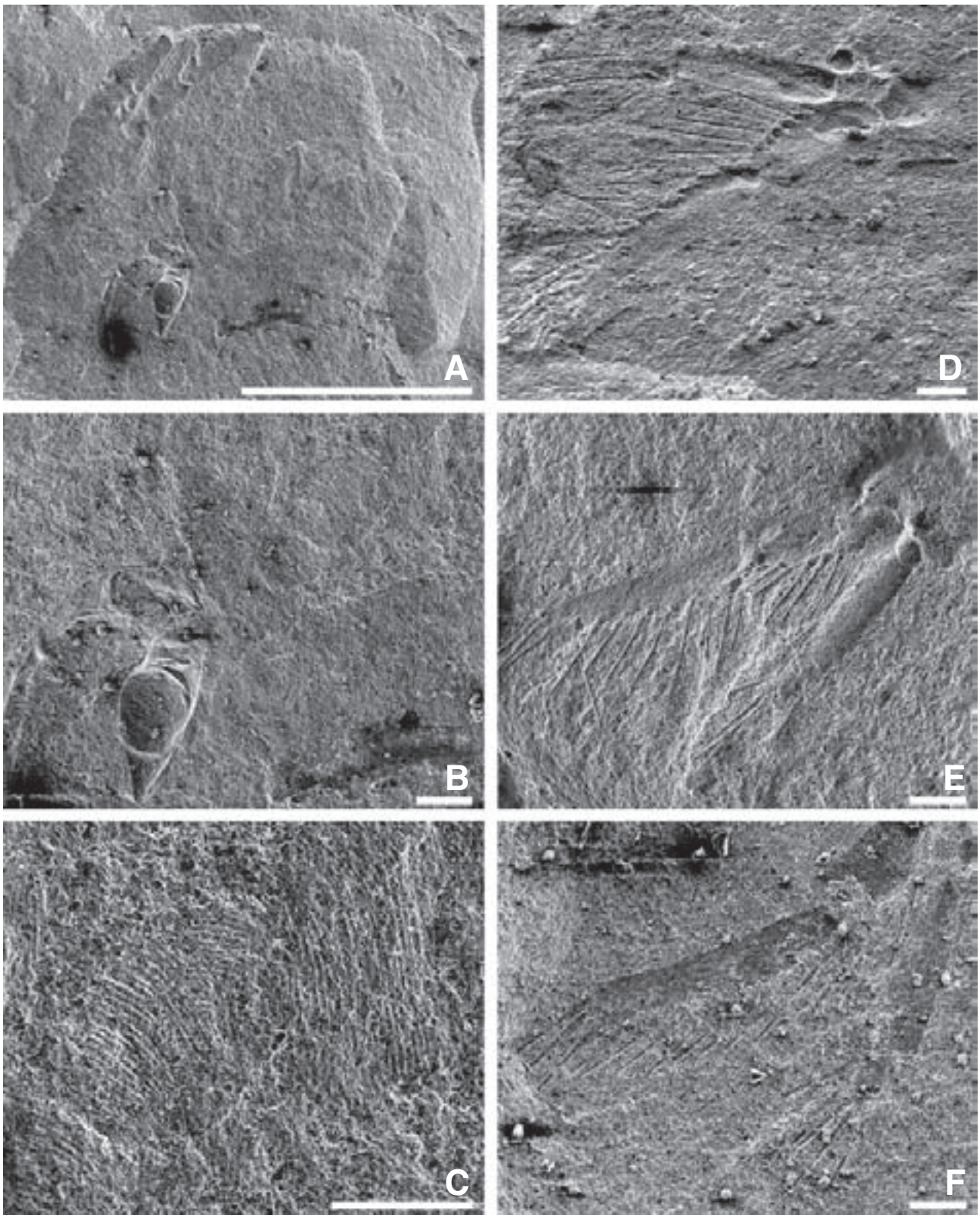

Figure 1. ***Archelatona zherikhini*** **gen. nov., sp. nov.**, paratypes, Khutel Khara, Mongolia, Lower Cretaceous. (A) Whole body, impression PIN 3965/3333. (B) The same fragment, mandibles and thoracic limbs. (C) Filtering setae on thoracic limbs. (D) Rami of swimming antenna, and other impressions on fragment PIN 3965/3333. (E) Rami of swimming antenna, PIN 3965/3334. (F) Rami of swimming antenna, PIN 3965/3332. Scale bars: A, 1000 μm; B–F, 100 μm.

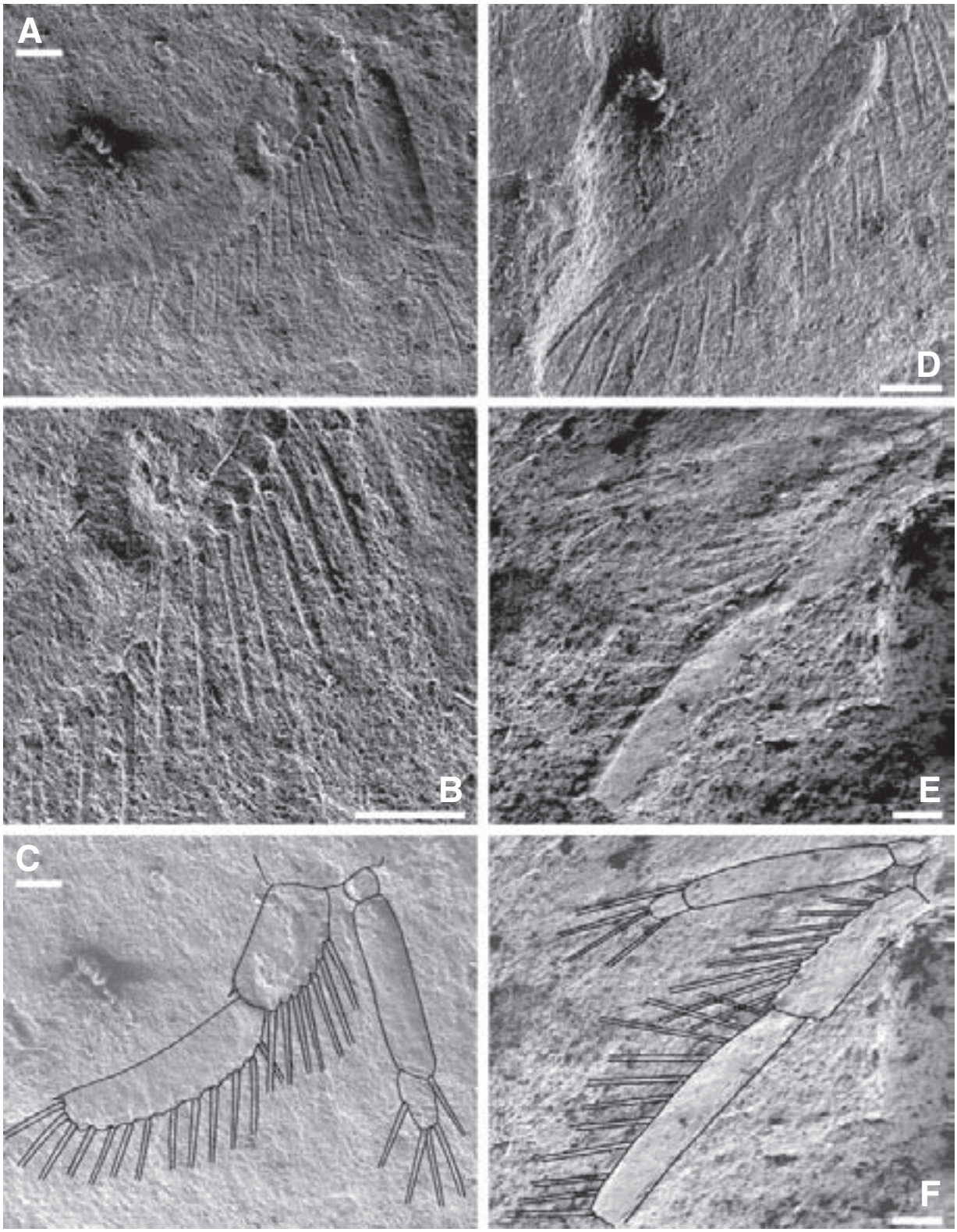

Figure 2. ***Archelatona zherikhini*** **gen. nov., sp. nov.**, holotype, Khutel Khara, Mongolia, Lower Cretaceous, PIN 3965/3332 (A–D), and Sididae indet. from Khotont, Jurassic/Cretaceous boundary, PIN 4307/2005 (E–F). (A) Rami of swimming antenna. (B) Articulation of segments of antennal exopod. (C) Reconstruction of antennal rami. (D) Distal segment of exopod. (E,F) Rami of swimming antenna, and their reconstruction. Scale bars: 100 μm.

there is a second seta on the middle segment, but this is probably an artefact because this seta is absent on clear impressions (Figs 1D–F, 2A–C). All setae of endopod uniform, unspecialized. Mandibles massive, asymmetrical (Fig. 1A,B). Several thoracic limbs similar, with numerous filtering setae (Fig. 1C). The proportion between body length and antennal exopod length in specimen 3965/3306 is about 3 : 1, similar to proportions of some Recent ctenopods. Thus, we may conclude that the approximate body size of these cladocerans was about 1.8–3.0 mm.

Sididae indet.

Locality. Rocks of the northern slope of Ukha Mtount, 6 km west of Somon Khotont, Ara-Khangay Aymag, Mongolia. Numerous freshwater insects (or/and their larvae) from several orders (more than 1500 impressions), characteristic for the latest Jurassic and Lower Cretaceous, were also collected (Rasnitsyn & Quicke, 2002). Only a single ctenopod specimen was found among numerous cladoceran remains (hundreds of impressions), the majority of which were assigned to adult prochydorids and ephippia of daphniids (see Smirnov, 1992).

Age. Jurassic/Cretaceous boundary, 145 Mya (Rasnitsyn & Quicke, 2002).

Material. (22) PIN 4307/2005. AII.

Description. Only rami of antenna II of this putative sidid cladoceran have been preserved, although not too distinct (Fig. 2E), antennal formula (9)–(> 11)/(0)–(≥ 1)–(≥ 3). The reconstruction of the impression is shown in Fig. 2(F). Both rami seem to be thin, but this may be an artefact. Exopod length 0.91 mm. Apical setae of the exopod, one of the apical setae of the endopod and distolateral spines of the ramal segments are apparently missing. Approximate body size 2.7 mm.

DISCUSSION

The fossil remains from Khutel Khara and Khotont belong to representatives of the family Sididae Baird, 1850 (order Ctenopoda Sars, 1865). Only these cladocerans possess the characteristic antenna II with large segments, numerous setae on the inner side of the exopod, and a series of thoracic limbs of similar structure, armed with numerous filtering setae. More closely, sidids from both localities belong to the tribe Latonini Korovchinsky, 1986 of the subfamily Sidinae Baird, 1850, because they have a two-segmented exopod with long segments and a three-segmented endopod with small basal and distal segments, and an elongated middle segment. Among recent members of the Latonini, species of the genera *Latona* Straus, 1820 (especially *L. tiwari* Biswas, 1964), *Latonopsis* Sars, 1888 (especially *L. brehmi* Petkovski, 1973, the largest member of this genus), *Sarsilatona* Korovchinsky, 1985, and *Pseudosida* Herrick, 1884 have the structure and armature of the antennal rami (see Korovchinsky, 1986, 1992) quite similar to those found in the Mongolian fossils. However, the aforementioned Recent sidids have two specialized ventralmost setae on their endopod (one on the distal segment one on the end of the middle segment). These are enlarged and often supplied with hooked tips, especially in *Pseudosida* (see Korovchinsky, 1992). By contrast, all setae of the antennal endopod of the fossil specimens are rather thin and uniform. Moreover, fossil specimens have small distolateral spines on both of the exopod segments, whereas in all Recent species of the aforementioned genera these spines are large. Only *L. brehmi* has a relatively small spine on the distal segment of the exopod, but a rather large spine on its middle segment (see Korovchinsky, 1992: fig. 69). Based on these characteristic traits of the ctenopods from Khutel Khara, we conclude that the fossil specimens represent a new extinct taxon of generic rank of the tribe Latonini, members of which are characterized by a set of plesiomorphic features.

Smirnov (1992: 114, fig. 14c) has studied the impression PIN 4307/2005 from Khotont and attributed it to 'one of the two orders into which the Conchostraca are now divided'. However, this is doubtful, because the latter crustaceans have both antennal rami consisting of small, numerous segments. The rami of antenna II from Khotont are of the Latonini-type, although they differ from those from Khutel Khara in having (possibly) much more slender exopodal segments, the most proximal of which is comparatively longer. However, all setae of the endopod are uniform as in specimens from the latter locality. We consider that the impression from Khotont belongs to another unknown extinct representative of the family Sididae, the taxonomic status of which remains unclear due to its poor preservation. Unfortunately, the impression lacks any further morphological structures, which are important for a more detailed systematic affiliation.

Keeping in mind that the related Recent representatives of Latonini are bottom-dwelling filter-feeders (Korovchinsky, 1986, 2004), we assume that this lifestyle may also be characteristic of *A. zherikhini*. This mode of life would be plesiomorphic among the cladocerans and existed already in the Mesozoic. In addition, the large number of antennal setae is a plesiomorphic feature of ctenopod morphology.

In the eastern hemisphere, representatives of the extant genera *Sarsilatona* and *Latonopsis* have been reported from a few localities in Africa, India and Australia (Korovchinsky, 1992, 2004). The more northerly

distribution of the Mesozoic relatives described here (i.e. Mongolia) may be due to the warmer global climate during that epoch or to a difference in thermal preferences.

We found that representatives of the tribe Latonini existed 145 Mya. Moreover, our data support the idea that cladocerans diverged prior to the Cretaceous (Frey, 1987; Fryer, 1995). Most probably, ctenopods, with their plesiomorphic morphology (for extant cladoceran taxa), are at least as ancient as the more advanced anomopods. Unambiguous fossil anomopods are known from the Jurassic (Smirnov, 1971, 1992; Fryer, 1991), and ambiguous anomopod-like fossils are described from the Permian (Smirnov, 1970). 'Molecular clock' calculations revealed that the genus *Daphnia* has an age of 200 Myr, and that the subgenera within this genus have been differentiated for about 180 Mya (Colbourne & Hebert, 1996). The subfamilies of the family Chydoridae are of Early Palaeozoic origin, and the chydorid genera probably differentiated in the Middle Palaeozoic, approximately 400 Mya (Sacherová & Hebert, 2003). No similar calibrations have been made for ctenopods, but the genetic divergences among some extant ctenopod genera (*Diaphonosoma*, *Holopedium*, *Sida* and *Latonopsis*) are very similar to the genetic divergences among daphniid genera (Swain & Taylor, 2003). Our new fossil descriptions provide robust evidence for the antiquity of ctenopods and offer hope for the discovery of additional fossils of cladoceran taxa that lack hard egg cases.

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