

Ecological Aspects of the Evolution of Caddisflies of the Family Philopotamidae (Insecta, Trichoptera) and a New Species of the Genus *Archiphilopotamus* from the Jurassic of Kyrgyzstan

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Abstract—The caddisfly *Archiphilopotamus sagulicus* Sukatsheva, sp. nov. (Philopotamidae) is described from the Lower Jurassic of Kyrgyzstan (locality Shurab III (Sai-Sagul)). A list of fossil Philopotamidae is provided, and ecology and taphonomy of fossil Philopotamidae is analyzed. Three extinct genera dominated in the Jurassic and Lower Cretaceous lacustrine deposits of various origins, while two extant genera were dominant in Late Cretaceous and Cenozoic fossil resins. This pattern supports the hypothesis of high oxyphily of preimaginal philopotamids through all their traceable history in spite of their limnic rather than lotic habits before the mid-Cretaceous. This might have been associated with high oxygen levels in the Mesozoic lakes before the mid-Cretaceous, a specific and extinct lake type that differed from the later lakes, according to competing hypotheses, in being either hypotrophic, or with abundant floating plant-and-bacterial mats.

Keywords: Caddisflies, Trichoptera, new species, hypotrophic lakes, floating plant-and-bacterial mats

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INTRODUCTION

This study is based on material from the Lower or Middle Jurassic of Kyrgyzstan (Osh Region, Batken District, Shurab III (Sai-Sagul) locality), collected in 1964 by an expeditionary team of the Paleontological Institute of the USSR Academy of Sciences (PIN USSR Academy of Sciences, now PIN RAS). Based on the type of wing venation, this fossil can be attributed to one of two ancient families of caddisflies with a similar type of forewing venation—Philopotamidae Stephens, 1829 and Necrotauliidae Handlirsch, 1906. The described fossil has only one character that is characteristic of necrotauliids, namely, a long anal loop and a rather short free apical segment A_1 . However, among modern philopotamids there are species with the same configuration of anal veins, for example, in the genus *Chimarra* Stephens, 1829, in the Australian species *Ch. uranka* Mosely et Kimmins, 1953. In addition, in necrotauliids the cells DC, MC and TC are open in most cases, and on the described wing from Shurab III they are closed, which, in combination with other characters, allows this fossil to be assigned to the genus *Archiphilopotamus* Sukatsheva,

1985 of the family Philopotamidae. As for closed cells DC, MC and TC, it should be noted that among representatives of Necrotauliidae there are also forms with closed cells, such as the genus *Pteromixanum* Sukatsheva et Jarzembowski, 2001 from the Early Cretaceous of southern England (Sukatsheva and Jarzembowski, 2001). However, in this case, all species of the genus lack fork F_4 and the additional branch on SC, and the wing impressions do not exceed 5 mm. Summing up the comparison of ancient philopotamids with necrotauliids and seeing how similar they may be, one can agree that necrotauliids, despite numerous revisions, still represent a composite family that includes quite diverse forms of ancient primitive caddisflies, possibly including some philopotamids.

Based on the venation of the forewings, which are most frequently preserved in fossils, the family Philopotamidae is one of the most primitive among modern caddisflies (Aristov and Sukatsheva, 2018; Sukatsheva and Sinitshenkova, 2023). The forewings usually have all five apical forks, occasionally lacking the first or fourth fork. The discoidal, medial, and thyridial cells are closed, with the medial cell often slightly or significantly longer than the discoidal one. The TC cell is

quite short. CuP and A₁ terminate at the posterior margin of the wing at a single point or close to each other. The anal field is wide.

The oldest reliable representatives of the family Philopotamidae are known primarily from Jurassic deposits. In total, the paleontological record has recorded more than 50 species of this family from the Jurassic, Cretaceous, Oligocene, and Miocene (Sukatsheva and Vasilenko, 2020; Wang et al., 2021; Sukatsheva and Sinitshenkova, 2023). Tables 1 and 2 show fossil philopotamids from deposits of varying ages and origins. They are associated with various types of continental water bodies (large plains, foothills, mountains, river oxbow lakes, and backwaters). However, fossil philopotamids are most often found in ancient resins and ambers.

More than a thousand species of philopotamids have been described in the modern fauna (Morse, 2011). They are distributed worldwide and develop primarily under rocks in fast-flowing, cold streams, mountain torrents, or in flowing and coastal areas of lakes, where the water retains the high levels of oxygen necessary for these insects. The larvae are filter feeders.

In total, over 3350 specimens of fossil insects belonging to 15 orders were collected from the Shurab III locality (Sai-Sagul) by expeditions of the Paleontological Institute over the years of collection (1957–1959, 1961, 1962, 1964, 1969, 1971) (Sukacheva and Rasnitsyn, 2004). According to the most recent data, only six specimens of caddisflies are recorded from this locality, of which two species have been described: *Dolophilodes (Sortosella) shurabica* Sukatsheva, 2004 and *Archiphilopotamus sagulicus* sp. nov.; the remaining finds are represented by wing fragments, the identification of which is difficult, but all of them are also assigned to the family Philopotamidae.

All materials used in the work are housed in the collections of the Arthropod Laboratory of the A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN RAS).

SYSTEMATIC PALEONTOLOGY

Order Trichoptera KIRBY, 1813

Family Philopotamidae Stephens, 1829

Genus *Archiphilopotamus* Sukatsheva, 1985

Key to species of the genus *Archiphilopotamus*
based on their forewings

- 1 (4) Small insects with front wings no more than 5.0 mm.
- 2 (3) CuP and A₁ terminate close to each other. Stem of fork F₁ is shorter than the stem of F₂.....*A. mancus* Sukatsheva, 1985
- 3 (2) CuP and A₁ terminate at one point. Stem of fork F₁ is as long as F₂.....*A. kubekovenssis* Sukatsheva et Vasilenko, 2020

- 4 (1) Insects of medium size, forewings more than 5.0 mm.
- 5 (6) Bases of F₁ and F₂ are at the same level.....*A. luxus* Sukatsheva, 1985
- 6 (5) Stem of fork F₁ is somewhat shorter than stem of fork F₂
- 7 (8) Vein RS₁ is bent toward RS₂, forming a short, small false fork, then again departs from RS₂, forming a real fork F₁.....*A. absurdus* Sukatsheva et Vasilenko, 2020
- 8 (7) Vein RS₁ straight, not bent toward RS₂
- 9 (10) Base of fork F₅ is at the same level as the base of the DC cell.....*A. sagulicus* Sukatsheva, sp. nov.
- 10 (9) Base of fork F₅ is more basal than the base of cell DC.....*A. expectatus* Sukatsheva et Sinitshenkova, 2023

Archiphilopotamus sagulicus Sukatsheva, sp. nov.

E t y m o l o g y. From *sagulicus* after the location of Shurab III (Sai-Sagul).

H o l o t y p e. PIN, no. 2389/578, direct imprint of an almost complete forewing; Kyrgyzstan, Shurab III (Sai-Sagul); Lower–Middle Jurassic, Sogul Formation.

D e s c r i p t i o n (Fig. 1). The wing is quite wide; its length is 2.3 its width. The greatest width of the wing is at the level where CuA₂ flows into the posterior margin. The greatest width of the wing is at the level of its confluence with the posterior margin. The anterior margin of the wing is slightly convex. The costal field is twice as wide at the base as at the apex. SC is rather long, entering the anterior margin of the wing in the middle of the third quarter of the wing length, slightly distal to the base of forks F₁ and F₂. R is straight, with a slight bend at the base of fork F₂. The additional branch of SC is oblique, located at the level of the middle of the second quarter of the wing length and slightly proximal to the base of fork F₅. There is an oblique, slightly curved cross-vein r–rs₁ located slightly distal to the base of fork F₁. RS is four-branched. Judging from the wing width, M is probably also four-branched, but this area of the wing is too poorly preserved to be certain. The trunk of the F₁ fork is slightly shorter than the trunk of the F₂. Cell DC is very short, closed by a straight crossvein rs₂–rs₃, located distal to the bases of forks F₁ and F₂. There is a slightly oblique cross-vein rs₄–m₁₊₂. M probably branches slightly distal to the branching site of RS (it is not possible to determine this more precisely due to the poor preservation of this area of the wing). Cell MC is closed by a straight cross-vein m₂–m₃, located at the base of fork F₃. Fork F₅ fork is long, its base is located at the level of the end of the second quarter of the wing length and at the level of the RS bifurcation. The TC cell is quite long, closed by a straight cross-

Table 1. Stratigraphic and geographic distribution of fossil Philopotamidae

Location/age	Taxon	Reference
Dominican Amber/Miocene	<i>Chimarra weitschati</i> Wichard, 1983 <i>Ch. resinae</i> Wichard, 1983 <i>Ch. palaeodominicana</i> Wichard, 1983 <i>Ch. dommeli</i> Wichard, 1983 <i>Ch. succini</i> Wichard, 1983 <i>Ch. palaenova</i> Wichard, 2007	Wichard, 1983 Wichard, 1983 Wichard, 1983 Wichard, 1983 Wichard, 1983 Wichard, 2007
Saxon amber/late Eocene	<i>Wormaldia contigua</i> Mey, 1986 <i>W. advenaria</i> Mey, 1988 <i>W. angularia</i> Mey, 1986	Mey, 1986 Mey, 1988 Mey, 1986
Baltic amber/late Eocene	<i>Wormaldia aequalis</i> Hagen, 1852 <i>W. wlipla</i> Ivanov et Melnitsky, 2005 <i>W. sukatshevae</i> Ivanov et Melnitsky, 2005 <i>Philopotamus hamatus</i> Ulmer, 1912 <i>Electrocanthinus klebsi</i> Ulmer, 1912 <i>Ubmorodina aequalis</i> Hagen, 1856 <i>Wormaldia impar</i> (Ulmer, 1912) <i>W. congener</i> (Ulmer, 1912) <i>W. medius</i> (Ulmer, 1912)	Hagen, 1852 Ivanov, Melnitsky, 2005 Ivanov, Melnitsky, 2005 Ulmer, 1912 Ulmer, 1912 Hagen, 1852 Ulmer, 1912 Ulmer, 1912 Ulmer, 1912
Rovno amber/late Eocene	<i>Wormaldia noscicenta</i> Melnitsky et Ivanov, 2010 <i>W. pheromonia</i> Ivanov et Melnitsky, 2005 <i>W. pobeda</i> Melnitsky et Ivanov, 2010	Melnitsky and Ivanov, 2010 Ivanov and Melnitsky, 2005 Melnitsky and Ivanov, 2010
Arkhar, Amur Region/Late Cretaceous	<i>Arkharina oblimata</i> Sukatsheva, 1982	Sukatsheva, 1982
Burmese amber/Late Cretaceous	<i>Wormaldia myanmar</i> Wichard et Poinar, 2005 <i>W. resina</i> Wichard et Wang, 2016 <i>W. cretacea</i> Wichard et Wang, 2016 <i>W. cercilongera</i> Wichard et al., 2020 <i>W. cercifurcata</i> Wichard et al., 2020 <i>W. squamosa</i> Wichard et al., 2020 <i>W. transversa</i> Wichard et al., 2020	Wichard, Poinar, 2005 Wichard, Wang, 2016 Wichard, Wang, 2016 Wichard et al., 2020 Wichard et al., 2020 Wichard et al., 2020 Wichard et al., 2020
New Jersey amber/Late Cretaceous	<i>Wormaldia praecursor</i> Botosaneanu, 1995	Botosaneanu, 1995
Tennessee amber, USA/Late Cretaceous	<i>Wormaldia praemissa</i> (Cockerell, 1916)	Cockerell, 1916
Kzyl-Dzhar, Kazakhstan/Late Cretaceous	<i>Kulickiella roziczkae</i> Sukatsheva, 2001	Sukacheva, 2001
Yantardakh, Taimyr/Late Cretaceous	Philopotamidae inc. sed.	This paper
Khasurty, Buryatia Baysa, Buryatia/Early Cretaceous	<i>Juraphilopotamus callidus</i> Sukatsheva et Aristov, 2020 <i>J. heteroclitus</i> Sukatsheva et Aristov, 2022	Sukatsheva and Aristov, 2020 Sukatsheva and Aristov, 2022
Bon Tsagan, Mongolia/Early Cretaceous	<i>Juraphilopotamus</i> , one species	Ponomarenko, Sukatsheva and Vasilenko, in press
Kholbotu-Gol, Mongolia/Early Cretaceous	<i>Juraphilopotamus</i> , one species	Ponomarenko, Sukatsheva and Vasilenko, in press
Kempendyay, Yakutia/Late Jurassic–Early Cretaceous	<i>Kempia piotri</i> Sukatsheva, 2018 <i>Mesoviatrrix paradoxa</i> Sukatsheva, 2018	Aristov and Sukatsheva, 2018 Aristov and Sukatsheva, 2018
Karatau, Kazakhstan/Late Jurassic	<i>Archiphilopotamus expectatus</i> Sukatsheva et Sinitshenkova, 2023	Sukatsheva and Sinitshenkova, 2023

Table 1. (Contd.)

Location/age	Taxon	Reference
Shevya, Transbaikalia/Late Jurassic	<i>Juraphilopotamus inopinatus</i> Sukatsheva et Sinitshenkova, 2023	Sukatsheva and Sinitshenkova, 2023
	<i>Liadotaulius shewjensis</i> (Sukatsheva, 1990)	Sukatsheva, 1990
Shar-Teg, Mongolia/Late Jurassic	<i>Baga pumila</i> Sukatsheva, 1992	Sukatsheva, 1992
B. Koruy, Transbaikalia/Middle Jurassic	<i>Liadotaulius korujensis</i> (Sukatsheva, 1990)	Sukatsheva, 1990
	<i>Juraphilopotamus funeralis</i> Sukatsheva et Vasilenko, 2020	Sukatsheva and Vasilenko, 2020
Kubekovo Krasnoyarsk Krai/Middle Jurassic	<i>Juraphilopotamus similis</i> Sukatsheva et Sinitshenkova, 2023	Sukatsheva and Sinitshenkova, 2023
	<i>Archiphilopotamus kubekovens</i> Sukatsheva et Vasilenko, 2020	Sukatsheva and Vasilenko, 2020
	<i>A. absurdus</i> Sukatsheva et Vasilenko, 2020	Sukatsheva and Vasilenko, 2020
	<i>A. mancus</i> Sukatsheva, 1985	Sukatsheva, 1985
	<i>A. luxus</i> Sukatsheva, 1985	Sukatsheva, 1985
Bakhar, Mongolia/Middle Jurassic	<i>Baga bakharica</i> Sukatsheva, 1992	Sukatsheva, 1992
Daohugou, China/Middle Jurassic	<i>Liadotaulius daohuguensis</i> Wu et Hang, 2012	Wu and Hang, 2012
	<i>L. limus</i> Zhang et al., 2016.	Zhang et al., 2016
	<i>Juraphilopotamus lubricus</i> Wang et al., 2009	Wang et al., 2009
	<i>Pulchercylinaratus punctatus</i> Gao et al., 2013	Gao et al., 2013
Shurab III (=Sai-Sagul), Kyrgyzstan/Early–Middle Jurassic	<i>Dolophilodes (Sortosella) shurabica</i> Sukatsheva, 2004	Sukacheva and Rasnitsyn, 2004
	<i>Archiphilopotamus sagulicus</i> , sp. nov.	This paper
Dobbertin, Germany/Early Jurassic	<i>Liadotaulius major</i> Handl., 1906	Handlirsch, 1906
Madygen, Kyrgyzstan/Middle–Late Triassic	? <i>Prophilopotamus asiaticus</i> Sukatsheva, 1973	Sukatsheva, 1973

Table 2. Number of species in the genera of fossil Philopotamidae in the fossil record

	Prophilopotamus	Liadotaulius	Pulchercylindratulus	Dolophilodes	Baga	Juraphilopotamus	Archiphilopotamus	Kempia	Mesoviatix	Kulickiella	Wormaldia	Chimarra	Arkharina	Ulmerodina	Philopotamus	Electrocatinus
Q				+							+	+			+	
Miocene											3	6				
Eocene											9			1	1	1
Paleocene													1			
K ₂										1	9					
K ₁ (+J ₃ -K ₁)						4		1	1							
J ₃		1				1	1									
J ₂ (+J ₁₋₂)		3	1	1	3	3	6									
J ₁		1														
T	1															

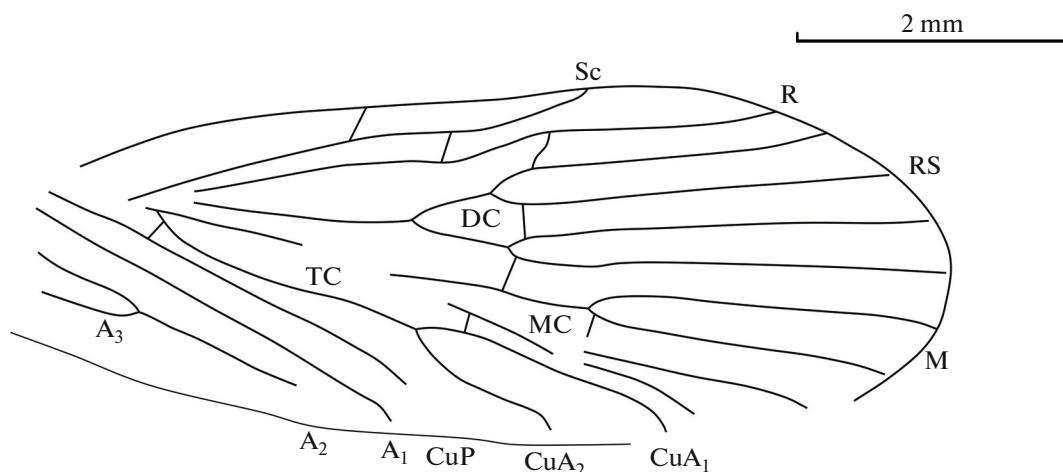


Fig. 1. Photograph and drawing of the forewing of *Archiphilopotamus sagulica* Sukatsheva, sp. nov., holotype PIN, no. 2389/578; Kyrgyzstan, Shurab III (Sai-Sagul) locality; Middle Jurassic, Sagul Formation. Scale bar 2 mm.

vein m_{3+4} -cua. There is a short oblique vein, the cuacup, at the base of the wing. A_1 is quite short, its entry into the posterior margin of the wing being located near the end of the second quarter of the wing's length. The end of the CuP is not preserved or has been desclerotized. A_2 is very long, A_3 is distinct and short. The anal area is quite narrow.

Dimension in mm: wing length 8.0, width 3.5.

Comparison. See the key to the species of the genus *Archiphilopotamus*.

Remarks. The new species is assigned to the genus *Archiphilopotamus* based on the similar arrangement of the crossveins enclosing the DC, MC, and TC cells, as well as the oblique accessory branch of the SC and the relatively short DC cell. The described species is close to *A. expectatus* Sukatsheva et Sinitshenkova, 2023 from the Upper Jurassic of the Karatau locality

(Kazakhstan) based on the relatively long SC, wide costal area, similar arrangement of the crossveins, and wing size. Unfortunately, the anal region of the wing of *A. expectatus* is almost completely effaced, and comparison with that of the new species is not possible.

Material. Holotype.

DISCUSSION

More than 50 families of caddisflies are known in the fossil record, and almost all of them have, to varying degrees, a restricted stratigraphic distribution. However, only representatives of the Philopotamidae and Polycentropodidae Brues et Melander, 1915 have been reliably recorded from the Jurassic to the present day. The earliest Philopotamidae finds are known from the Lower Jurassic and possibly the Middle to Upper Triassic, and the oldest Polycentropodidae

finds have been described from Upper Jurassic deposits in Yakutia, at the Kempendyay locality (Aristov and Sukatsheva, 2018). Finds from the Lower Cretaceous of Mongolia (Khutel-Khara), previously identified as Polycentropodidae (Sukatsheva, 1993), according to our data, should be assigned to the family Vitimotauliidae Sukatsheva, 1968.

It is interesting that the small family of modern caddisflies Kambaitipsychidae Malicky, 1991, consisting of a single genus *Kambaitipsyche* Malicky, 1991 with two species *K. hykriion* Malicky et Chantaramongol, 1991 and *K. schmidi* Malicky, 1991, distributed in Burma and Thailand (Malicky, 1991; Malicky and Chantaramongol, 1991), is similar to the family Philopotamidae in the primitive type of venation of the forewings. This similarity (specifically in the venation of the forewings, which are mostly preserved in the fossil state) is especially noticeable when compared with philopotamids of the genera *Hydrobiozella* Tillyard, 1924 and *Archiphilopotamus*. Modern species of endemic kambaitipsychids are common in Burma, in the same localities where Cretaceous Burmese amber containing *Kambaitipsyche malaisei* is known (Wichard et Wang, 2020). Such consistent endemicity may confirm the antiquity and primitiveness of not only this family but also, most likely, the family Philopotamidae, to which kambaitipsychids are very closely related. The main difference between fossil and modern kambaitipsychids is wing size. Extant representatives of *K. schmidi* have forewings measuring 12–14 mm, while the fossil *K. malaisei* has forewings measuring 5 mm.

This unusual endemic situation is observed not only in the order Trichoptera. For example, beetles of the family Sphaeriusidae (Jäch, 1999), genus *Beresporum* (Fikaček, 2022), have been found in Burmese amber, as well as under modern conditions in the same region of Burma (Fikaček et al., 2022).

The families Philopotamidae and Polycentropodidae contain genera that can be traced from the Jurassic or mid-Cretaceous to the present day. Representatives of Polycentropodidae are currently distributed worldwide and inhabit mainly running waters, less often in bodies of stagnant water. The main flowering of Polycentropodidae occurred in the Cenozoic; for example, 69 species have been found in Baltic amber, and in the Mesozoic, Burmese amber alone contains a fairly large number of different genera (11), four of which (*Neureclipsis* McLachlan, 1864, *Plectrocnemia* Stephens, 1836, *Holocentropus* McLachlan, 1878, and *Neucentropus* Martynov, 1907) have survived to the present day. All of these genera currently inhabit both running and stagnant bodies of water, sometimes even temporary pools.

Representatives of the Philopotamidae demonstrate a much clearer association with running water. The family includes genera that have existed for a long geological period (from the mid-Cretaceous to the

present), which can most likely be explained by their habitat in ecological conditions that have changed little over long periods. A ritral—a fast-flowing stream with relatively cold, oxygen-rich water—may be precisely such an environment. During the Mesozoic, aquatic ecosystems underwent fundamental changes; the types of water bodies changed significantly, particularly affecting not only lakes but also rivers (for more details, see Rasnitsyn and Quicke, 2002, p. 388), but the ritral was least affected.

Taking this into account, looking at the data in Tables 1 and 2, we see the most dramatic change in the composition of fossil philopotamids at the Early/Late Cretaceous boundary: until the mid-Cretaceous, only representatives of extinct genera are present, while afterward, almost exclusively modern genera are present. Furthermore, before the mid-Cretaceous, philopotamid remains were found only buried directly in sedimentary rocks, while afterward, they were found mainly in fossil resins. The only exceptions are two Upper Cretaceous and one Eocene find in sedimentary rocks of Kzyl-Zhar, Arkhara, and Bembridge, respectively, where only extinct philopotamid genera are found in the Cretaceous, while in the Eocene, only the modern genus is found. Additionally, we note that in the Lower Cretaceous sedimentary deposits, which have been studied entomologically perhaps better than any other, only four species of philopotamids are known, only slightly more than in the Upper Cretaceous and Cenozoic (three), while in the Jurassic there are 21 species.

Well-known patterns of insect burial (Zherikhin, 2002, 2009) provide a good explanation for the peculiarities of the philopotamid fossil record in the Cenozoic and, to some extent, in the Cretaceous. Like other ritrobiont insects (living in fast-flowing water as larvae or nymphs), these adult caddisflies only occasionally enter lakes, the primary burial environment where the insect fossil record is formed. Their remains were usually in stream sediments and other small bodies of water in the landscapes where they lived. However, all these sediments were infrafacies located high above the erosional base and therefore destined for erosion and reworking during subsequent landscape evolution. Only the remains of insects buried in fine-grained ultrafacies, primarily in sediments of larger lakes (and especially in the sea), have a good chance of preservation. However, this is normally inaccessible to ritrobionts, so instead of lake sediments, amber becomes the primary source of data on past ritrobionts. The banks of streams and other fast-flowing rivers overgrown with amber forests were, in the past, fairly common habitats, and the erosion and reworking of resin-laden sediments in these forests was completely natural for such infrafacies. The resin would be unaffected, i.e., resin with inclusions would simply be carried by the river from infrafacies to ultrafacies and reburied there. The remarkable stability over geological timescales and other features of the ritral biota will be preserved

and become visible to paleontologists in the form of the dominance of surviving philopotamid genera, even in Cretaceous resins.

The situation with philopotamid burials directly in sedimentary rocks is significantly different. In particular, finds of extant genera are extremely rare there and are completely unknown from Cretaceous deposits. Since such finds are random not only in the Cenozoic but also in the Cretaceous, it makes sense to begin the analysis with more frequent Jurassic fossils. As mentioned, more than twenty such occurrences are known in Lower, Middle, and Upper Jurassic deposits (we will not discuss here the less reliable Triassic find). This is too many to attribute them to random transport from infrafacies (ritral) to ultrafacies (lake deposits). It is therefore necessary to assume that Jurassic philopotamids may have lived in lakes.

Extant philopotamid larvae are typical filter-feeding microphages living in long tubes with a swollen end made of spinneret secretions, which they construct on the dense bottom of a body of water or on the surface of rocks. The larvae collect silt particles, small detritus, and microscopic animals and bacteria from the walls of their living tubes, both internally and externally. The larvae's primary requirement is clean, oxygen-rich water. These conditions are found not only in the ritral zone, but also sometimes in the lake littoral, as well as in specific environments such as springs and waterfalls.

In the Jurassic, especially in the Jurassic of Asia, unique lakes existed, with no modern equivalents: they had a rich oxyphilic fauna, now characteristic only of the ritral (for example, with a variety of stonefly nymphs) and are classified as hypotrophic lakes. Such lakes are characterized by specific conditions resulting from the presumed antibiotic effect of *Ginkgo* and *Czekanowskia* leaf litter (for more details, see: Rasnitsyn and Quicke, 2002, pp. 394–400; Zherikhin, 2003, p. 130). The majority of Jurassic philopotamids have been found in the sediments of such lakes, so it is logical to assume that the abundance of Jurassic philopotamid remains at least in part reflects their development directly in the reservoirs of burial, and not only in the fast-flowing streams typical of the family.

Ponomarenko (2007, pp. 245–246) criticized the theory of hypotrophic lakes and considers the antibiotic effect of *Ginkgo* and *Czekanowskia* litter on the biota of Mesozoic reservoirs to be greatly exaggerated. He highlights the absence of submerged macrophytes as the main difference between the ecosystems of ancient and modern lakes and believes that the main role among producers, along with plankton, was played by floating mats on a framework of lycopsids and mosses, on which an abundant fauna of invertebrates, including insects, existed. The oxyphilic nature of the fauna is explained by its habitation on floating subaerial mats. Examining Mesozoic lakes in volcanic regions, Ponomarenko does not find significant

differences in the type of bottom sediments and the structure of the biocenosis with reservoirs called hypotrophic. Thus, both V.V. Zherikhin and A.G. Ponomarenko acknowledge the existence of special lake environments that disappear by the middle of the Cretaceous, which is entirely consistent with our data on the development of philopotamids in burial reservoirs.

The supposedly important difference between the Jurassic philopotamids in their way of life and the Cenozoic ones, namely the ability to develop in lacustrine environments, can be compared with their taxonomic differences—with one not very reliable exception, all Jurassic philopotamids belong to extinct genera, some of which were widespread (*Juraphilopotamus* Wang, Zhao et Ren, 2004, *Archiphilopotamus* Sukatsheva, 1985, and *Liadotaulius* Handlirsch, 1939).

This fact can be used to better understand the evolution of the family during the Early Cretaceous, when their remains were particularly rare. All known Early Cretaceous Philopotamidae belong to the characteristic Jurassic genus *Juraphilopotamus*, while all Late Cretaceous ones belong to the modern genus *Wormaldia* (except for a single species from Kyzyl-Zhar, which is classified as a distinct extinct genus). Therefore, it can be concluded that, in its most general form, the paleontological history of the family can be divided into two main stages. Throughout their history, philopotamids remained a highly oxyphilic group in their preimaginal stages of development. However, during the Jurassic and possibly the Early Cretaceous, they were able to develop in particularly oxygen-rich lakes, which ensured their widespread presence in the paleontological record, even in the absence of amber as a specific means of transporting their remains from infra- to ultrafacies. The extinct genera *Juraphilopotamus*, *Archiphilopotamus*, and *Liadotaulius* are markers of the faunas of this stage.

By the mid-Cretaceous, these unusual lakes disappeared, as did the characteristic Jurassic genera of Philopotamidae. The family remains in the fossil record almost exclusively as inclusions in amber. From the early Cenomanian onward, it is represented there almost exclusively by the most common modern genera—first *Wormaldia*, and from the Neogene onward, *Chimarra*. *Chimarra* is the largest genus in the family (universal, but with two-thirds of its species in the Neotropics), while *Wormaldia* is the second-largest genus (universal except Australia, with the highest diversity in the Oriental region). Together, they comprise the overwhelming majority of Philopotamidae species. The presence of only these extant genera in the Cenozoic and their dominance—*Chimarra* in Dominican amber, *Wormaldia* in Eurasian faunas—is consistent with their modern distribution.

It is noteworthy that, in the Jurassic and Early Cretaceous, Philopotamidae remains are found in deposits of widely varying origin, but the taxonomic compo-

sition of caddisflies does not significantly depend on these differences. Most likely, the distribution of caddisflies in the original faunas was determined by entirely different factors: in our opinion, this was, first and foremost, a requirement of the preimaginal stages of Philopotamidae, consistent throughout their history, for high oxygen content in the developmental reservoir (which did not necessarily coincide with the burial reservoir). This is especially true for the subsequent stage of the family's history (Late Cretaceous–Cenozoic), when the place and time of caddisfly development (watercourse), the place and time of primary burial of the emerging imago (resin), and the place and time of reburial of the resin in the ultrafacies were very distant, especially during the final stage of the taphonomic process.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not include any studies involving human or animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

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