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The First Record of Dicosmoecinae from the Cenozoic of the Russian Far East with a Brief Global Overview of Fossil Limnephilidae (Insecta: Trichoptera)

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Abstract—A new genus and species, *Prodicos rasnitsyni* gen. et sp. nov. (Trichoptera, Limnephilidae), from the Upper Eocene–Lower Oligocene of Russia is described. The global fossil record of adult Limnephilidae is reviewed.

Keywords: Insecta, caddisflies, Limnephilidae, Lower Miocene, new genus and species
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INTRODUCTION

The family Limnephilidae Kolenati, 1848 is one of the youngest integripalpian caddisfly families (Phryganeina = Integripalpia), which had reached flourishing only by the beginning of the Early Neogene, mostly in the Miocene (Table 1). The first reliable, but rare Limnephilidae come from the terminal Eocene of the United States (Florissant locality, Colorado) and Baltic amber (see below). An extensive collection of insects from the Florissant locality includes only a few caddisflies, only 1% of which belongs to Limnephilidae, whereas the family Hydropsychidae composes 95% of all specimens (Carpenter, 1931).

The Florissant locality is tuffogenic deposits of a large lake, where Limnephilidae could have been extremely abundant (Sukatcheva and Vasilenko, 2013). However, they were rare in North America during that period. The dominant position could have been held by more primitive Hydropsychidae. At present, they live mostly in running water or unquiet nearshore part of lakes, which was presumably characteristic of Florissant. Generally speaking, the lacustrine fauna of the modern type developed gradually during the Oligocene–Lower Miocene (Zherikhin and Sinitshenkova, 2002). Therefore, it is quite natural that limnic caddisflies of the modern type, including Limnephilidae, did not occur at all or were rare.

Subsequently, the Limnephilidae expanded from east to west, i.e., from the United States through eastern Asia to Europe (Zherikhin, 1978). In addition to the specimens from the Late Eocene of the United States (Table 1), this family has recently been discovered in the Upper Eocene Baltic amber (Wichard, 2013). Remains of Limnephilidae are relatively frequently found in the Upper Eocene–Lower Oligocene of the United States (Ravi River, Montana) and the northern Sikhote-Alin (basin of the Granatnaya River = Amgu) as well as in the Upper Oligocene of Primorye (Smezhnyi Creek, tributary of the Samarga River) (Table 1). However, they are still not recorded in Europe, even in rich localities, such as in the Upper Oligocene of Germany (Rott). Caddisflies are represented there by the ancient family Phryganeidae (Sukatcheva, 2016). As was believed previously (Zherikhin, 1978), limnephilids appeared in Europe not earlier than the Miocene and immediately became abundant. As a result, the faunal composition of caddisflies during that time changed considerably, which is evident from the materials from Iceland, the western Carpathians, and several localities of the Stavropol Region (Table 1). The Stavropol Region (Vishnevaya gully and Temnolesskaya localities) provides unique examples of mass burials (about 700 specimens) of almost exclusively the family Limnephilidae, dominated by one species. Fossil remains of caddisflies inform the Stavropol Region were found in lagoon rather than freshwater deposits. However, their larvae apparently inhabited lakes, rivers, or oxbow near the burial sites (Sukatcheva and Vasilenko, 2013). Another example of the dominance of Limnephilidae concerns lake burials of the Upper Miocene of Washington, United States (Leitha Formation). Carpenter (1931) described therefrom the genus *Miopsyche,* with two species *M. alexanderi* and *M. martynovi,* which is related to the genus *Limnephilus* Leach, 1815. Subsequently, Carpenter (1992), having failed to find significant differences, synonymized *Miopsyche* under the genus *Limnephilus*. Interestingly, the species *Miopsy-*

Table 1. Geological and geographical distribution of fossil adults of the family Limnephilidae

Age		Locality	Taxon	Reference
Pliocene		Auvergne, France	*Limnephilus antiquus* Piton	Piton, 1935
Miocene	Upper	Khanka, Primorye	Limnephilidae gen. sp.	original data
		Washington, USA, Leitha	Limnephilidae gen. sp.	Carpenter, 1931
		Washington, USA, Leitha	*Miopsyche martynovi* Carpenter	Carpenter, 1931
		Washington, USA, Leitha	*Miopsyche alexanderi* Carpenter	Carpenter, 1931
	Middle	Hrutogil, Iceland	Drusinae gen. sp.	Wappler et al., 2014
		Western Carpathians, Slovakia	*Vodnik prapovodnik* Suk. et Vršanský	Sukatsheva et al., 2006
		Vishnevaya gully, Russia	*Miopsyche kaspievi* O. Mart.	Martynova, 1939
		Temnolesskaya, Russia	*Miopsyche* sp. nov.	original data
	Upper Oligocene–Lower Miocene	Velikaya Kema (Tikhii Spring), Russia	Limnephilidae gen. sp.	original data
Oligocene	Upper	Samarga (Smezhnyi Creek), Primorye, Russia	Limnephilidae gen. sp.	original data
		Ferry Canyon, Montana, USA	? *Miopsyche* sp.	Cobabe et al., 2002
	Upper Eocene–Lower Oligocene	Amgu (= Granatnaya), Russia	*"Limnephilus" recultus*	Cock. Cockerell, 1925
		Amgu (=Granatnaya), Russia	*"Limnephilus" kudiensis* Cock.	Cockerell, 1926
		Amgu (=Granatnaya), Russia	*Prodicos rasnitsyni* sp. nov.	this paper
		Ravi River, USA	*Miopsyche (?) rubiensis* Lewis	Lewis, 1973
		Ravi River, USA	Limnephilidae gen. sp.	Lewis et al., 1990
Eocene	Upper	Florissant, USA	*Limnephilus* (sensu lato) *exenicus* Cock.	Cockerell, 1920
		Florissant, USA	*Limnephilus* sp.	Scudder, 1890
		Florissant, USA	*Platyphylax (Eopteryx) florissantensis* Cockerell	Cockerell, 1907
		Baltic amber	*Electrocryptochia wigginsi* Wichard	Wichard, 2013

che kaspievi O. Mart., 1939 (Martynova, 1939) described from Vishnevaya gully turned out to be very similar to the above-mentioned species from the Leitha Formation. This once again proves that European and North American entomofaunas were rather similar in the Miocene (Martynov, 1927). It is noteworthy that Limnephilidae were found in several other Eocene–Oligocene localities of the United States (Scudder, 1890; Cockerell, 1907, 1920; Piton, 1935; Lewis, 1973; Cobabe et al., 2002) (Table 1). The findings from the Renova Formation (Upper Oligocene–Lower Miocene) of the Ferry Canyon (Montana), where numerous remains of Limnephilidae are not only adults, but also larval cases built of fragments of bugs of the family Corixidae, are of particular interest (J.J. Giersch, personal communication).

Significant changes in the aquatic insect fauna in the Late Paleogene–Early Neogene are probably accounted for by changes in vegetation, such as wide distribution of submerged plant mats, which formed numerous microstations favorable for aquatic insects (Kalugina and Zherikhin, 1975). Insects were able to develop safely inside and on the surface of these mats. Furthermore, the regime of many water bodies was influenced by the mass development of herbivorous ungulates in the Oligocene and Miocene due to the formation of herbaceous landscapes. The inflow of biogenic elements in the watering areas must have caused an increase in water trophicity and simulated the development of actively filtering microphages, such as chironomids (Kalugina, 1980). Actually, most Neogene faunas are generally similar to the modern fauna of eutrophic lakes with rich aquatic vegetation.

The specimens of adult Limnephilidae from Eocene–Oligocene deposits are mostly wing imprints. However, in the Miocene, body and even whole insect imprints become abundant. As mentioned above, this is especially noticeable in the rich collection from the Miocene of the Stavropol Region. In the fossil record, wing imprints of Limnephilidae are often accompanied by transportable larval cases, which are similar to those of extant Limnephilidae in size, shape, and arrangement of the building material. Such cases were first found in the Green River locality of the United States (Scudder, 1890) in deposits dated Middle Eocene (Smith et al., 2010). They were also found in the Lower Oligocene of Primorye (Kraskino locality; Pavlyutkin and Petrenko, 2010). Furthermore, cases and wings of Limnephilidae were found in the Upper Eocene or Lower Oligocene of Primorye, Russia (Amgu and Velikaya Kema localities) (Table 1). Interestingly, the Upper Eocene Bol'shaya Svetlovodnaya (=Biamo) locality in Primorye lacks adult Limnephilidae, although other caddisfly families are abundant there.

Only the presence of adult insects is evidence of the occurrence of true Limnephilidae. Fossil larval cases alone, even those from the Paleogene and Neogene, found separately from wing imprints cannot be identified as limnephilid. Modern Limnephilidae build their cases of various materials (plant fragments, detritus, sand particles, small shells); therefore, it is difficult to identify fossil cases to family, even if they come from late deposits. For better understanding, the list of adult Limnephilidae (Table 1) is given separately, while the list of presumable larval cases of this family was published previously (Vyalov and Sukatcheva, 1976; Sukatcheva, 1982).

A few other new localities with limnephiloid caddisfly cases have recently been found in Europe, for example, in the Oligocene of Germany (Enspel locality), in volcanic deposits, where all living organisms were instantly buried during ash precipitation. These paleontological "Pompeii" are characterized by the occurrence of larvae coming out of their cases, as observed in Enspel (Wedmann and Poschmann, 2010). Furthermore, limnephiloid cases were recorded in the Oligocene of Brazil (Martins-Neto, 1989).

Let us return to the caddisfly fauna from the Baltic amber. This extremely rich Eocene fauna contains only one specimen identified as Limnephilidae. This is a representative of the most primitive limnephilid subfamily Dicosmoecinae (Wiggins, 1984), the monotypic genus *Electrocryptochia wigginsi* Wichard, 2013 (Wichard, 2013). It is known that Limnephilidae in general prevail among case-building caddisflies of the Northern Hemisphere, being most typical for the high latitude water bodies. Four limnephilid subfamilies only occur in the Northern Hemisphere. Only the Dicosmoecinae have been recorded in both Northern and Southern hemispheres. A total of 11 genera are known in the Northern Hemisphere and eight are in the Southern Hemisphere (seven genera in South America and one in Australia and Tasmania). In both hemispheres, the Dicosmoecinae live in cold streams of mountain areas, which are probably their original native habitats (Wiggins, 2002). Most larval Dicosmoecinae are detritophagous, although some feed on diatoms.

Almost complete absence of Limnephilidae in the Baltic amber is probably accounted for by their occurrence as a mass group in the Oligocene of the United States (Table 1), i.e., when the formation of primary Eocene amber beds in Europe was accomplished. This supports the conclusion that representatives of the family Limnephilidae were still very rare in this territory during the Eocene and almost did not fall into resin of amber-producing trees (Kulicka and Sukaczewa, 1990).

The wing described in this paper is assigned to the subfamily Dicosmoecinae based on the so-called "dicosmoecus" type of the crossvein m-cu in the posterior anastomosis part of the forewing (Vshivkova et al., 2007). The vein m-cu is directed backwards, which is typical of Dicosmoecinae, as well as the wide wing with a rounded apical margin. This wing is the first nonamber fossil of Dicosmoecinae.

SYSTEMATIC PALEONTOLOGY

Order Trichoptera

Suborder Integripalpia (=Phryganeina)

Family Limnephilidae Kolenati, 1848

Subfamily Dicosmoecinae Schmid, 1955

Genus *Prodicos* Sukatcheva, gen. nov.

E t y m o l o g y. From the Latin *pro-* and the genus *Dicosmoecus*.

T y p e s p e c i e s. *P. rasnitsyni* sp. nov.

D i a g n o s i s. Large insects with wide wings. Sc straight; R simple, curved apically. Cell DC very long. Cell MC open. Cell TC closed. Fork F_1 starting noticeably proximal to forks F_2 and F_3. Fork F_5 moderately long. M_{1+2} fork trunk ending at point of divergence of crossvein m_{3+4}–cua_1. CuP and A_1 parallel. A_1 long, ending at desclerotized line running from arculus to CuA_2 slightly above posterior wing margin.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. The genus *Prodicos* is most similar to the genera *Dicosmoecus* Mac Lachlan, 1875, *Amphicosmoecus* Schmid, 1955, and *Allocosmoecus* Banks, 1943. It is similar to *Dicosmoecus* in the ratio of DC length to its trunk length and in the end of the M_{1+2} trunk exactly at the point of divergence of the crossvein m_{3+4}–cua_1. The genus *Prodicos* is similar to *Amphicosmoecus* and *Allocosmoecus* mainly in the type of A_1 ending at the desclerotized line above the hind wing and the preapical curvature of R and differs from them in the significantly longer A_1 (and, hence, short A_2). *Prodicos* differs from *Dicosmoecus* in the R

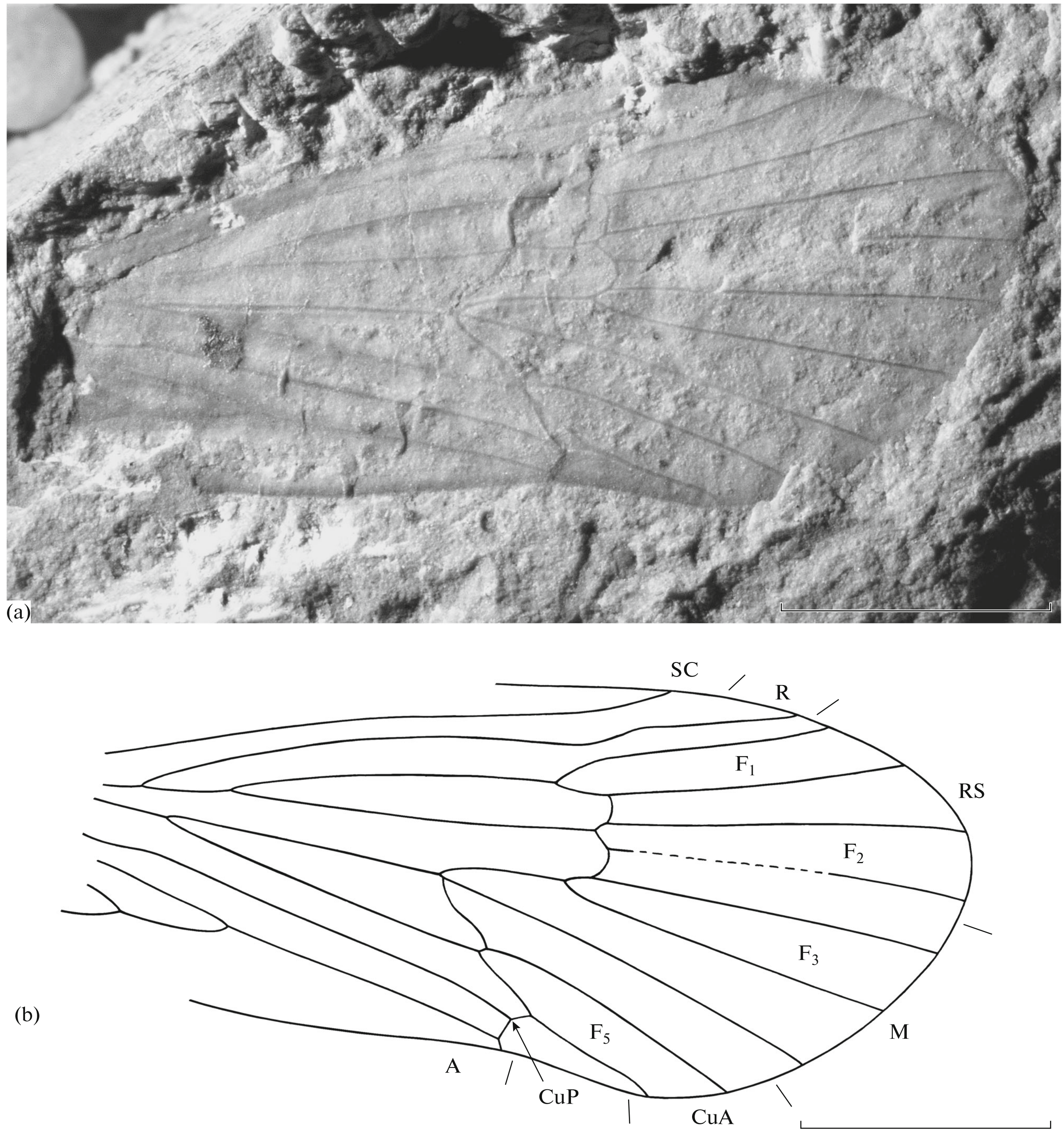

Fig. 1. *Prodicos rasnitsyni* gen. et sp. nov., holotype PIN, no. 3135/135: (a) general view, (b) venation. Scale bar, 5 mm.

curved near the apex and the place where A_1 falls into the desclerotized line rather than directly into the posterior wing margin. The new genus differs from other three genera of the tribe Dicosmoecini in the shorter trunk of the DC cell (*Onocosmoecus* Banks, 1943, *Eocosmoecus* Wiggins et Rich., 1989) and in the more proximal position of F1 base (*Allocosmoecus*).

R e m a r k s. The similarity of *Prodicos* to the above-mentioned genera of the tribe Dicosmoecini show that it is close to the modern genera dwelling in the Northern Hemisphere.

Prodicos *rasnitsyni* Sukatcheva, sp. nov.

E t y m o l o g y. In honor of A.P. Rasnitsyn.

H o l o t y p e. PIN (Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow), no. 3135/135, part and counterpart of almost complete forewing; Promorskii Region, Terneiskii District, Granatnaya River (=Amgu = Amagu = Kud'ya); Upper Eocene–Lower Oligocene.

D e s c r i p t i o n (Figs. 1a, 1b). The wing is wide; the anterior margin is straight; the apex is rounded. The subcostal field is narrowed. The Sc is straight. R is slightly curved at the apex. The DC cell is long (7.0 mm), 3.5 times as long as its trunk. All forks are sessile. Fork F_5 starts more proximally than other forks. F_2 and F_3 start at almost the same level, distal to the F_1 base. The DC cell is covered by slightly convex crossvein rs_2–rs_3. A very convex crossvein rs_4– m_1 is present between forks F_2 and F_3. F_4 is absent. Cell TC is long, strongly widened toward the apex, closed by a long slightly curved crossvein m_{3+4}–cua. CuP and A_1 are parallel to each other and end on the desclerotized vein running from CuA_2 to the posterior margin. A_1 is moderately long, ends at the middle of the wing length. A_2 is short. A_3 is very short. The anal field is very wide.

M e a s u r e m e n t s, mm. Wing length, 19.0; wing width, 9.0.

R e m a r k s. The absence of F_4 is probably evidence that this is a male wing.

M a t e r i a l. Holotype.

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