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The family Prosopistomatidae (Ephemeroptera): a review on its ecology and distribution, with particular emphasis on the European species *Prosopistoma pennigerum* Müller, 1785

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Although the monogeneric mayfly family Prosopistomatidae is almost globally distributed, remarkably few records have been made. Evidence available to date indicates that this taxon is very rare. We present ecological data on the European species *Prosopistoma pennigerum* which were assessed during a monitoring programme in the headwaters of River Volga. As a result of a bibliographic review, the historic distribution of this species throughout Europe is provided and its ecological demands (lithophil, rheophil, potamophil) are summarised.

Keywords: biogeography; mayflies; large rivers; indicator; reference community

Introduction

The Prosopistomatidae is a monogeneric family, and within the genus *Prosopistoma* Latreille 1833, 20 species have been described at present (Table 1). A further eight species from sub-Saharan Africa, five species from Madagascar and one from the Comores will be described soon (Barber-James 2009). A *Prosopistoma* larva that was recently found during the project '*ASSESS-HKH*' in the Hindu Kush-Himalayan region possibly also represents a new species (A. Hartmann, personal communication).

These exceptional mayflies were first classified as Crustacea (Geoffroy 1762; Fourcroy 1785; Latreille 1833) but only over 100 years after their discovery it was realised that the '*prototype de mon crustacé*' was a mayfly larva (Joly 1871; Joly and Joly 1872). The primary erroneous associations are not entirely surprising, when the odd morphology of this taxon is considered. The head of the lens-shaped larvae is recessed into the thorax, the notal shield ('carapace') extends to the sixth abdominal segment and the caudal filaments can be completely retracted into the abdomen (Figure 1). The shape of the mandibles is unusual, since the mola is lost. Consequently, the mouth apparatus of *Prosopistoma* was assumed to be modified for carnivorism (Trägårdh 1911; Haybach 2006). In contrast, Fontaine (1980) stated that carnivorous habits cannot be concluded only from the observation of mouthparts and claimed that *P. pennigerum* feeds on detritus and algae. Another remarkable feature is the gill chamber, containing six distinct pairs of tracheal gills (Kluge 2004). Detailed

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Table 1. Distribution (Zoogeography: Af – Afrotropical, Au – Australian, O – Oriental, wP – Western Palaearctic, eP – Eastern Palaearctic,) and ecological preferences of Prosopistomatidae.

		Altitude			Stream width		Water depth		Substratum		Records	
	Zoogeography	Low: <200 m	Middle: 200–800 m	High: >800 m	Stream ≤10 m	River >10 m	Littoral, shallow zones ≤0.5 m	Deep zones >0.5 m	Stones, gravel (predominant)	Macrophytes/ Algae (presence)	Larvae	Adults
P. africanum Gillies, 1954	Af		x	x	x	x	x	x	n.a.	n.a.	x	x
P. annamense Soldán and Braasch, 1984	O	x			x	x	x	x	x	n.a.	x	
P. boreus Peters, 1967	O		x		x		x		x	n.a.	x	
P. crassi Gillies, 1954	Af		x			x	n.a.	n.a.	n.a.	n.a.	x	
P. deguernei (Vayssière, 1893)	Af	x				x	n.a.	n.a.	n.a.	n.a.	x	
P. funanense Soldán and Braasch, 1984	O	x			x		n.a.	n.a.	x	n.a.	x	
P. indicum Peters, 1967	O	x				x	x	x	x	x	x	
P. lieftincki Peters, 1967	O			x	x		x		n.a.	n.a.	x	
P. olympus Sartori and Gattolliat, 2003	O	x	x		x		x		x	n.a.	x	
P. orhanelicum Dalkıran, 2009	wP	x	x		x		x		x	n.a.	x	
P. palawana Peters, 1967	O	x			x		x		x	n.a.	x	

(*continued*)

Table 1. (*Continued*).

		Altitude			Stream width		Water depth		Substratum		Records	
	Zoogeography	Low: <200 m	Middle: 200–800 m	High: >800 m	Stream ≤10 m	River >10 m	Littoral, shallow zones ≤0.5 m	Deep zones >0.5 m	Stones, gravel (predominant)	Macrophytes/ Algae (presence)	Larvae	Adults
P. pearsonorum Campbell and Hubbard, 1998	Au	x			x		x	x	x	n.a.	x	x
P. pennigerum (Müller, 1785)	wP	x	x		x	x	x	x	x	x	x	x
P. phoenicium Alouf, 1977	wP		x		x		x		x	n.a.	x	
P. sedlaceki Peters, 1967	Au			x	x	x		x	x	n.a.	x	
P. sinense Tong and Dudgeon, 2000	eP			x	x		x		x	n.a.	x	
P. trispinum Zhou and Zheng, 2004a	eP			x	x		x		x	x	x	
P. unicolor Zhou and Zheng, 2004b	eP			x	x		x		x	n.a.	x	
P. variegatum Latreille, 1833	Af				x	x	n.a.	n.a.	n.a.	n.a.	x	
P. wouterae Lieftinck, 1932	O			x	x			x	x	n.a.	x	

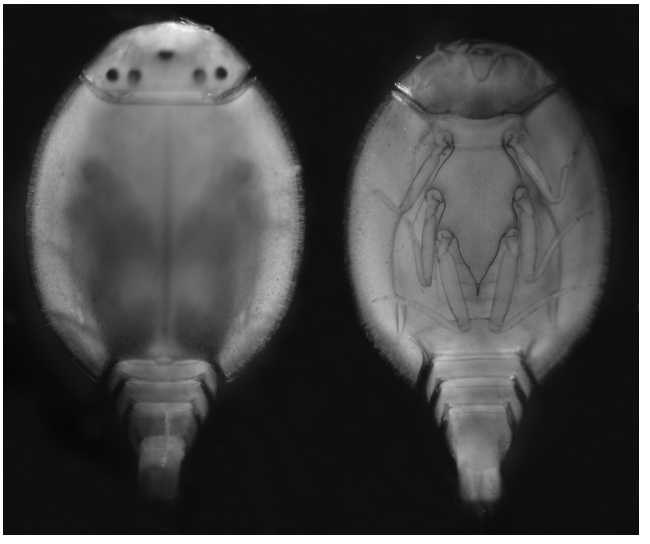

Figure 1. *Prosopistoma pennigerum*, dorsal and ventral view (TL = 5.6 mm).

morphological descriptions can be found e.g. in Joly and Joly (1872), Vayssière (1890, 1925), Trägardh (1911), Lafon (1952), and Kluge (2004). A revision of the nomenclature was provided by Hubbard (1979). Entomological notes on all described species are provided in Schletterer and Füreder (2009).

Up to now, adults of only three species (*P. pennigerum, P. africanum, P. pearsonorum*) have been found. *Prosopistoma pennigerum* was recorded to fly for only about 30 minutes after its emergence at dawn (Fontaine 1982), in June and July (Vayssiére 1881; Fontaine 1955, 1982; Degrange 1955). The females of this species are known to be reproductive as subimago (Edmunds and McCafferty 1988). Emergence at dawn is likely to be a family trait, because it is also described for *P. africanum* (Gillies 1954) and *P. pearsonorum* (Campbell and Hubbard 1998). For *P. pearsonorum*, Campbell and Hubbard (1998) hypothesised a parthenogenetic life cycle, because despite intensive efforts, no male imagines or subimagines were ever collected. The emergence at dawn, possibly a result of predator avoidance (predators are less active in the morning), is typical for the tropics and supports Edmunds' idea (Edmunds 1972, 1979) of a tropical Gondwanan origin of the Prosopistomatidae, which is also indicated by the high number of species found in Africa, Madagascar and Asia (Barber-James 2003, 2009).

Methods

To describe relevant environmental conditions for the European representative of the family, we provide data from fieldwork which was carried out during surveys in the headwater of the Volga River in spring and summer 2006 and 2007. Samples were taken with a multi-habitat sampling method (modified after Hering et al. 2003). The material was rinsed through a 500 μm net and stored in ethanol. *Prosopistoma* was sorted immediately after sampling and preserved in 96% ethanol. In order to assess the historical distribution patterns of the species *P. pennigerum* in Europe, a bibliographic synthesis was performed.

Results

Recent data on Prosopistoma pennigerum (Müller, 1785) from Russia

Pristine sites in the Upper Volga River are still inhabited by typical potamal species (e.g. *Ephoron virgo*, *Heptagenia sulphurea*, *Potamanthus luteus* and *Prosopistoma pennigerum*) that are nowadays rare in European rivers. The Volga River emerges in the lowland (elevation at source = 228 m), thus its headwater region bears the character of a (summer warm) lowland river. Due to low anthropogenic pressures it is an important refugial habitat for rare and endangered potamal species (Schletterer and Füreder, in press). Our findings from the Upper Volga River in 2006 were the first record of *P. pennigerum* on the territory of the Russian Federation (Schletterer and Kuzovlev 2007). The present records provide valuable information about densities as well as ecological demands and habitat requirements of *Prosopistoma pennigerum*. At a location near Rzhev (Figure 2) the species was found in a fast flowing section (about 0.6 m s^{-1}) of the Volga River in approximately 0.5 m depth (littoral), where the substrate was formed by gravel and small stones. Settlement densities (mean values of two sampling campaigns in summer 2006 and 2007) amounted to 11 larvae per square metre, which is 5% of the mayfly community, or 0.73% of the total community respectively.

Prosopistoma pennigerum is a typical component of the reference community of large European rivers. In Table 2 we present data from three large rivers (Volga, Daugava, Rhine), where the species occurred or is still present. The accompanying fauna is also taken into account: the basis for the list is the reference community

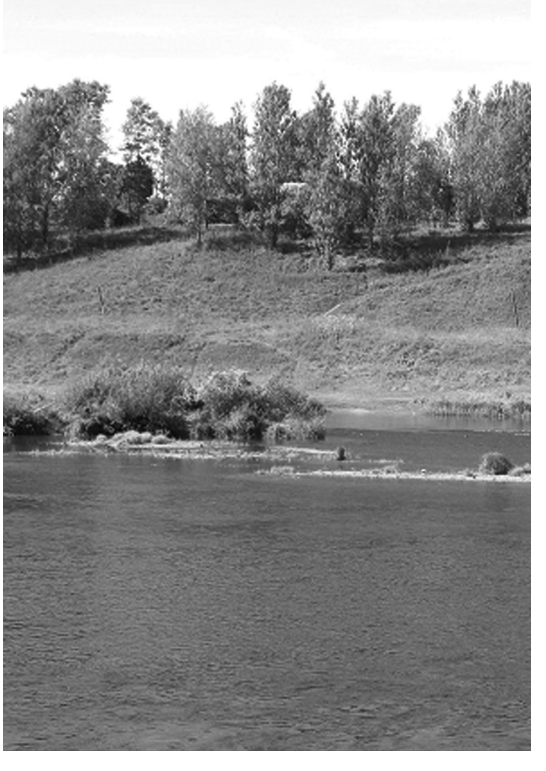

Figure 2. Locality Rzhev at the Volga River.

Table 2. *Prosopistoma pennigerum* as a part of the reference community (0 extinct, x present, xx abundant) of large European rivers: elements of the reference community (RC) of River Rhine are highlighted in grey (some are missing, see text); some additional species that are relevant in east-European rivers are added. Chemical data for River Rhine is from HLUG (2008), the hydrochemical parameters from the Volga River were assessed by Russian partners in August 2005.

	Volga	Daugava (Kačalova 1962)	Rhine (Pottgiesser et al. 2005)
Ancylus fluviatilis	xx	x	x
Unio crassus	x		xx
Theodoxus fluviatilis		x	xx
Bithynia tentaculata	x	xx	
Valvata piscinalis	x		
Baetis muticus	x		x
Centroptilum luteolum	xx		
Heptagenia sulphurea	x	xx	
Paraleptophlebia submarginata	x	x	
Serratella ignita	xx	x	
Oligoneuriella rhenana			xx
Potamanthus luteus	xx	xx	xx
Prosopistoma pennigerum	x	x	0
Brachyptera braueri			xx
Isoperla obscura	x		0
Leuctra fusca	xx		
Perla burmeisteriana			xx
Xanthoperla apicalis	x		0
Helobdella stagnalis	x	x	
Erpobdella octoculata	x		
Aphelocheirus aestivalis	xx	x	xx
Brachycentrus maculatus			xx
Cheumatopsyche lepida	x	x	xx
Hydropsyche sp.	xx	xx	xx
Polycentropus flavomaculatus	x	x	
Psychomia pusilla	xx		
Setodes punctatus		x	xx
Ablabesmyia	x	x	
Gomphus vulgatissimus	x	x	x
Rheotanytarsus spec.	x	x	xx
Stream width (m)	180	approx. 150	<150
Depth at sampling location (m)	0.5	0.5–4.4	0.3
Current speed (m/s)	0.60	up to 2	n.a.
Discharge (m^3, MQ)	94.24	n.a.	1420 (at Worms)
Vegetation cover along the bank %	100	100	100
Floating macrophytes %	5	20	n.a.
pH	7.2	n.a.	7.4–8.3
Conductivity μS/cm	191	n.a.	16.4–66.9
Nitrate NO3-N mg/l	2.30	n.a.	n.a.
Nitrite NO2-N mg/l	n.a.	n.a.	0.01–0.15
Ammonium NH4-N mg/l	0.53	n.a.	<0.09–0.11
total N mg/l	2.90	n.a.	1.7–4.3

from the River Rhine (according to Pottgiesser et al. 2005; without *Baetis vardarensis*, *Caenis macrura*, *Rhithrogena beskidensis*, *Chloroperla tripunctata*, *Protonemura meyeri*, *Siphonoperla burmeisteri* and *Esolus* sp. – because these species did not occur in the rivers Volga and Daugava). An overall estimation of the faunal composition shows that the other animals are also adapted to currents, underlining

that *Prosopistoma* is part of a natural community in large rivers, along stony littoral areas with strong current. It is also shown that other species that became extinct in large western European rivers (e.g. *Isoperla obscura*, *Xanthoperla apicalis*) are still present in intact East European Rivers.

Prosopistoma pennigerum (Müller, 1785) in Europe

The mayfly *P. pennigerum* is considered to be extinct in most parts of Europe (Bauernfeind and Humpesch 2001), and also in Russian literature it is described as a very rare species (Kluge 1997). The species is also included in the European Ephemeroptera species list (Schalk et al. 2005), where it is recorded for Germany, France, Sweden, Spain, and Portugal. In the Scandinavian Ephemeroptera list, included in Schalk et al. (2005), *P. pennigerum* is treated as extinct. Under the synonym *P. foliaceum* Fourcroy, 1785 there are further records of this species from Portugal and Spain. The present literature review revealed records of the species in 19 European countries (Figure 3, Table 3).

Figure 3. Distribution of *Prosopistoma pennigerum* (Müller, 1785) in Europe.

Table 3. Distribution of *Prosopistoma pennigerum* (Müller, 1785) in Europe.

Country	Location	Literature
Algeria	Isser (Sidi Abdelli)	Gagneur and Thomas 1988, Thomas 1998
Austria	The reference most likely corresponds to findings from the formerly large territory of the Austrian-Hungarian Empire	Vayssière 1890a
Czech Republic	Vltava (Zofinsky island, Prague), Labe, Blanice	Vayssière 1893, Komárek 1916, Sámal 1933, Lafon 1952
France	Seine (Paris, Poit du Jour, Bas-Meudon, between Epone and Mantes), Meurthe (Nancy), Rhone (Avignon, Valence, Lyon), Garonne (Toulouse), Gironde, Loire (Lamothe), Vienne, Ardèche	Vayssière1890a, Vayssière 1893, Dorier 1925 Fontaine and Wautier 1953, Joly 1871, Wautier 1955, Bertrand and Verrier 1949, Gauthier 1952
Georgia	Kura River (Borzhomi Nature Reserve)	Sadovsky 1946; Kasymov 1972
Germany	Rhine (Ottenheim, Ludwigshafen, St. Goar/Loreley, Mainz, Koblenz and between Breisach and Straßburg), Main (Aschaffenburg), Tauber (Rothenburg)	Noll 1867, Lauterborn 1908, Ulmer 1927, Schoenemund 1930
Greek	Thiamis (about 30 km north-east of Igoumenitsa)	Hoffmann 1994
Hungary	Szilas stream (near Budapest)	Hufnagel and Gaál 2005
Italy	Ombrone (near Grosseto)	Bellmann 2000
Latvia	Daugava River (Koknese)	Kačalova 1962, 1965; Kačalova and Skrube 1971, Spuris 1974, 1982
Luxembourg	Mosel (Bullay, Grevenmacher)	Schoenemund 1930, Hoffmann 1950
Macedonia	Vardar River (near Veles and Demir Kapija)	Ikonomov 1964
Netherlands	Small ponds along Lake Ijssel	Vos 1954, Mol 1984, 1985
Portugal	Tâmega (Frariz – Amarante, Região Norte)	Terra 1984
Romania	Mures, Cerna (Hunedoara region)	Bogoescu 1958
Russia	Volga (near Rzhev)	Schletterer and Kuzovlev 2007
Spain	Tajo, Cabriel, Mundo, Júcar and Segura	Baltanás 1990, Pujante 1993, Vidal-Abarca et al. 1991, Puig et al. 1989, Ubero-Pascal 1996, Ubero-Pascal et al. 1998
Sweden	Lagan River, Morumsaa	Trägårdh 1911, Alm 1918
Turkey	Dicle (Tigris) River in Diyarbakır, southeastern Anatolia	Koch 1985, Kazancı 2001

The data are grouped into Central Europe (France, Luxembourg, Germany, Austria), Western Europe (Portugal, Spain), southern Europe/Mediterranean (Italy, Macedonia, Greece, Turkey, Algeria), northern Europe (Netherlands, Sweden) and Eastern Europe (Czech Republic, Hungary, Romania, Latvia, Georgia, Russia).

Central Europe

For France there are several records of this species from the rivers Seine, Rhone, Garonne (Vayssière 1893), Meurthe (Joly 1871), Vaucluse (Vayssière 1882), Vienne (Leger 1924), Drôme (Dorier in Leger 1924), Gironde (Bertrand and Verrier 1949), Ardèche (Gauthier 1952) and Loire (Wautier 1955). The first larvae were found in 1762 by Geoffroy in the Seine near Paris and further larvae were collected there in 1842 by Montandon; in 1856 Lucas collected specimens at Poit du Jour, Bas-Meudon, and between Epone and Mantes (Anonymous 1883). At Nancy, larvae were found in the river Meurthe (Joly 1871). From the Garonne River, larvae are known from Toulouse (Joly 1868; Despax 1929 – see Lafon 1952). In the Loire River specimens were caught in 1938 near the village of Lamothe by H. Bertrand (Wautier 1955). From the Rhone River *Prosopistoma pennigerum* is known from a location at Avignon (Vayssière 1890a) and Valence (Dorier 1925) and at the end of September 1951 a student of J. Wautier collected about 20 larvae near Lyon (Fontaine and Wautier 1953; Wautier 1955). The last records from the Rhone are published by Usseglio-Polatera and Bournaud (1989). Although it may still be present in the Rhone River (BAL 2001), the genus *Prosopistoma* has to be considered as threatened nowadays in southwestern France by water pollution and surface water abstraction. It was also portrayed as 'already disappeared from this region' (Thomas 1996). In Luxembourg the species occurred in the river Mosel at Bullay (Schoenemund 1930) and at Grevenmacher (Hoffmann 1950). Haybach and Malzacher (2003) mention some historical records of *P. pennigerum* in Germany but assume that this species is lost or extinct nowadays. In the river Rhine, *Prosopistoma* was found at Ottenheim, Ludwigshafen (Lauterborn 1908), St.Goar/Loreley, Mainz, Koblenz (Noll 1867) and at some locations between Breisach and Straßburg (Ulmer 1927). According to Haybach (2006), R. Wagner from the 'Limnologische Fluss-Station Schlitz' reported that *Prosopistoma* was collected by Köpp in the 1950s in the middle Rhine. The species was further found in Main River at Aschaffenburg (Schoenemund 1930) and in Tauber River at Rothenburg (Ulmer 1927). In Bavaria, the species has not been recorded since 1927 and is considered to be extinct (Adam 2003), but in any case the record from the river Tauber is questionable (Malzacher 1981; Haybach 2006). In reaches with stones or gravel and high discharge, *P. pennigerum* was a typical species, thus it is included in the reference community, e.g. in the lower Rhine River at mean altitude, but it is extinct there (Pottgiesser et al. 2005). *P. pennigerum* is also extinct in the Upper Rhine, where typical epipotamal elements have decreased due to hydroelectric power plants (Rey and Ortlepp 2002). There is one reference indicating that the species was also found in Austria (Vayssière 1890a), but it was not possible to find more specific publications to verify this record. This reference most likely corresponds to findings from the formerly large territory of the Austrian-Hungarian Empire.

Western Europe

The first record from the Iberian Peninsula was made in Portugal: in 1983 the species was found in the Tâmega River at Frariz – Amarante, Região Norte (Terra 1984). In Spain the species is restricted to a few places in central parts and the south of the country (Robles et al. 2002). From central Spain the species is known from the Tajo River (Baltanás 1990). Further records exist from some rivers in the South of Spain:

Cabriel (Pujante 1993), Mundo (Vidal-Abarca et al. 1991) as well as Júcar and Segura (Puig et al. 1989; Ubero-Pascal 1996; Ubero-Pascal et al. 1998).

Southern Europe

In Italy, *Prosopistoma pennigerum* was recorded in 1979 in the region Toscana, where it occurred in a stream in a stony reach with a strong current (Bellmann 2000). The larvae were collected in the river Ombrone near Grosseto (C. Belfiore and A. Haybach, personal communication). Ikonomov (1964) recorded the species within a faunistic survey from the Varda River (Macedonia) and emphasised that the larvae are typically rheophilous. Bauernfeind (2003) included the species in a checklist for Greece, due to a record of Hoffmann (1994) from a braided section of the river Thiamis (H.W. Bohle, personal communication). The species was found in a section dominated by gravel under big rocks and the chironomid *Lithotanytarsus* was abundant, indicating water enriched with calcium carbonate (A. Hoffmann, personal communication). In Turkey *Prosopistoma pennigerum* is known from Dicle (Tigris) River near Diyarbakır, southeastern Anatolia (Koch 1985). This material has to be revised since Dalkıran (2009) has described a new species from northwestern Turkey. There is even a record of *P.* cf *pennigerum* from North-Western Algeria (Gagneur and Thomas 1988; Thomas 1998), which was made in the beginning of the 1980s in river Isser near Sidi Abdelli (altidude 300 m a.s.l.). During the dry season the width of the river was 6 m and the current was slow (A. Thomas, personal communication). In the 1980s, attempts have been made to find the species again, but it was not possible – maybe due to increasing pollution of the river system (J. Gagneur, personal comunication) and nowadays the Sidi Abdelli Dam is located at the place where *Prosopistoma* once was found.

Northern Europe

In the Netherlands the species was found in small ponds ('buitendijkse kolken') along lake Ijssel (Vos 1954), but this record is very doubtful (Mol 1985). From Scandinavia the species is known from two localities in Sweden: in the Lagan River two larvae were found in two stomachs of salmons (Trägårdh 1911) and another record is from the river Mörrumsån (Alm 1918).

Eastern Europe

The species was known from Vltava near Prague (Vayssière 1893; Komárek 1916), Blanice (Stephan in Lafon 1952), but it is considered to be extinct in the Czech Republic nowadays (Soldán 2000). In Hungary, a subimago of *Prosopistoma* was found in autumn 2002 at Szilas stream (left-side tributary of the Danube River) near Budapest (Hufnagel and Gaál 2005). In Romania, *Prosopistoma pennigerum* was recorded in the region Hunedoara from the river Mures and its tributary Cerna (Bogoescu 1958). In Latvia, the species was found in the Daugava River (Kačalova 1962, 1965; Kačalova and Skrube 1971; Spuris 1974, 1982). In the literature, the species *P. daugaviense* Spuris 1974 is mentioned, but this is a nomen nudum and without doubt referring to *P. pennigerum* (Poppels and Kalniņš 2002). After the hydroelectric station 'Pļaviņu' was built, this species disappeared from the Daugava River (N.J. Kluge, personal communication). In October 1965, about 120 larvae

from the Daugava River were transferred into the tributary Venta to preserve the species (Kačalova 1965), but there is no information about the result of this activity. In Georgia, *Prosopistoma* was discovered by R. S. Kazlauskas in the Kura River, within the Borzhomi Nature Reserve, and he wanted to describe a new species (N.J. Kluge, pers. comm.). Other researchers also collected larvae from Kura and identified them as *P. pennigerum* (Sadovsky 1946; Kasymov 1972). Due to these records, the species was included in the Red Book of the USSR. Nowadays it is listed in the Red Book of Smolensk Region/Russia (Kruglov 1995) and in the Red Book of Belarus (Republic of Belarus 2004; Moroz 2006). We recorded the species for the first time in the territory of the Russian Federation.

Ecology of Prosopistomatidae

It is generally recognised that larvae of *Prosopistoma* live under rocks or stones at medium depths (see e.g. Joly 1871; Schoenemund 1930; Gillies 1954). In Australia, the first records are from drift samples, thus Pearson and Penridge (1979) hypothesised that the larvae inhabit large rocks or boulders in rapidly flowing or deep water. The present records from the Volga River showed the association of this species with pebble and gravel substrates. The larvae can be clearly described as lithophilous. Flow velocity is considered to be important for the presence of Prosopistomatidae (Soldán and Braasch 1984; Ubero-Pascal 1996; O'Keeffe and Dickens 2000; Sartori and Gattolliat 2003). Larvae from the river Segura (Spain) were found in a location with a high velocity (0.21–0.49 m/s) and a discharge of about 5 m^3/s (Ubero-Pascal 1996). *P. funanense* was found at locations with a current speed between 0.1 and 0.3 m/s and for *P. annamnese* it has been shown that the densities are 0.05% (of the total mayfly community) at a current speed of 0.1–0.3 m/s, a maximum of 2.6–3.5% at 0.3–0.8 m/s and 1.2–1.8% at 0.8–1.2 m/s (Soldán and Braasch 1984). A study in South Africa revealed that *Prosopistoma crassi* prefers velocity ranges above 0.8 m/s (O'Keeffe and Dickens 2000). Surprisingly, different researchers were able to keep animals in an aquarium for several months (Vayssiére 1881; Kačalova 1965). However, according to their natural habitat the larvae of Prosopistomatidae can be clearly assigned to be rheophilous. Lafon (1952) claims that *P. pennigerum* is a potamophile, while Illies and Botosaneanu (1963) consider the species as a rhithrophile. An analysis of the mean annual discharge patterns of the locations in Europe shows that more than 50% of the sites can be assigned to large rivers (>100 m^3/s). About 30% of the stations are located along small (<10 m^3/s) and 20% mid-sized streams (10–100 m^3/s), showing that the species is not restricted to large river systems. But most of the settled reaches are of epi- and metapotamal type, because there the temperature regime is favourable. Thus, we can summarise that the larvae of Prosopistomatidae are lithophilous, rheophilous and *P. pennigerum* is most likely potamophilous.

Discussion

Increasing anthropogenic pressures resulting in habitat alteration, pollution or introduction of alien species (Léveque et al. 2005) are threatening freshwater biodiversity (Stiassny 1999). In North America, the extinction rate for freshwater animals is estimated to be five times higher than for the terrestrial fauna (Ricciardi and Rasmussen 1999); similar figures can be expected globally. An assessment of a

worldwide status of biodiversity is difficult, because data are insufficient (Léveque et al. 2005), thus the knowledge on distribution and ecological demands of a family, figuring out the threats, gives important hints for water policy plans.

The Fauna Europaea (FEWS 2004) points out that *P. pennigerum* is present in seven countries (Czech Republic, Greek mainland, Hungary, Macedonia, Romania, Spanish mainland, The Netherlands) and that in five countries (the French mainland, Italian mainland, Latvia, Luxembourg, Sweden) its presence is doubtful. The results of the literature synthesis for this study shows that the European Ephemeroptera species list (Schalk et al. 2005) and the Fauna Europaea (FEWS 2004) provide only fragmentary data about *Prosopistoma*. With this paper we were able to compile a reliable dataset on the historic and present distribution of this species in Europe, thus it is suggested to use this as a basis for further research.

Prosopistoma pennigerum was a typical component in the European freshwater fauna. The most frequent records came from potamal water bodies in France, Germany and Latvia, but the species is apparently now extinct at these sites. All other findings throughout Europe were single records. Nowadays it is only possible to regularly find the species in Spain and Russia (Ubero-Pascal et al. 1998; Schletterer and Kuzovlev 2007). It is possible that due to the special habitat or due to the small size, the species is overlooked in standard sampling programmes. However, the densities as shown by the recent records from the Volga River are generally low. These settlement patterns can be due to the possibly carnivorous feeding habits of this mayfly. Although Fontaine (1980) claimed non-predacious feeding habits for *P. pennigerum*, other authors reported that the species is feeding on Chironomidae and oligochetes (Trägårdh 1911). Thus it is likely that this species is predaceous at least in some life stages.

A main factor on the distribution of mayfly larvae is the substratum (Landa 1969; Brittain 1982; Dolédec 1988; Cogerino et al. 1995), but also water temperature, water quality, oxygen saturation, nutrition, as well as current and hydro-morphology play a role. For the family Prosopistomatidae we identified substratum (lithophilous) and current (rheophilous) as key factors for their distribution. The distribution of the European species *P. pennigerum* is considered to be linked to basin scale and temperature regime (potamophilous).

The main threats for *Prosopistoma pennigerum* are (1) intensive land use and water pollution (Thomas 1996), (2) water abstraction (Thomas 1996) and (3) hydroelectric power plants (Rey and Ortlepp 2002). A worldwide comparison indicates similar threats but also contrary indications. In contrast to the European species, which disappeared after the construction of dams on localities on the Rhine or Daugava Rivers, Prosopistomatidae are still present below the Vaal Dam (South Africa), though in reduced numbers and localities (Barber-James 2003). From the Lower Vaal River, downstream of the Vaal Triangle Industrial area (South Africa), no Prosopistomatidae were collected as a result of their sensitivity to pollution, showing that the present distribution of this family in South Africa is also affected by anthropogenic activities (Barber-James 2003). A study in Indonesia revealed that *P. olympus* is among the rarest mayflies and that it never occurs in locations where logging activities were carried out (Derleth 2003; Sartori and Gattolliat 2003).

Overall, Prosopistomatidae can be considered to be found in intact freshwater habitats in the Afrotropical, Oriental, Australian and Palaearctic region. One reason might be that the family is highly sensitive to environmental changes of either natural or anthropogenic origin. Furthermore it is known that larvae of Prosopistomatidae

are intolerant or moderately intolerant to organic pollution (Zhou and Zheng 2004a; Alam et al. 2008). Thus we assume that the presence of *Prosopistoma* indicates ecological integrity, i.e. high status water quality of a water body. Little is known about these unusual mayflies, because most of the species are found only sporadically and can be considered as being very rare. Thus, for better conservation, all described species have to be added to the IUCN-directory and as well to national red lists. Further research on the habitats, biogeography and the taxonomic status of this family is needed.

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