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RESEARCH ARTICLE

On the variation and distribution of the lake minnow, *Eupallasella percnurus* (Pall.)

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Abstract. The lake minnow, *Eupallasella percnurus* (Pall.), has a vast distribution range which extends from Poland to the Chukchi Peninsula, Sakhalin, Hokkaido, and Korea. This area and its adjacent regions are inhabited by an array of other minnow species which are morphologically close to the lake minnow and are currently included in the genera *Phoxinus* and *Rhynchocypris*. However, their systematic relationships remain largely obscure. The vast distribution range of the species, including numerous river systems divided by many mountain ranges that provide it with a very diverse and rich hydrographic and glaciological history, favors the evolution of locally differentiated forms. As a result, five subspecies have been distinguished within the lake minnow: *E. p. percnurus*; *E. p. stagnalis*; *E. p. ignatowi*; *E. p. mantschuricus*; *E. p. sachalinensis*. Because of great morphological variation, their status is still the subject of debate. The most recent morphological studies suggest a separate specific status of the Volga minnow *E. p. stagnalis*.

Keywords: lake minnow, variation, distribution, morphology, systematics

Introduction

The lake minnow, *Eupallasella percnurus* (Pall.), is a Eurasian representative of cyprinid fishes (Cyprinidae) of a vast distribution range which extends from the Oder River system in the west to the Anadyr River system in the Chukchi Peninsula, Sakhalin, Hokkaido, Korea, northern China, Mongolia, and Kazakhstan. Throughout this area it inhabits almost exclusively small, usually isolated, distrophic water bodies. It is very rarely found in rivers.

The systematic position of the lake minnow remains very controversial. According to the most up-to-date morphological analysis (Howes 1985), it is a member of the genus *Eupallasella*, to which it was transferred from the genus *Phoxinus*. The hypothesis was supported by the results of allozyme studies by Ito et al. (2002). Based on a limited-range genetic study Sakai et al. (2006) placed it in the genus *Rhynchocypris*.

The extremely large distribution range and the fact that the fish inhabits small and most often isolated water bodies favor great morphological variation, which has been emphasized by all the authors who have dealt with the infraspecific systematics of the lake minnow (Berg 1949, Thienemann 1950, Kaj 1954, Gąsowska and Rembiszewski 1967, Howes 1985, Mitrofanov 1987). In the past, this variation led to establishing numerous subspecies which were then subject to a few limited systematic revisions (Kaj 1954, Gąsowska and Rembiszewski 1967). Based on the literature (Berg 1949, Kaj 1954, Gąsowska and Rembiszewski 1967, Mitrofanov 1987, Nikitin and Safronov 2009), the following subspecies are distinguished at present: *E. percnurus percnurus* inhabiting most of Siberia and the territories of Poland,

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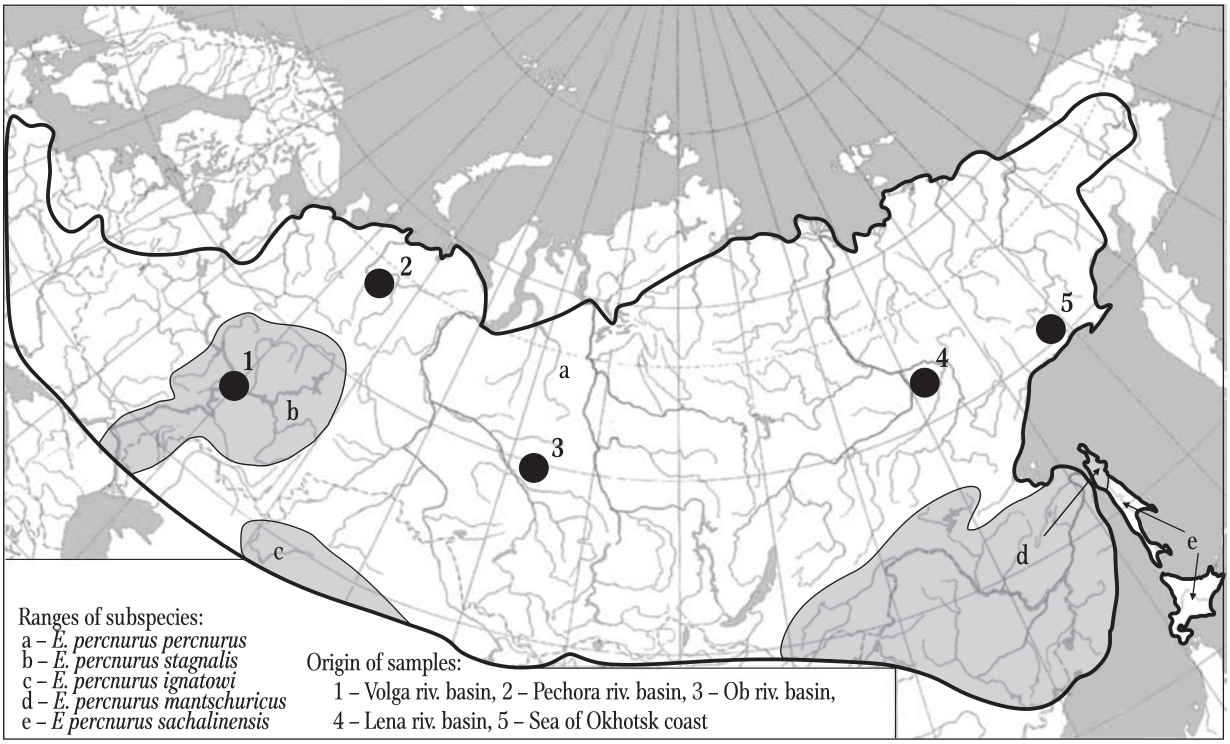

Figure 1. Distribution range of *Eupallasella percnurus* (Pall.) subspecies and sampling site locations.

Table 1
Sampling site location and number of specimens of *Eupallasella percnurus* (Pall.)

Subspecies	River system	Locality	N
Eupallasella percnurus percnurus	Pechora	Ust-Tsilma	15
	Ob	Sarafanovka village	14
	Lena	Yakutsk	25
	Sea of Okhotsk (Tauy R.)	Talon village	15
Eupallasella percnurus stagnalis	Volga	Nizhniy Novgorod	31

western Ukraine, and northwestern Russia; *E. percnurus stagnalis* which occurs in the Volga, Kama, and Oka river systems; *E. percnurus ignatowi* from undrained areas of northern Kazakhstan; *E. percnurus mantschuricus* which is found in the Amur River system, Sakhalin, and Korea; *E. percnurus sachalinensis* distributed in Sakhalin and Hokkaido. The relationships among these subspecies remain obscure.

According to earlier studies, the European populations of the lake minnow (Berg 1949, Gąsowska and Rembiszewski 1967) represent the nominate subspecies *E. percnurus percnurus*, most of whose range is located east of the Urals. Considering the role of these mountains as a barrier, it seems more likely that Europe was populated by the minnow originating from the Volga River system.

The aim of this paper was to analyze morphological variation of the lake minnow using geometric morphometry based on the distribution of the subspecies, and to attempt to specify the origin of the European populations of the species.

Material and methods

The material included 100 specimens of the lake minnow representing 5 populations from the Pechora, Volga, Ob, and Lena river systems and the Sea of Okhotsk coast (Fig. 1, Table 1). The fish were caught with nets and preserved in 4% formaldehyde in horizontally positioned plastic containers, thus the specimens were not deformed and mostly well stretched. In the laboratory, the specimens were rinsed in running water for two hours and then prepared to be photographed. Each photographed fish was placed on its right side and pinned to a cork board using thick entomological needles in such a way that the sagittal plane of the specimen was parallel to the board surface. Thinner entomological needles were used to mark the landmarks. This facilitated the localization of the landmarks in the photographs. A millimeter scale was placed at the level of the sagittal plane of each specimen for the purpose of later calibration of the measurements taken from the photographs. Thus prepared, the specimens were photographed with a Canon EOS D350 digital camera. Only non-deformed straight specimens were used for the photographs and, consequently, measurements. Twelve landmarks were designated on each specimen according to the Truss Network scheme (Strauss and Bookstein 1982) as modified by Paśko and Maślak (1997) (Fig. 2). The landmarks were: I – anteriormost point of the premaxillary bone; II – posterior margin of the posterior naris; III – posteriormost point of the mandible; IV – base of the last (interior) ray of the pectoral fin; V – posterior margin of the supraoccipital bone; VI – base of the first ray of the dorsal fin; VII – base of the first ray of the ventral fin; VIII – base of the first ray of the anal fin; IX – base of the last ray of the dorsal fin; X – base of the last ray of the anal fin; XI – origin of the dorsal lobe of the caudal fin (anteriormost point of the first ray base); XII – origin of the ventral lobe of the caudal fin (anteriormost point of the last ray base).

Distances between the landmarks were measured with the SigmaScan Pro 5.0 program (SPSS Inc.)

Statistical analyses

Statistical calculations were done with Microsoft Excel 2003 (Microsoft Corporation), NTSYS 1.8 for DOS (Rohlf), NTSYS 2.21l for Windows (Rohlf), and Statistica 9.1 (StatSoft Inc.). The data were log-transformed, and the effect of varied body size of the specimens was removed by Allometric Burnaby's Method (Bookstein 1991, Reyment 1991). In order to detect patterns of inter-population variation, the number of variables (characters) was subject to reduction in data matrices freed from the effect of the first eigenvector using Canonical Variate Analysis (CVA) since the data met the assumption of normality of distribution of characters in the populations and of homogeneity of their variance which were tested with Shapiro-Wilk's test of normality of the distribution of characters and with Levene's test of the homogeneity of variances.

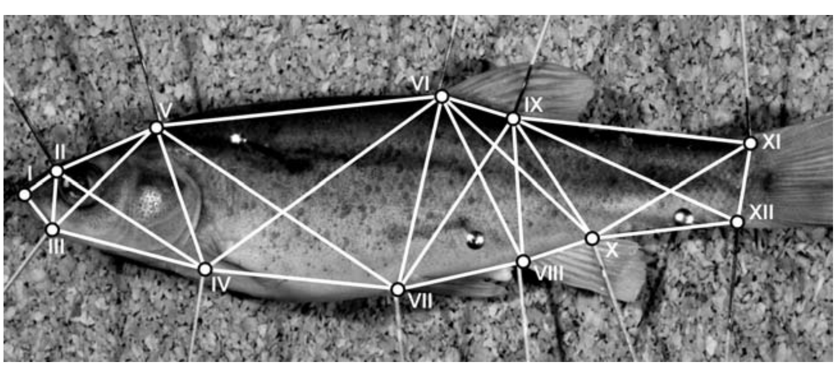

Figure 2. Landmark location and the Truss Network scheme used for morphometric measurements.

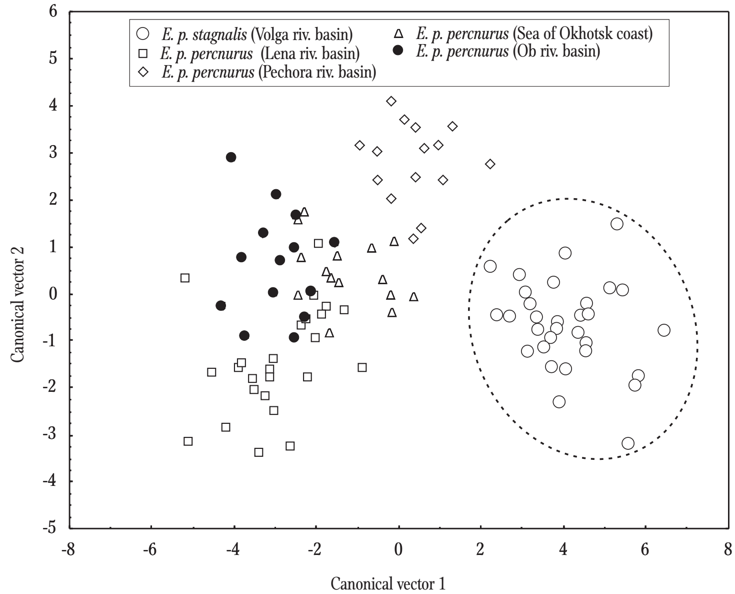

Figure 3. Results of the Canonical Variate Analysis (CVA) of the Truss Network morphometric features of *Eupallasella percnurus* (Pall.).

Results

Wilks' Lambda for the general model obtained in the analysis was 0.00 at $P \leq 0.05$, indicating the very strong, statistically significant discrimination power of the model. The correctness of the classification (based on the generalized distance for particular specimens from cluster centroids) for the data matrix used to calculate the model was very high and ranged from 72 to 100% for individual populations. On average, nearly 92% of each population was correctly classified within the model. The first three canonical vectors were significant at $P \leq 0.05$, but already the first two explained 78% of the total variation.

The discrimination localization of the studied populations within the space of the first two canonical vectors is presented in Figure 3. The population of *E. percnurus stagnalis* from the Volga River system is distinctly separated along vector I which explains 63% of the total variation observed. The remaining populations form essentially one cluster, although the population of *E. percnurus percnurus* from the Pechora River system occupies an intermediate position between the Volga population and the remaining populations which originate from the areas east of the Urals. Vector II does not discriminate distinctly any of the populations studied.

Discussion

The results justify the separation of *E. percnurus stagnalis* as a distinct taxon which should most probably have species status. The population of this form differs decidedly from the populations of nominate form, which is slightly surprising, considering the spatio-temporally extensive palaeohydrographic contact of the present Volga system with the areas of Siberia and northeastern Europe inhabited by *E. percnurus percnurus*.

According to most authors, and especially Berg (1949), most of the range of the lake minnow (except the Volga and Amur river systems, Sakhalin, Hokkaido and an undrained region of northern Kazakhstan) is inhabited by lake minnow populations representing the nominate subspecies. In the case of Siberia, the situation can be accounted for by its glaciological past which is much less complex as compared to that of Europe. However, the fact that the subspecies also inhabits Europe at present is surprising. According to Kaj (1954), the lake minnow is a post-glacial immigrant from the northeast, or a glacial relic of the Central European mixed fauna. The results of previous genetic studies (Kusznierz et al. 2006), which revealed small genetic variation among Polish populations, suggest that Europe was recolonized by the lake minnow returning from the so-called northern refugia located in present-day Hungary and Slovakia (Willis et al. 2000, Stewart and Lister 2001). This partly confirms Kaj's (1954) view, the more so that the presence of lake minnow populations in western Ukraine (Movtchan and Smirnov 1981) and their absence between the Dnieper and Volga rivers indicate that recolonization did not proceed from the Volga system, though at first glance such a migration route would seem most likely. The extensive contact between the Volga River system and the region of central and northeastern Europe (Mangerud et al. 2004) in the not very remote past suggests that the populations inhabiting the Oder, Vistula, Dnieper, Dnester, North Dvina, and Pechora river systems should be closer to *E. percnurus stagnalis* from the Volga system than they are to the Siberian populations of the nominate subspecies, which are separated from Europe by the Urals. The very distinct morphological differences between *E. percnurus stagnalis* and *E. percnurus percnurus* seem to confirm the results of the most recent palaeohydrographic studies (Mangerud et al. 2004), which suggest the possible existence of a connection between the Pleistocene periglacial Lake Komi with the Ob River system; the connection, located on the northern fringe of the Urals, could explain the presence of *E. percnurus percnurus* in the Pechora River system. The species could have reached European waters along this route.

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Streszczenie

O zróżnicowaniu i rozmieszczeniu strzebli błotnej *Eupallasella percnurus* (Pall.)

Strzebla błotna *Eupallasella percnurus* (Pall.) odznacza się bardzo szerokim zasięgiem występowania sięgającym od Polski po Półwysep Czukocki, Sachalin, Hokkaido i Koreę. Na tym rozległym obszarze oraz terenach bezpośrednio do niego przyległych występuje ponadto szereg innych gatunków strzebli morfologicznie zbliżonych do strzebli błotnej, zaliczanych aktualnie do rodzajów *Phoxinus* i *Rhynchocypris*. Ich relacje systematyczne w znacznej mierze pozostają ciągle niejasne.
Ogromny zasięg występowania gatunku obejmujący szereg dorzeczy wielkich rzek, podzielony wieloma pasmami górskimi i w związku z tym odznaczający się bardzo zróżnicowaną, bogatą historią hydrograficzną i glacjologiczną, z założenia sprzyja powstaniu zróżnicowania lokalnych form. W efekcie u strzebli błotnej wyróżniono pięć podgatunków *E. p. percnurus*, *E. p. stagnalis*, *E. p. ignatowi*, *E. p. mantschuricus*, *E. p. sachalinensis*. Ze względu na dużą zmienność morfologiczną status tych form w dalszym ciągu budzi wiele wątpliwości.
W prezentowanej pracy przedstawiono wyniki badań morfometrycznych przeprowadzonych z wykorzystaniem metody Truss Network oraz analizy kanonicznej, do których użyto 100 osobników strzebli błotnej reprezentujących 5 populacji pochodzących z dorzeczy Peczory, Wołgi, Obu i Leny oraz z wybrzeża Morza Ochockiego. Uzyskane rezultaty wskazują zasadność nadania strzebli wołżańskiej *E. p. stagnalis* statusu samodzielnego taksonu, najprawdopodobniej na poziomie gatunkowym. Uzyskany obraz zróżnicowania morfometrycznego potwierdza większe podobieństwo populacji z dorzecza Peczory do populacji występujących na wschód od Uralu niż do znacznie bliższej, w sensie geograficznym, populacji z dorzecza Wołgi. Wskazuje to na możliwość zasiedlenia dorzecza Peczory, a prawdopodobnie także Północnej Dźwiny, Dniepru, Dniestru, Wisły i Odry przez strzeble pochodzące z dorzecza Obu, które do dorzecza Peczory mogły dostać się przez połączenie tych dorzeczy usytuowane na północnych stokach Uralu.