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Taxonomy of the spring dwelling amphipod *Synurella ambulans* (Crustacea: Crangonyctidae) in West Russia: with notes on its distribution and ecology

Dmitry SIDOROV [1,*] & Dmitry PALATOV [2]

[1] Department of Zoology, Institute of Biology and Soil Science FEB RAS, 100-let Vladivostoku Av. 159, Vladivostok 690022, Russia. E-mail: sidorov@biosoil.ru
urn:lsid:zoobank.org:author:55C1264F-67C0-4C3F-8E6B-ECE1E821457B
[2] Department of Hydrobiology, Moscow State University, Leninskie Gory 1/12, Moscow 119991, Russia. E-mail: triops@yandex.ru
urn:lsid:zoobank.org:author:25BBE8A0-81C4-4B42-859A-3A7BA3EE3C0E
* Corresponding author: E-mail: sidorov@biosoil.ru

Abstract. This study deals with taxonomic problems of the semi-subterranean crangonyctid amphipod *Synurella ambulans* (F. Müller, 1846), well-known from various freshwater habitats in Europe. The taxonomy of the species *S. ambulans* and the generic diagnosis for the genus *Synurella* are revised. A new synonymy is proposed: *Synurella ambulans* (F. Müller, 1846) = *Synurella ambulans meschtscherica* Borutzky, 1929, **syn. nov.** The affinity with the related groups, distribution and ecology of the species are examined.

Key words. Amphipoda, Crangonyctidae, *Synurella ambulans*, stygophile, distribution, ecology, springs.

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Introduction

The amphipod genus *Synurella* Wrześniowski, 1877 is stygophile, but lacking typical stygomorphic features such as anophthalmy, depigmentation and reduced fecundity (the females normally produce no less than 11−20 small-sized eggs). *Synurella* occurs in semi-subterranean freshwaters and coastal plain brackish habitats throughout the Holarctic region (Karaman 1974a, 1990; Barnard & Barnard 1983). To date, approximately 19 species of *Synurella* have been described, including 6 from Russia. The geographical records of *Synurella* in western Russia are confined to three described species: *S. donensis* Martynov, 1919 (springs of Rostov-on-Don vicinity), *S. derzhavini* Behning, 1928 (wells of Saratov vicinity) and *S. meschtscherica* (Borutzky, 1929) (springs and spring-runs of Meschtschera).

The goal of our study was to examine taxonomic boundaries between *S. ambulans* and *S. meschtscherica*. Some authors previously had doubts about the validity of *S. meschtscherica* (see Karaman 1974a) and assumed it was a junior synonym of *S. ambulans,* because of the lack of clear differences between these taxa. However, it was thus far never formally synonymized. It should be noted, that initially *S. meschtscherica* was reported by Borutzky (1927) under the name *S. ambulans*, who then later described it as a subspecies of that species (Borutzky 1929). Birstein (1948) provisionally evaluated the status of *S. ambulans meschtscherica* and suggested that it deserved species status. However, this was done without sufficient argumentation.

The taxonomy of the genus is confusing. Some forms of the large species-complex *S. ambulans* are considered distinct species by some researchers, whereas other workers only rank them as subspecies or consider them as local forms. Moreover, poorly known nominal species such as *S. donensis*, *S. ambulans taurica* Martynov, 1931 and *S. philareti* Birstein, 1948 may simply be aberrant forms of other, better-known, species. Consequently, the number of species to be included in the genus is uncertain. The species *S. ambulans* was described as *Gammarus ambulans* by Friedrich Müller (1846) from ditches at Greifswald in Mecklenburg-Vorpommern (N Germany) (Müller 1846). It has been suggested previously that the species is extremely polymorphic and widespread in Europe and Asia Minor (Ruffo 1974; Karaman 1974a, 2003; Nesemann 1993; Muskó 1994; Kontschán 2001; Pezzoli 2010). However, the morphological variability of the species was interpreted too liberally by the former authors and without good reasons. As a consequence of this incomplete taxonomic knowledge, erroneous conclusions about species origin and distribution were formulated. Since the recent discovery of *S. ambulans* in the Black Sea area (Ketelaars 2004), Ukraine (Alexandrov *et al.* 2007) and in the Belgian province of West-Flanders (Boets *et al.* 2010), it was assigned to a group of Ponto-Caspian invaders, although there is no sound evidence for this assumption.

Some authors have considered integrating the genus *Synurella* into the genus *Stygobromus*, owing to the lack of clear morphological and geographical boundaries between these groups (Birstein 1948; Karaman 1974a, 1974b), or directly united them (Barnard & Barnard 1983). However, some researchers have expressed the opposite view (Holsinger 1977; Bousfield 1977). In our opinion, significant morphological differences between these genera are primarily observed in the general body morphology. Moreover, the genus *Synurella* is not monophyletic according to Martynov (1931), who assigned all the Far Eastern-Siberian and one Alaskan species to the subgenus *Eosynurella.* The latter group differs markedly from the European taxa, except for *Synurella dershavini* Behning, 1928 and from the North American *Synurella*, by the pear-shaped gnathopod 2 propodi and the structure of uropod 3 with a strongly reduced terminal segment. It is possible that the biogeography of the genera *Synurella* and *Stygobromus* cannot be explained by a simplified barrier-insulation approach proposed by several authors (Birstein 1948; Karaman 1974a, 1974b), but should apparently be explained by isolation through the existence of ancient seas, straits, and by evolutionary differences.

Synurella meschtscherica from the Meschtschera Lowland is now formally considered a junior synonym of *S. ambulans*. In our study we examined samples from the topotype locality of *S. meschtscherica*. We further include detailed distributional information based on morphological comparison of material from scattered localities in West Russia.

Material and Methods

Taxonomic sampling

The specimens of *S. meschtscherica* were collected and studied from an extensive territory on the East European Plain (Fig. 1), ranging from the Baltic Sea basin (Pskov administrative area) to the Meschtschera Lowland in the east (Moscow, Ryazan, Vladimir areas) and in the south to the Central Russian Upland in the Oka River basin (Kaluga area) as far as the upper part of the Dniepr River basin (Bryansk area). The comprehensive collection of specimens was carried out mostly by the second author using a common hand net. The samples were preserved in 80% ethanol and are kept at the Institute of Biology and Soil Science (Vladivostok). Preserved material of *S. ambulans* at the Museum of Naturkunde (Berlin), collected and determined by M.L. Zettler from Kassow near Rostock (Mecklenburg-Vorpommern, Germany), was also used in this study for comparison of two species.

Morphology

All relevant morphological structures were examined and measured. To measure the body length, more precisely the distance along the dorsal side of the body from the base of the first antenna to the base of

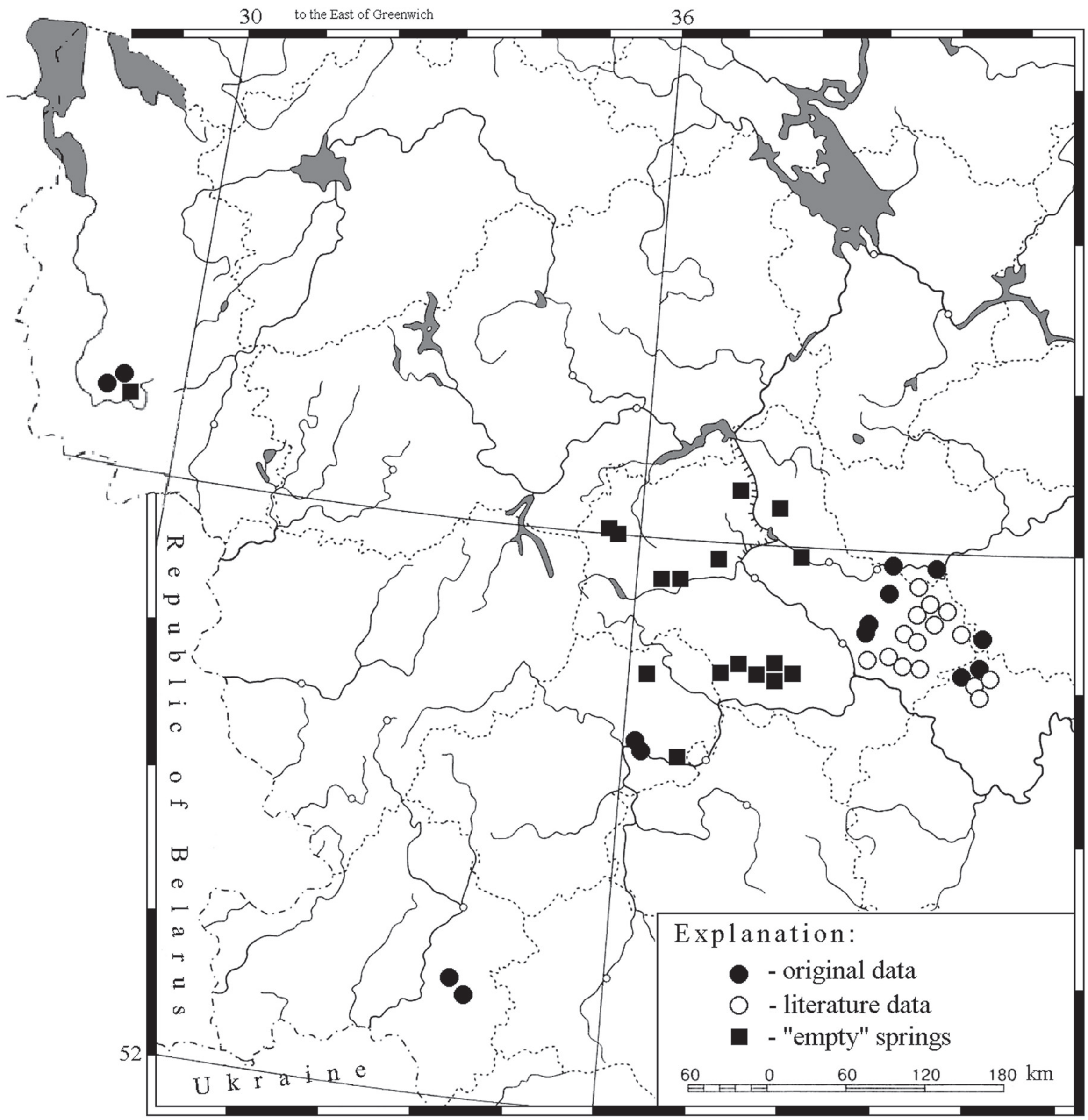

Fig. 1. Map indicating the geographic distribution of *Synurella ambulans* (F. Müller, 1846) in western Russia. Legend: "empty" springs display undisturbed springs with a rich crenophilous fauna without *S. ambulans.* Literature data: Borutzky (1929), Chertoprud (2006a, 2006b). Source: Blank Mapping Tools, Moscow (2009).

the telson, the specimen was held in a ventro-dorsal position. A Lomo MBS-9 stereomicroscope with a scaled micrometer eyepiece was used to make this measurement and appendages were drawn using a Carl Zeiss NU-2 compound microscope equipped with a drawing device as modified by Gorodkov (1961). The permanent preparations were made using polyvinyl lactophenol (PVL) and a methylene blue staining solution. A lens adapter LSN-23D by Zarf Enterprises for Nikon CoolPix 995 was used for digital photomicrography of the lateral cephalic lobes and appendages.

The term "defining angle" of the gnathopod propodi refers to the angle formed at the end of the palm and beginning of the posterior margin or the point at which the tip of the dactylus closes on the propodus (see Holsinger 1974). The nomenclature for setal patterns on segment 3 of the mandibular palp follows the standard introduced by Karaman (1970). The descriptive terminology follows a classification system based on the homology concept proposed by Watling (1989). The following description was generated from a DELTA database (Dallwitz 2005) for the crangonyctid genera and species of the world.

Abbreviations

BN = Bryansk area, Navlinsky.
FENU = Zoological Museum of the Far East National University, Vladivostok.
IBSS = Institute of Biology and Soil Science, Vladivostok.
KF = Kaluga area, Ferzikovsky.
MO = Moscow area, Orekhovo-Zuevo.
MSU = Zoological Museum of Moscow State University, Moscow.
PP = Pskov area, Pustoshkinsky.
RK = Ryazan area, Klepiki.
VP = Vladimir area, Petushinsky.

Results

Taxonomy

Order Amphipoda Latreille, 1818
Family Crangonyctidae Bousfield, 1973

Genus ***Synurella*** Wrześniowski, 1877

Synurella Wrześniowski, 1877: 403.
Goplana Wrześniowski, 1879: 299.
Boruta Wrześniowski, 1888: 44.
Eosynurella Martynov, 1931: 531.
Diasynurella Behning, 1940: 43.

Type species

Gammarus ambulans F. Müller, 1846 (= *Synurella ambulans* (F. Müller, 1846) designated by Wrześniowski (1877)).

Revised diagnosis (related to sub-family group 1 *sensu* Bousfield 1977: 302)

Closely allied with *Stygobromus* Cope, 1872, but with the following characteristic features: head, lateral cephalic lobe broadly rounded without inferior sinus (except *Synurella osellai*); antenna 2 of male with paddle-shaped calceoli; gnathopod 1 propodi sub-quadrate; gnathopod 2 propodi with well-developed posterior margins, propodi always larger than the same of gnathopod 1; coxal plates 1–3 deep, much longer than broad; coxal plate 4 deep, with excavation; urosomites partially or entirely fused; telson apical margin distinctly notched or lobate; oöstegites 2–5 large, ovoid.

Remarks

In our opinion, the Crimean form *Synurella ambulans taurica* Martynov, 1931, with a slightly extended basipodite of pereopod 7, is related to the southern species complex of *S. intermedia* and *S. tenebrarum* rather than to the nominative species. However, owing to the poor description it is difficult to reach a definite conclusion.

Synurella ambulans (F. Müller, 1846) (*sensu stricto*)
Figs 2-9

Gammarus ambulans F. Müller, 1846: 296, Taf. 10, figs A-C (original description).
Synurella ambulans Stebbing, 1906: 369.
Synurella polonica Wrześniowski, 1877: 403.
Synurella ambulans meschtscherica Borutzky, 1929: 30, figs 1-17, **syn. nov**.
Synurella meschtscherica Birstein, 1948: 70.
Stygobromus ambulans Barnard, 1983: 438.
Stygobromus meschtschericus Barnard, 1983: 440.

Synurella ambulans – Schäferna 1922: 57, tab. 1 (10), tab. 2 (1-4), text-figs 26-29. — Borutzky 1927: 63. — Schellenberg 1942: 85, Fig. 66.
Synurella polonica – Stebbing 1906: 369. — Jarocki & Krzysik 1924: 555.
Synurella ambulans meschtscherica – Straškraba 1962: 132.
Synurella meschtscherica – Barnard 1958: 75. — Straškraba 1967: 208. — Karaman 1974a: 124.
Stygobromus meschtschericus – Starobogatov 1995: 192. — Chertoprud 2006a: 19; 2006b: 382.

Diagnosis

Medium-sized species with marked secondary sexual dimorphism. Body pigmented. Gnathopod 2 larger than gnathopod 1. Pereopod 6 longer than pereopod 7. Pereopod 7 basis without distinct posterior lobe. Coxal gills on pereopods 2–7, gill 7 very small. Sternal gills arrangement as following: pereonite 2 (-2-), pereonite 3 (-2-), pereonite 6 (1-1), pereonite 7 (1-1), pleonite 1 (1-1). Brood plates 2–5 (oöstegites) rather broad, with long marginal setae. Body length 3.5 – 6.0 mm (♀), 3.0 – 4.5 mm (♂).

A distinctive feature of this species is a well-marked broad yellowish spot (Fig. 2A) located on the dorsal surface of the head between eyes. The spot is discernible only in living animals.

Fig. 2A-C. *Synurella ambulans* (F. Müller, 1846). **A**. Yellow spot on the dorsal surface of the head of live specimens (front and left side), MO. **B**. ♂, 4.2 mm, FENU X34906/Cr-1406, KF. **C**. ♀, 5.5 mm, FENU X34906/Cr-1406, BN, left side (preserved specimens).

Material examined

GERMANY. All specimens (3 ♀♀, 1 ♂) completely dissected and mounted on a single slide per number: [MSU Mb-1146] ♀ (oöstegites developed, setose) 5.7 mm and ♂ 4.2 mm, [FENU X34906/Cr-1406] ♀ (oöstegites developed, setose) 5.5 mm and ♀ (oöstegites developed, setose) 5.2 mm. Mecklenburg-Vorpommern, Kassow (53°87'76.3"N 12°07'67.2"E), 21 May 1997, collected by M. Zettler.

RUSSIA. All specimens completely dissected and mounted on a single slide [FENU X34906/Cr-1406], 8 ♀♀, 2 ♂♂: ♀ (oöstegites developed, setose) 6.0 mm, Pskov area, Pustoshkinsky, near Yezerische Lake, Kholodny brook (56°24'10"N 29°08'33"E), 20 Aug. 2010, collected by D. Palatov; 2 ♀♀ (oöstegites developed, setose) 3.5 mm and 5.5 mm, Bryansk area, Navlinsky, Desna River basin, near Partizanskoye, pond (52°45'77"N 34°22'72"E), 17 Sep. 2009, collected by D. Palatov; ♀ (oöstegites developed, non-setose) 5.5 mm and ♀ (oöstegites developed, setose) 4.0 mm, Kaluga area, Ferzikovsky, Oka River basin, spring (54°29'47"N 36°21'41"E), 02 Jul. 2007, collected by D. Palatov; ♀ (oöstegites developed, non-setose) 5.2 mm and ♂ 4.5 mm, Moscow area, Orekhovo-Zuevo, ~ 3.5 km E of Voinovo, Chernaya River (55°50'42"N 39°04'82"E), 02 May 2009, collected by D. Palatov; ♀ (oöstegites

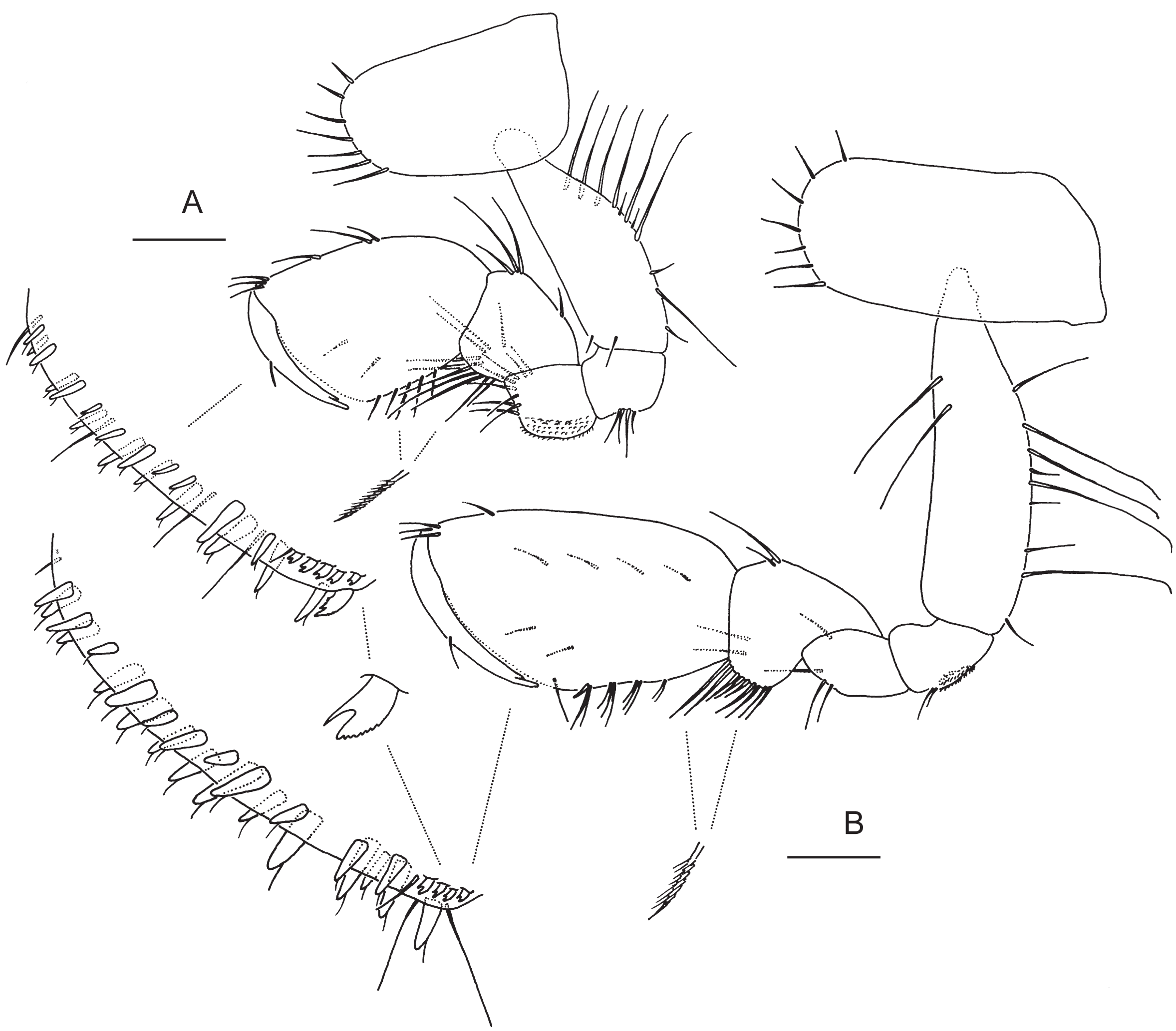

Fig. 3A-B. *Synurella ambulans* (F. Müller, 1846), ♂, 4.5 mm, FENU X34906/Cr-1406, MO. **A**. Gnathopod 1. **B**. Gnathopod 2. Scale bars 0.2 mm.

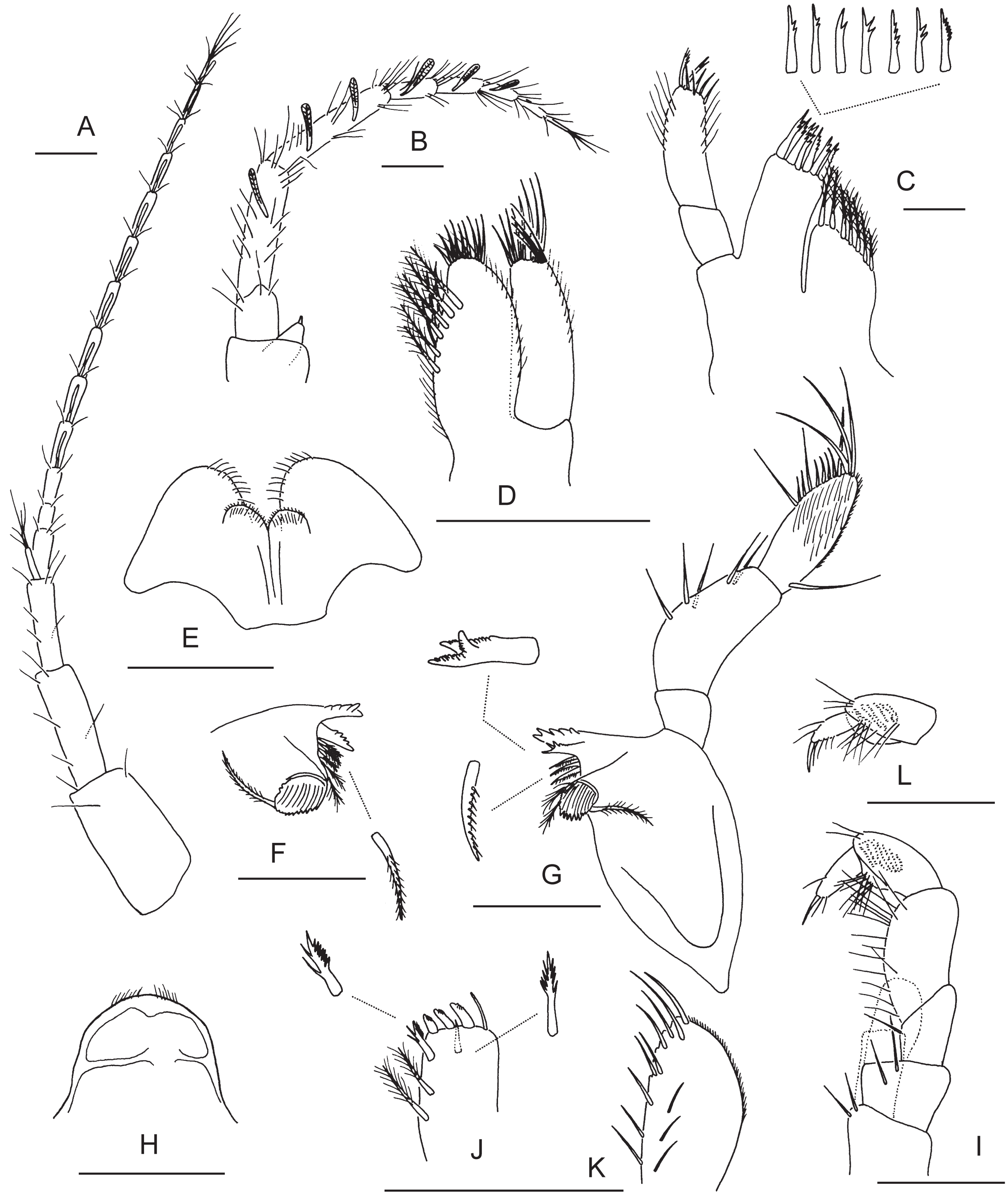

Fig. 4A-L. *Synurella ambulans* (F. Müller, 1846), ♂, 4.5 mm, FENU X34906/Cr-1406, MO. **A**. Antenna 1. **B**. Antenna 2. **C**. Maxilla 1. **D**. Maxilla 2. **E**. Lower lip. **F**. Left mandible. **G**. Right mandible. **H**. Upper lip. **I**. Maxilliped. **J**. Maxilliped, inner plate. **K**. Maxilliped, outer plate. **L**. Distal part of maxilliped palp, female, 6.0 mm, FENU X34906/Cr-1406, PP. Scale bars 0.2 mm.

developed, setose) 5.0 mm. Nerskaya River basin, near Podosinky, brook (55°34'18"N 38°49'12"E), 27 Aug. 2005, collected by D. Palatov; 2 ♀♀ (oöstegites developed, non-setose) 4.0 mm and 3.8 mm, ~ 2.5 km NE of Anciferovo, "Anciferovsky Spring" (55°33'85"N 38°48'17"E), 8 Jan. 2010, collected by D. Palatov; ♂ 4.0 mm. Vladimir area, Petushinsky, Markovo, brook (55°52'11"N 39°17'15"E), 22 Apr. 2007, collected by D. Palatov.

Additional material examined

All specimens measured, partially dissected and stored in different vials [IBSS 17/2SD], ca. 82 ♀♀, 33 ♂♂: 3 ♀♀, 4 ♂♂, Vladimir area, Petushinsky, ~ 3 km SE of Usad, small floodplain lake (55°51'27"N 39°08'76"E), 02 May 2009, collected by D. Palatov; 4 ♀♀, Gus-Khrustalny, near Shestimirovo, Buzha River basin, brook (55°27'09"N 40°13'68"E), 14 May 1994, collected by M. Chertoprud and D. Palatov;

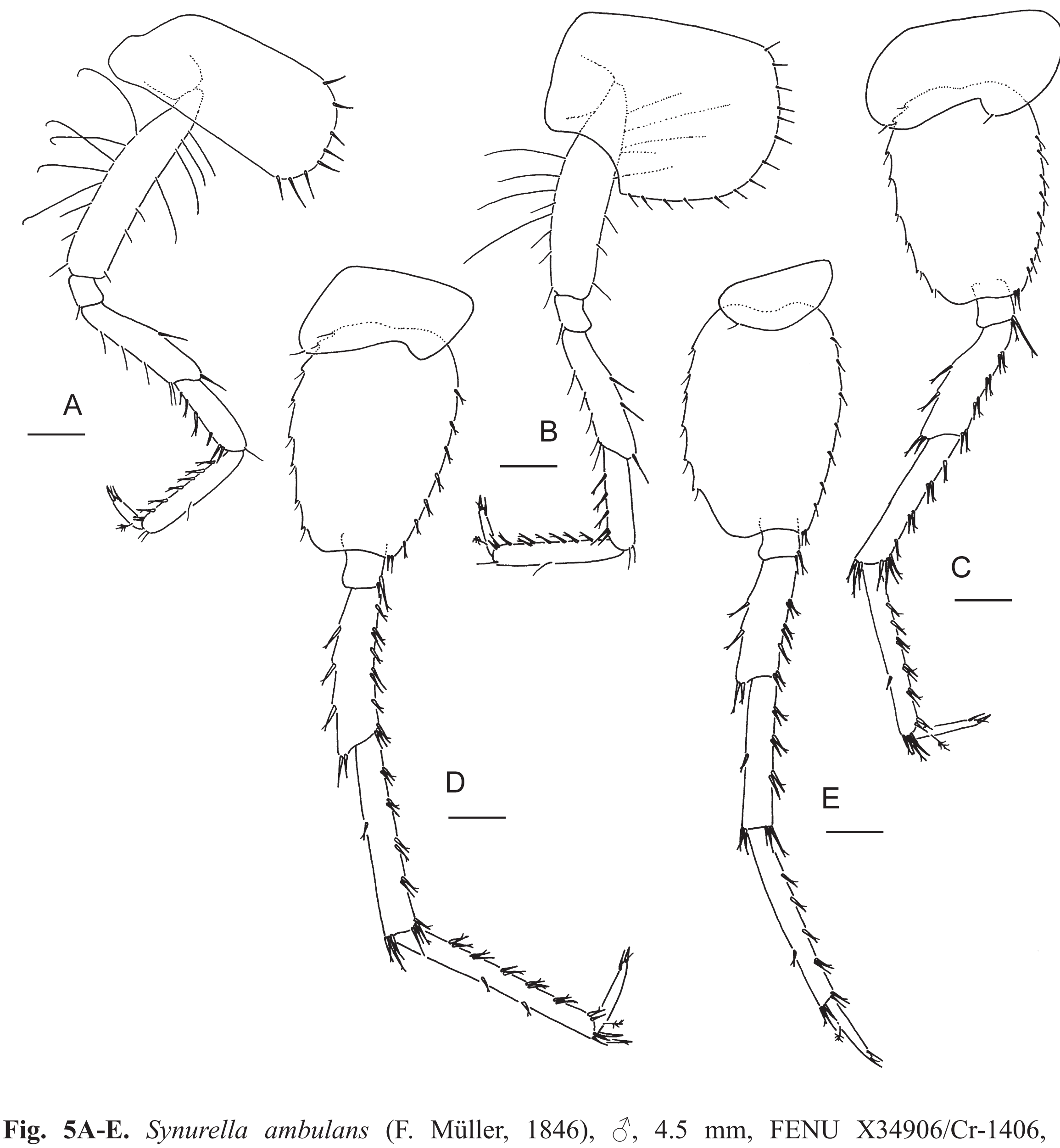

Fig. 5A-E. *Synurella ambulans* (F. Müller, 1846), ♂, 4.5 mm, FENU X34906/Cr-1406, MO. **A**. Pereopod 3. **B**. Pereopod 4. **C**. Pereopod 5. **D**. Pereopod 6. **E**. Pereopod 7. Scale bars 0.2 mm.

4 ♀♀, Ryazan area, Klepiki, ~ 1.5 km NW Shmeli, Yalma River basin, spring (55°12'93''N 39°55'63''E), 02 Oct. 2006, collected by M. Chertoprud and D. Palatov; 38 ♀♀: near Velikodvorye, Yalma River basin, springs (55°12'46''N 39°59'12''E), 20 Oct. 2006, collected by D. Palatov; ca. 50 ♀♂, Kaluga area, Ferzikovsky, ~ 2 km E of Majakovsky, Oka River basin, spring (54°29'47''N 36°21'41''E), 30 Apr. 2011, collected by D. Palatov; 5 ♀♀, 4 ♂♂, Bryansk area, Navlinsky, near Dumcha, Dumcha River basin, springs (52°49'35''N 34°10'48''E), 19 Sep. 2009, collected by D. Palatov; 2 ♀♀, Pskov area, Pustoshkinsky, Velikaya River basin, ~ 2 km W of Vysotskoe, brook (56°26'68''N 29°22'06''E), 16 Aug. 2010, collected by D. Palatov.

Type locality

Germany, Mecklenburg-Vorpommern, Greifswald (approx. 54°5'N, 13°23'E), ditches (F. Müller, 1846). Type material stored in the zoological collection of the Greifswald University (Zettler 1998: 57).

Redescription

Male

Length. 4.5 mm, FENU X34906/Cr-1406.

Habitus. (Fig. 2B) Not stygomorphic.

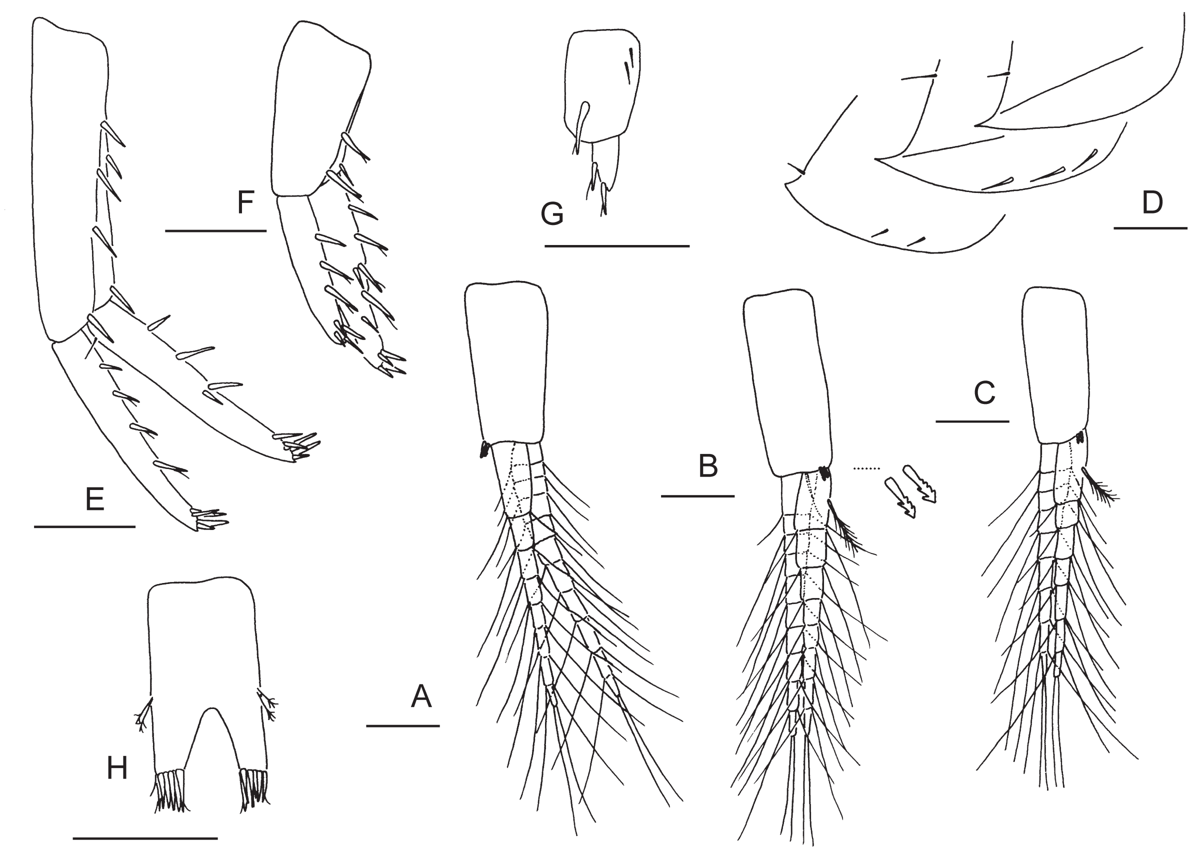

Fig. 6A-H. *Synurella ambulans* (F. Müller, 1846), ♂, 4.5 mm, FENU X34906/Cr-1406, MO. **A**. Pleopod 1. **B**. Pleopod 2. **C**. Pleopod 3. **D**. Epimera 1-3. **E**. Uropod 1. **F**. Uropod 2. **G**. Uropod 3. **H**. Telson. Scale bars 0.2 mm.

Body. Slender with elongate appendages, color yellowish.

Head. Eyes (Figs 2B; 9) vestigial, black; yellow spot (Fig. 2A) located on the dorsal surface of the head between eyes characteristic for living specimens. Antenna 1 (Fig. 4A) 55% length of body, 30% longer than antenna 2; peduncular segments 1–3 in length ratio 1:0.8:0.6; primary flagellum with 13 segments; aesthetascs present. Antenna 2 (Fig. 4B), peduncular segments 4 and 5 in lengths ratio 1:1; flagellum with 5 segments; calceoli present. Left mandible (Fig. 4F) incisor 5-dentate; lacinia mobilis 5-dentate; setal row with 3 serrate setae. Right mandible (Fig. 4G) incisor 5-dentate; lacinia mobilis trifurcate. Molar process (Fig. 4F, G) triturative, with accessory seta. Palp mandible (Fig. 4G) segment 2 slightly longer than segment 3; segment 3 with 1 A-seta, 2 C-setae, 6 D-setae and 4 E-setae. Lower lip (Fig. 4E), inner lobes present; mandibular process indistinct (broad). Maxilla 1 (Fig. 4C), inner plate with 7 plumose setae; outer plate with 7 serrate setae; palp segment 2 about 2x longer than segment 1. Maxilla 2 (Fig. 4D), inner plate with 6 plumose setae. Maxilliped (Fig. 4I-K) inner plate with 3 strong apical setae; outer plate broad. Foregut lateralia with 8 strong pectinate setae.

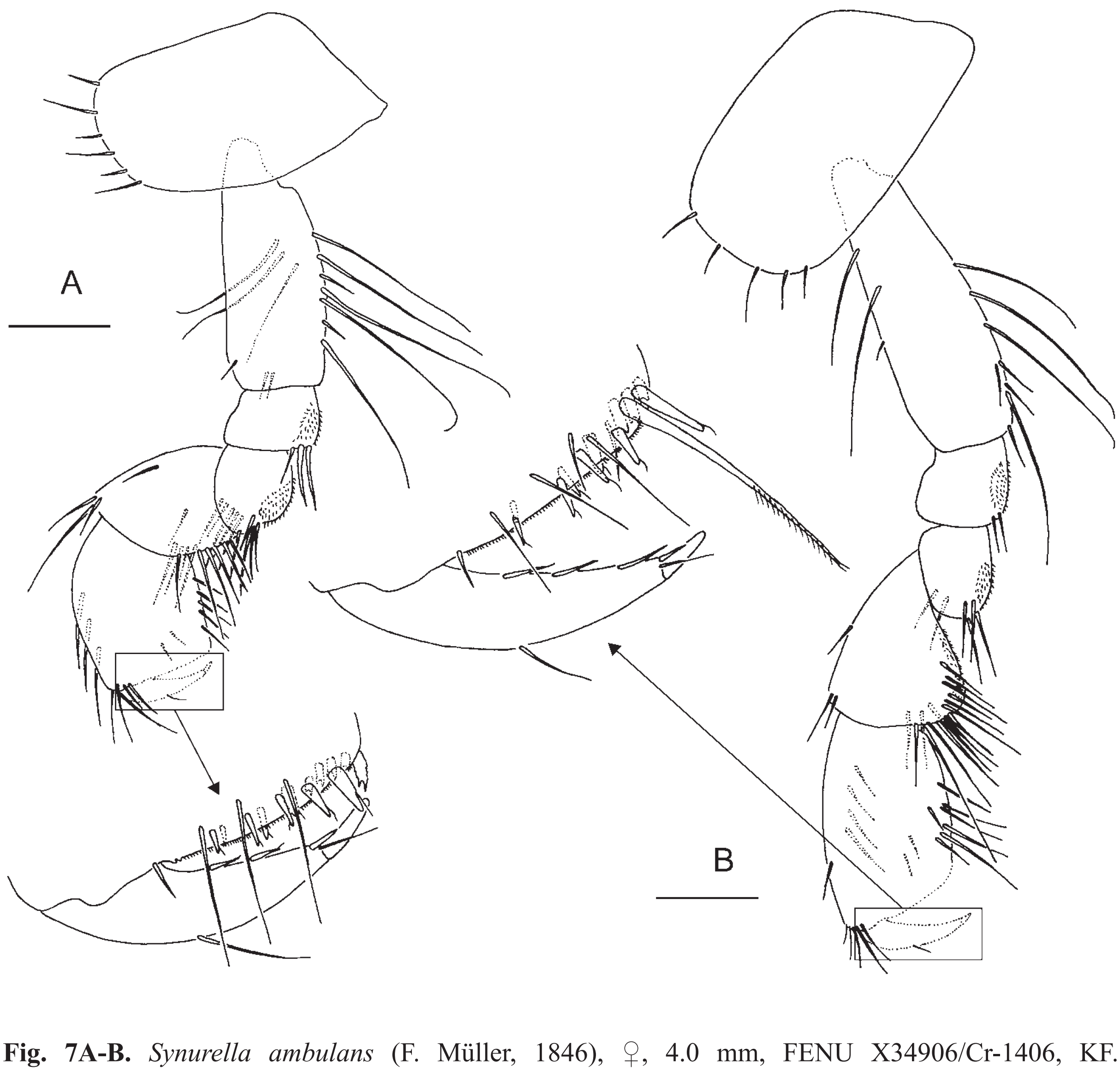

Fig. 7A-B. *Synurella ambulans* (F. Müller, 1846), ♀, 4.0 mm, FENU X34906/Cr-1406, KF. **A**. Gnathopod 1. **B**. Gnathopod 2. Scale bars 0.2 mm.

Pereon. Gnathopod 1 (Fig. 3A), propodus palm beveled, defining angle distinct, palmar modified setae at defining angle present, palm with cutting margin smooth, palm with 19 simple strong setae in two rows; dactylus, inner margin smooth. Gnathopod 2 (Fig. 3B), propodus larger than gnathopod 1 propodus; palm distinctly beveled, defining angle distinct, palmar modified setae at defining angle present, palm with cutting margin smooth, palm with 24 simple strong setae in two rows; dactylus, inner margin smooth. Pereopod 6 longer than pereopod 7. Pereopods 5–7 (Fig. 5C-E) bases expanded, posterior margins with serration. Pereopods 3–7 (Fig. 5A-E) dactyli elongated, about 40–50% length of corresponding propodi. Coxal gill 7 present. Paired median sternal gills on pereonite 2 and pereonite 3. Single lateral sternal gills on pereonite 6, pereonite 7 and pleonite 1.

Pleon. Epimeron 1 (Fig. 6D), posteroventral corner acute or sub-acute, ventral margin unarmed. Epimera 2–3 (Fig. 6D), posteroventral corner acute or sub-acute, ventral margins armed. Pleopods 1–3 (Fig. 6A-C), peduncular segments with 2 coupling setae (retinaculae). Uropod 1 (Fig. 6E), inner ramus 80% as long as peduncle, distal peduncular process absent. Uropod 2 (Fig. 6F) about 65% as long as uropod 1,

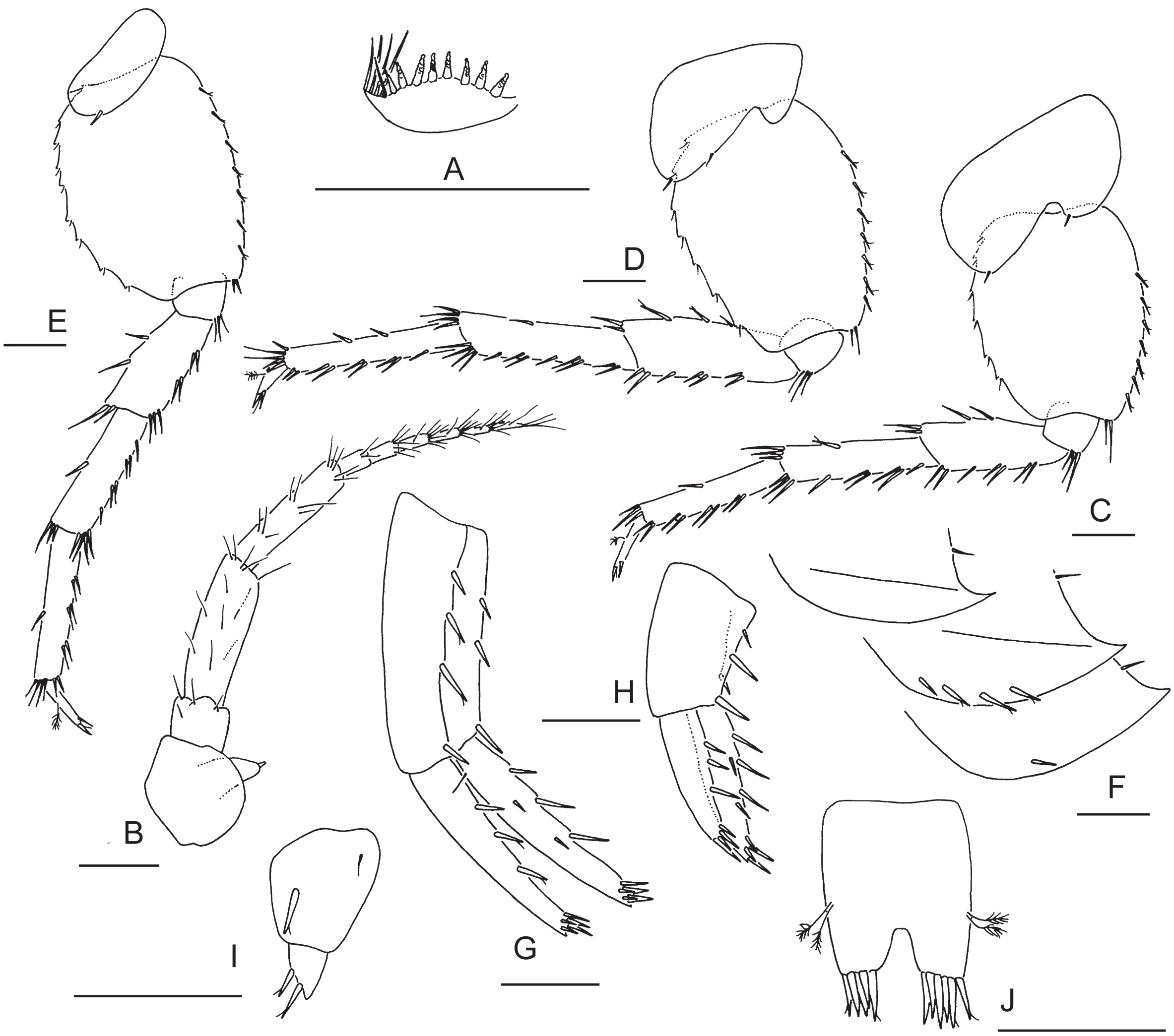

Fig. 8A-J. *Synurella ambulans* (F. Müller, 1846), ♀, 4.0 mm, FENU X34906/Cr-1406, KF. **A**. Lateralia. **B**. Antenna 2. **C**. Pereopod 5. **D**. Pereopod 6. **E**. Pereopod 7. **F**. Epimera 1-3. **G**. Uropod 1. **H**. Uropod 2. **I**. Uropod 3. **J**. Telson. Scale bars 0.2 mm.

peduncle shorter than inner ramus; inner ramus longer than outer ramus. Uropod 3 (Fig. 6G) uniramous, peduncle or/and lateral margin of ramus armed. Telson (Fig. 6H) not tapered distally, rather elongate, 1.8x longer than broad, about 10% longer than uropod 3, apical margin cleft on 1/3 of total length, with 6 strong notched setae on each lobe.

Dimorphism

Female

Length. 5.5 mm, FENU X34906/Cr-1406), sexually dimorphic characters.

Body. (Fig. 2C) Stout, appendages shortened. Antenna 1 45% longer than antenna 2. Antenna 2 (Fig. 8B) flagellum with 6 segments; calceoli absent. Gnathopod 1 (Fig. 7A), propodus palm transverse or scarcely sub-transverse with cutting margin acanthaceous, palm with 8 simple strong setae in two rows; dactylus, inner margin with setae. Gnathopod 2 (Fig. 7B), propodus palm with cutting margin acanthaceous, palm with 7 simple strong setae in two rows; dactylus, inner margin with setae. Pereopods 3–7 (Fig. 8C-E), dactyli about 45–50% length of corresponding propodi. Uropod 1 (Fig. 8G), inner ramus as long as peduncle. Uropod 2 (Fig. 8H) about 60 % as long as uropod 1. Telson (Fig. 8J) somewhat tapered distally, slightly elongate, 1.1x longer than broad, as long as uropod 3. Oöstegites 2–5 large, ovoid with long marginal setae.

Variability

Karaman (1974a) pointed out a significant variability in several morphological features for *S. ambulans*. However, in our analysis of individuals from the different parts of its range in Russia and Germany, we could not discover any significant variance in the shape of the lateral cephalic lobes, epimera, uropods, telson or bases of pereopod 7 (Fig. 9). In adults we observed elongation of the pereopod 7 bases and the presence of many robust setae on the lower edge of the epimera 2–3. Ommatidia were larger in young animals but their number was smaller than the one in adults. We also noted a slight variation in the length of the antenna 1 50–55% length of body and 40–45% longer than antenna 2, and a considerable variation in the length of pereopods 3–7 dactyli (35–50% length to corresponding propodi). The number of segments in the flagellum of antenna 1 equals 12–16. The specimens from Kholodny brook, near Yezerische Lake (Russia, Pskov area, Pustokshinsky) have a slightly different setation pattern of maxilliped palp segments 3 and 4 (Fig. 4L), but are otherwise indistinguishable.

Remarks

Borutzky (1929: 32) adduced several distinctive characters which, in his opinion, were sufficient to distinguish *S. a. meschtscherica* from *S. a. ambulans*: relative length of the both antennae, the stronger armament of mouthparts (viz., presence of scopiform bundles of setules on palpi of mandibles and maxilliped, presence of molar setae), armament of uropod 3 peduncle, the shape and armament of telson. After analyzing Borutzky's description, we are convinced that he has mixed details (p. 33) of males and females without explanation: the cited characters of the antenna 2 and the gnathopods belong to the female, while the telson characters are typical of the male. Moreover, Borutzky (loc. cit.) compared his own "mixed" description to the incomplete description by Schäferna (1922), who also depicted the female's telson without indication of gender. Borutzky (loc. cit.) evidently did not have Müller's (1846) original description at hand, in which the latter explains why he attributed subspecies status to his specimens.

The comparison of the material of *S. ambulans* from Russia, previously identified as *Synurella meschtscherica*, with that from Germany revealed no morphological differences between them. Comparison of the variability of the original samples with species descriptions by Müller (1846), Schäferna (1922) and Borutzky (1929) showed that both species are identical. We therefore consider

Synurella ambulans meschtscherica Borutzky, 1929 a junior synonym of nominative *S. ambulans* (F. Müller, 1846).

The taxonomic status and geographic distribution of previously described forms of *S. ambulans* are in need of a substantial revision. In our opinion the complex classification of *S. ambulans* is caused by: 1) a poor first description of the species by F. Müller and 2) a relatively wide distribution of the genus in Europe. It is possible that *S. ambulans*, ranging widely in Europe and Asia with significant variability reported by some authors (see above), is actually a series of several cryptic species.

A few discrepancies were found in the comparison with the original description. Borutzky (loc. cit.) reported the body length of individuals within the range of 6–12 mm for mature specimens without an indication of the method of measurement. Our largest individual has a body length of 6.0 mm. We have also studied the samples from Velikodvorskye springs of Ryazan area, previously also explored by Borutzky, where females up to 5.0 mm body length were found. Borutzky (1929: 32) also found a somewhat larger number of segments of the flagellum of the antenna 1, 18–24 (males) and 16–22 (females), and reported on eyeless individuals which are absent in our collections. However, the observed

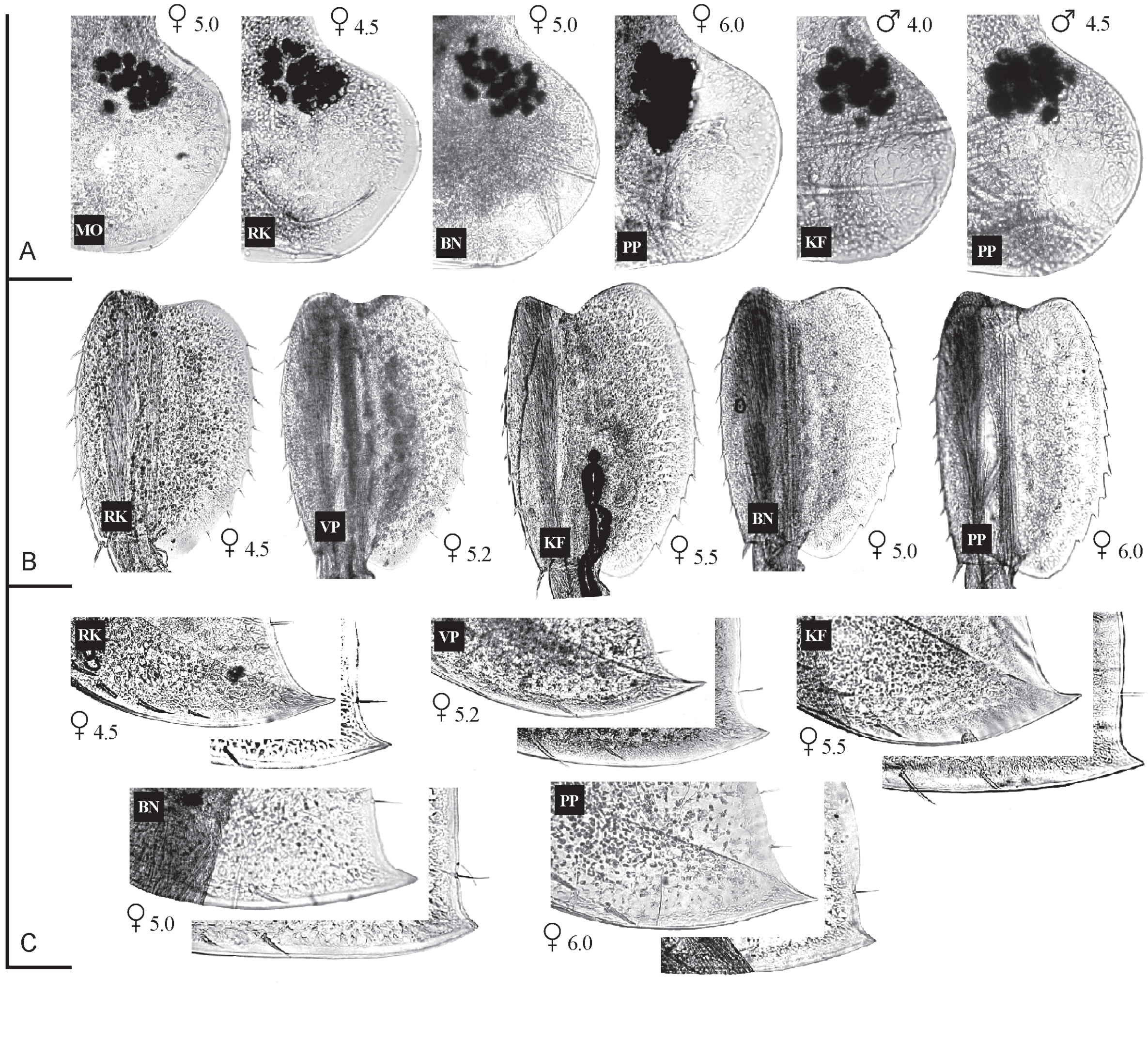

Fig. 9. Variability of (**A**) lateral cephalic lobe of *Synurella ambulans* (F. Müller, 1846) from different populations; (**B**) posterior margin of pereopod 7 basis; (**C**) epimera 2 and 3. (Digital Photomicrography).

variability was not documented by this author, eyeless individuals were not described and had not been given a special status. The inaccuracy of Borutzky's description confirmed our doubts about the validity of *S. meschtscherica* and convinced us that only one form of *Synurella* is present in the Meschtschera Lowland.

Distribution

RUSSIA. Pskov area: Pustoshkinsky region. Vladimir area: Petushinsky and Gus-Khrustalny regions. Moscow area: Orekhovo-Zuevo, Egoryevsk and Shatura regions (Chertoprud 2006a, 2006b). Ryazan area, Klepiki (Borutzky 1927, 1929). Kaluga area: Ferzikovsky region. Bryansk area: Navlinsky region.

Although *S. ambulans* was found in extensive territories in West Russia, it was absent in a number of different springs (see map) with a rich crenophilous fauna. This mosaic distribution is apparently caused by environmental factors.

Synurella ambulans has been reported from many countries situated on the Great European Plain including Belgium (Boets *et al.* 2010), Germany (Heckes *et al.* 1996; Zettler 1998; Eggers & Martens 2001), Poland (Konopacka & Sobocinska 1992), Lithuania (Arbačiauskas 2008) and Belarus (Giginyak & Moroz 2000).

Ecology

Stygophile, predominantly occupying semi-subterranean habitats. Biotopes mostly including wetlands, bogs, wetland areas of streams with swampy shores nearly everywhere overgrown with *Alnus* (see Borutzky 1929).

Synurella ambulans dwells in various springs, stagnant parts of the rivers and brooks connected with the ground outlets of subterranean waters, frequently associated with the asellid isopod *Asellus aquaticus* (Linnaeus, 1758). A characteristic features of all microhabitats are their stagnant or very slowly flowing waters, not exceeding 0.1 m/sec; a water temperature generally ranging between 2.0 and 16.0 °C, a low oxygen concentration of 3.0–9.0 O^2 mg/l, a pH between 5.0–8.0 and low mineralization not higher than 197.5–353.1 mg/l (once 510.0 mg/l) (Nesemann *et al.* 1995; Giginyak & Moroz 2000; Chertoprud 2006a). Springs are often covered with *Lemna* and *Hydrocharis*, or densely grown with *Elodea* and *Fontinalis*; bottoms are composed of detritus, sand, mud, snags and leaf litter. *Dendrocometes paradoxus* Stein, 1852 (Protozoa, Infusoria, Suctoria) is a common ectoparasite on the coxal gills of *S. ambulans* (see Taylor & Sanders 2001).

The rare findings of *S. ambulans* in a number of a small floodplain lakes in the spring could be explained by the flood drift. However, most interesting is the accidental discovery (by DP) of a mass congestion of *S. ambulans* on the shallows of a large lake in the Velikaya River basin (Pskov area) in winter. It is possible that these crustaceans can survive adverse winter conditions by "warming up" near oozing from the bottom fontanels.

Discussion

Comments on biogeography of *Synurella* species complex

The biogeography of any group is closely linked with its phylogenetic relationships (Holsinger 1986), which in turn is related to a system of trustworthy diagnostic features. It is well-known that the taxonomy of the family Crangonyctidae is based largely on the structure of uropod 3, although the plasticity of this character had already been discussed (Bousfield 1983) and a recent molecular phylogeny confirms this (Hiwatari *et al.* 2011). The latest results of 18S phylogeny also revealed an ancient radiation of *Synurella* with a paraphyletic relationship to the North American and European groups (Kornobis *et al.* 2011).

Morphologically, the family Crangonyctidae is not homogeneous and can be tentatively divided into two groups of uneven size, but equivalent in terms of their "biogeographical weight". The first group includes taxa with the "free coxal plates 1–4" or commonly diagnosed as shallow coxae, when their width is greater than, or equal to, the height (this group includes: *Bactrurus*, Siberian *Stygobromus* and the majority of the North American *Stygobromus*). Two poorly described Eurasian species – *Stygobromus apscheronicus* (Derzhavin, 1945) and *Stygobromus kazakhstanicus* Kulkina, 1992 – occupy an intermediate position but they might belong to this group, because of their shallow coxal plates 3 and 4. The second large group, however, consists of species with deep coxal plates and is distinguished by a coxal plate 4 with excavation. This group includes the North American and European *Crangonyx*, *Synurella*, *Lyurella hyrcana* Derzhavin, 1939, *Stygonyx courtneyi* Bousfield & Holsinger, 1989, *Amurocrangonyx arsenjevi* (Derzhavin, 1927) and *Palaeogammarus*. The same character was used previously by Bousfield (1977) and Holsinger (1986) in a hypothesized phylogenetic relationship among Crangonyctidae. They ascribed a plesiomorphic state for the deep coxae and an apomorphic state for shallow or reduced coxae in overall size (see Holsinger 1986: 90). The front edge of the Crangonyctidae head is rather diverse in morphology (Holsinger 1977) and can be roundish (Fig. 9) or characterized by the presence of the inter-antennal lobe and inferior sinus. However, this feature apparently may not be appropriate for phylogenetic analyses, as we have observed non-uniform gradation from the roundish form (*S. ambulans*) with intermediate form (*S. derzhavini*) to the expressed "sinusoidal form" (*S. osellai*) (see Sidorov *et al.* 2012). Meanwhile, we have concluded that both features of general body morphology are most important for separation of heterogeneous phyletic groups in future testing of biogeographic hypotheses.

Taxonomic boundaries and eco-geographic distribution of *Synurella ambulans*

Synurella ambulans has a large distribution in the lowlands of northern Europe, ranging from NW to NE Europe and possibly reaching the Black Sea area (Dedju 1967). Previously, from pieces of Baltic amber dated as far back as the Eocene, several forms of *Synurella* have been described as being closely related to the southern species *S. intermedia*, because of the somewhat extended pereopod 7 bases and the non-acute posteroventral epimeral corners (see Coleman 2004: 3). Perhaps the northern distribution of *S. ambulans* may be a relatively recent phenomenon, after the retreat of the glaciers in the early Holocene. However, we do not know the southern and western boundary of the distribution of this species. The findings of *S. ambulans* in Southern Europe and Asia Minor indicate that its range is discontinuous. This assumption is questionable and requires additional verification. In our view, all references to *S. ambulans* in Asia Minor (Ruffo 1974; Karaman 2003; Ustaoğlu *et al.* 2004) as well as in Southern Europe (Bonacina *et al.* 1992; Stoch & Dolce 1994; Pezzoli 2010) are ambiguous and should be re-compared carefully with *S. ambulans* from other areas.

Synurella ambulans is absent from a number of intact springs, unaffected by anthropogenic stress (Fig. 1). These springs were almost always rich in crenophilous fauna. As noted by Giginyak & Moroz (2000), *Synurella ambulans* inhabits springs with water close to melt water in physical and chemical properties. The natural tolerance of the studied amphipod specimens of *S. ambulans* was limited to low concentration of oxygen and mineralization (see Giginyak & Moroz 2000: 82). Previously, a similar relationship between life in springs and low water hardness of 1.2–1.6° dGh (= 214.1–285.6 mg/l) was noted for the Far Eastern *Amurocrangonyx* (Birstein & Levanidov 1952). It is interesting that *S. ambulans* apparently has a feature that can distinguish it from the other species of the genus, namely a yellowish spot (url: www.biospeleo.ru/S_ambulans.htm) which is the hypertrophied digestive gland. Previously, the observation of a yellowish (orange) spot for the species was mentioned by Müller (1846), Stebbing (1906), Borutzky (1929) and Boets *et al.* (2010). The hypertrophied digestive gland (HDG) is characteristic also of several deep-sea marine amphipods, e.g. *Eurythenes gryllus* Lichtenstein, 1822 where it performs the leading role in the metabolic response of the defense antioxidant system (Camus & Gulliksen 2004). In subterranean amphipods the HDG has also been observed in *Amurocrangonyx*.

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