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Synurella odessana sp. n. (Crustacea, Amphipoda, Crangonyctidae), first report of a subterranean amphipod from the catacombs of Odessa and its zoogeographic importance

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Abstract

A new species from the catacombs of Odessa (South Ukraine), *Synurella odessana* **sp. n.** is described and its taxonomic affinity with congeners are discussed. This is the first record of the subterranean amphipod crustacean of the genus *Synurella* from an artificial biotope. The new species has numerous plesiomorphic features states allowing a more detailed evaluation of the taxonomy of the genus *Synurella*. The most remarkable feature of this new species is the presence of a "synurellid type" gnathopod 1 and a "crangonyctid type" gnathopod 2. Herein, we propose three groups in the genus *Synurella* distributed within the Volga-Black Sea basin: *ambulans*-group (epigean inhabitants of coastal lowlands, stygophiles), *dershavini*-group (hypogean or spring inhabitants of karstic regions, preadapted stygobionts), *wachuschtii*-group (minute inhabitants of interstitial waters, stygobionts). The *dershavini*-group occupies isolated taxonomic position among the synurellids. We suggest that the modern distribution of *dershavini*-group reflects the formation of ancient river basins in the region.

Keywords

Amphipoda, Crangonyctidae, *Synurella*, Odessa, catacombs, zoogeography, new species

Introduction

The area of the modern Black Sea was covered by Tethys Sea, which became isolated from other oceanic waters some 10–13 Myr ago. The predecessors of the Black Sea–Sarmatian, Meotian, Pontian, Ancient Euxininan, Karangatian, Neoeuxinian and other seas–were different in size, outline and salinity (Zaitsev and Mamaev 1997). Changes in salinity have led to periodic replacement of freshwater fauna and flora by marine taxa. This rich history has resulted in the development of significant limestone deposits, which, under the influence of karstification processes, are now permeated by many underground cavities ranging from small caverns and channels to spacious water caves. The origin and evolution of the subterranean animals in this region arose within this complex history of seas and karst development.

The territories surrounding the Black Sea are rich in terrestrial troglobionts (Jordana et al. 2012) and stygobionts (Birstein and Ljovuschkin 1967), including endemic genera. Recently, a number of new studies of subterranean fauna were conducted in this region (Marin and Sokolova 2014; Sidorov 2014; Vinarski et al. 2014). Within the genus *Synurella* Wrześniowski, 1877, the highest diversity of semi-subterranean species is found in the Ponto-Caspian region and adjacent lands (Sidorov 2015), while the genus *Synurella* as a whole has a Holarctic distribution with its greatest species richness in the Palearctic, from where 13 recent species are known (Karaman 1974; Sidorov and Palatov 2012).

Recent biological exploration of the subterranean waters in the catacombs located under the city of Odessa (Ukraine) have yielded a new species belonging to *Synurella* (Kovtun and Sidorov 2014). Similar habitats in other regions are also inhabited by subterranean crustaceans, as for example the eyeless amphipod *Echinogammarus catacumbae* Karaman and Ruffo, 1977 was described from the catacombs of St. Lucia in Syracusa (Karaman and Ruffo 1977).

The geological history of the Odessa limestone, its structure, karst, and the accumulation of the fossil remains in karst caves, as well as the catacombs themselves are detailed in the works of Pronin (1989, 2009) and Klimchouk et al. (2010). Many fossils (mostly mammals) have been documented from the taphocenoses of Odessa karst caves (catacombs) (Orlov 1989), but the present study is the first mention on stygobionts.

Material and methods

Taxonomic sampling

Samples containing stygobionts were collected in the catacombs under Odessa (Figures 1, 2) using a dip net with a 250-µm mesh and preserved in 80% ethanol.

Figure 1. Map showing the distribution of the *dershavini*-group in the Volga-Black Sea basin: **1** *S. dershavini* Behning, 1928 **2** *S. donensis* Martynov, 1919 **3** *S. odessana* sp. n. **4** *S. osellai* Ruffo, 1972.

Morphology

Body length of the amphipods was recorded by holding the specimen straight and measuring the distance along the dorsal side of the body from the base of the first antenna to the base of the telson using a micrometer eyepiece in a Lomo MBS-9 dissecting microscope.

Appendages were drawn using a Carl Zeiss NU-2 compound microscope equipped with a drawing device as described in Gorodkov (1961). Permanent preparations were made using polyvinyl lactophenol (PVL) and a methylene blue staining solution was used as mounting medium.

In the descriptions, utilization of the descriptive term “defining angle” of the gnathopod propodi refers to the “angle” formed at the end of the palm and beginning of the posterior margin (see Holsinger 1974); “recess” at “defining angle” pertains to the pouch into which the tip of the dactyl may be submerged. According to the shape and structure of propodi two types of gnathopods were defined: the “synurellid type” with linear or sub-linear anterior and posterior margins, palmar margin transverse or subtransverse; inherent to majority of *Synurella*. The “crangonyctid type” of gnathopod with palmar margin developed and bevelled, palm S-shaped, slightly sinusoidal or convex, longer than posterior margin and deep “recess” fitted with 1 strong lateral spine on inner face of propodus; inherent to the *dershavini*-group. The nomenclature for setal patterns on article 3 of the mandibular palp follows the standard introduced by

Stock (1974). Nomenclature for presence/absence of sternal gills in medial and lateral positions follows the numeric descriptor: (-1-)–single medial position, (1-1)–single lateral position.

The following description is based on the type series, and the material examined is deposited in the Zoological Museum of the Far East Federal University, Vladivostok, Russia (FEFU hereafter) and in the research collection of the Institute of Biology and Soil Science, Vladivostok, Russia (IBSS hereafter).

Systematic section

Malacostraca Latreille, 1802
Order Amphipoda Latreille, 1818
Family Crangonyctidae Bousfield, 1973

Genus *Synurella* Wrześniowski, 1877

syn.: *Synurella* Wrześniowski, 1877: 403 (type spec., *Gammarus ambulans* F. Müller, 1846, original designation). *Goplana* Wrześniowski, 1879: 299. *Boruta* Wrześniowski, 1888: 44. *Eosynurella* Martynov, 1931: 531. *Diasynurella* Behning, 1940: 43.

***Synurella odessana* sp. n.**
http://zoobank.org/D8FCD91C-3A82-49AE-A3F0-024FCC1A86FF
Figures 2–7

syn.: *Synurella* sp. Kovtun, Sidorov, 2014, p. 70, fig. 1.

Material examined. Holotype: male, 11.5 mm, X42024/Cr-1541-FEFU, Ukraine, catacombs under Odessa, (depth -30 m from surface, lower level), Slobodka District (approx. 46.480593, 30.700242), 02.03.2014, leg. O.A. Kovtun. Paratypes: male (9.0 mm), 2 females (6.5 mm, 9.0 mm), X42025/Cr-1542-FEFU, same data as holotype.

Additional specimens examined (not included in type series). All specimens measured, partially dissected and stored in different vials [17/3sd-IBSS]: 22 females (2×9.0 mm, 7×8.0 mm, 5×6.5 mm, 8×5.5 mm), 5 males (2×8.5 mm, 3×7.5), 7 juveniles, all with same data as type series.

Diagnosis (both sexes). Large-sized species with marked sexual dimorphism (see below). Body semitransparent, alive whitish or yellowish. Eyes black, with reduced number of ommatidia; yellow mass located on the dorsolateral surface of the head between eyes. Rostrum pointed. Inferior antennal sinus distinct. Antenna 1 of males very long, comprised about 90% of total body length; more than twice as long as antenna 2; calceoli absent in both sexes. Gnathopod 2 larger (stouter and longer) than gnathopod 1; carpal lobe narrow; propodus bearing 1 strong lateral spine at "recess" near defining

Figure 2. Habitus of *Synurella odessana* sp. n., left side (preserved specimens): **A** male, 11.5 mm, holotype X42024/Cr-1541-FEFU **B** female, 9.0 mm, paratype X42025/Cr-1542-FEFU.

angle. Pereopod 7 longer than pereopod 6. Pereopod 7 basis with distinct posterior lobe. Pleopods well developed with 5–6 retinacula (coupling setae) each. Urosomal somites completely fused, but sutures visible. Coxal gills on pereopods 2–7, gill 7 very small. Sternal gills arrangement as following: pereonite 2 (-1-), 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 5.5–9.0 mm (females), 7.5–11.5 mm (males).

Description. *Male*, 11.5 mm long, [X42024/Cr-1541-FEFU]. **Head**. *Eyes* (Figures 2, 3A) vestigial 7 detached ommatidia, black; yellow mass located on dorsolateral surface of head between eyes. *Antenna 1* (Figures 2A, 5B): 90% length of body, more than twice as long as antenna 2; peduncular articles 1–3 with a length ratio of 1 : 0.9 : 0.5, articles 1 and 2 with stiff short setae on medioventral face; primary flagellum with 32 articles, some flagellar articles bearing short lanceolate aesthetascs, accompanied by setae; accessory flagellum 2-articulate, longer than accompanying flagellar article. *Antenna 2* (Figure 5A): gland cone short; peduncular article 4 20% longer than article 5, both sparsely setose, with stiff, simple setae; flagellum with 9 articles bearing rod-like structures accompanied with sparse setae, calceoli absent. *Upper lip* (labrum) (Figure 5C): sub-triangular, with minute setae at apex, clypeus elongate. *Mandibles* subequal: left mandible (Figure 5G) incisor 5-dentate, lacinia mobilis 5-dentate, setal row with 7 serrate setae, triturative molar strong, without accessory seta; incisor of right mandible (Figure 5H) 4-dentate, lacinia mobilis trifurcate, both parts with serrations, setal row with 6 serrate setae, molar with plumose accessory seta; *palp* (Figure 5I) article 1 33% length of article 2; article 2 as long as article 3, 6 setae on inner margin; article 3 with 3 A-setae, 4 C-setae, 6 E-setae and row of about 11 D-setae. *Lower lip* (labium)

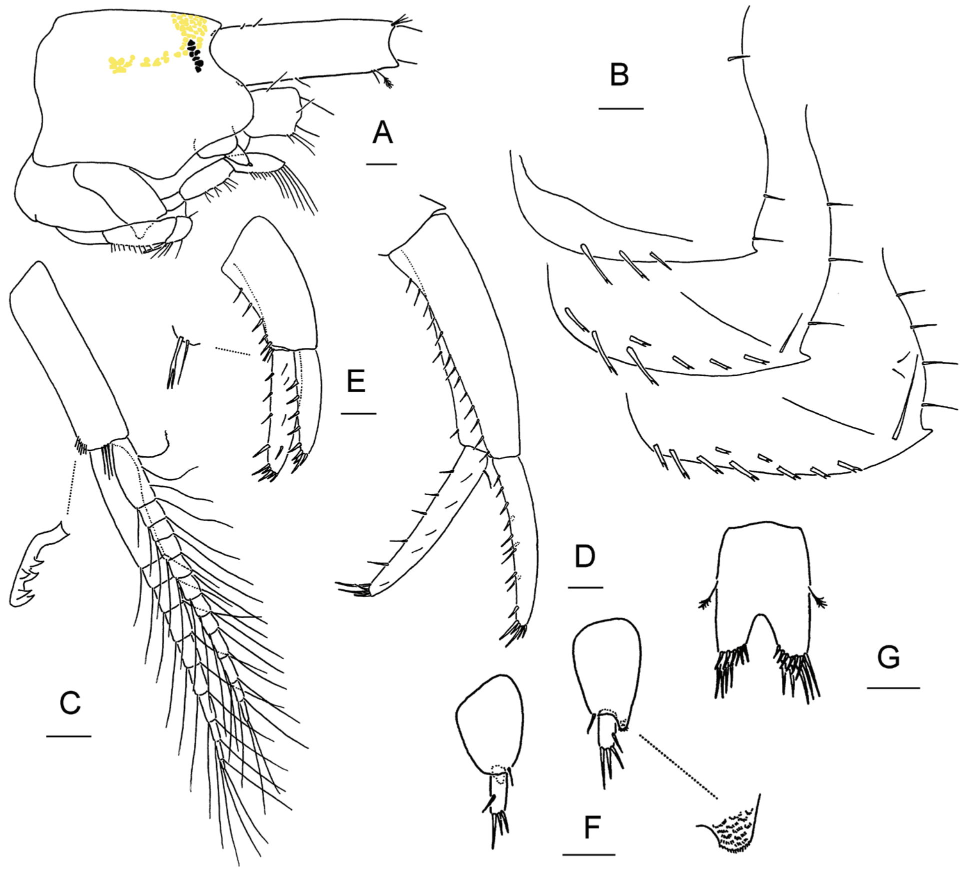

Figure 3. *Synurella odessana* sp. n.: male, 11.5 mm, holotype X42024/Cr-1541-FEFU: **A** head **B** epimera 1−3 **C** pleopod 3 **D** uropod 1 **E** uropod 2 **F** uropod 3 **G** telson. Scale bars 0.2 mm.

(Figure 5D): outer lobes broad, densely setose with setules, mandibular lobes obtuse, inner lobes broad. *Maxilla 1* (Figure 6F): inner plate broad with 6 plumose setae; outer plate with 7 robust spines (most bifid); palp articles 1 and 2 length ratio 0.3 : 1, article 2 bearing 6 stiff, simple setae apically. *Maxilla 2* (Figure 6E): inner plate about twice as broad as outer plate, with oblique row of 5 plumose setae, two rows of plumose and naked setae on apex; outer plate with 12 slender setae on apex (one group longer); both plates densely setose with setules. *Maxilliped* (Figure 5J): inner plate with 6 strong peg-like spines on apex, 4 plumose setae extending from inner margin to apex; outer plate with a row of 16 simple setae extending from inner margin to apex; palp quadriarticulate, palp articles 1–4 length ratio 0.3 : 1 : 0.5 : 0.6, article 2 stout with row of simple setae on inner margin, article 3 stout with group of stiff setae on outer face; dactylus without setae along inner margin, nail long with 2 minute setae at hinge. Foregut *lateralia* with 10 strong pectinate setae. **Pereon**. *Coxal plates 1–2* similar, shallow, sub-rectangular (Figures 4A, B), with 5–6 marginal setae; *coxal plates 3–4* (Figures 6A, B) sub-quadrate, *coxa 3* narrowly rounded, with 8 stiff short setae on

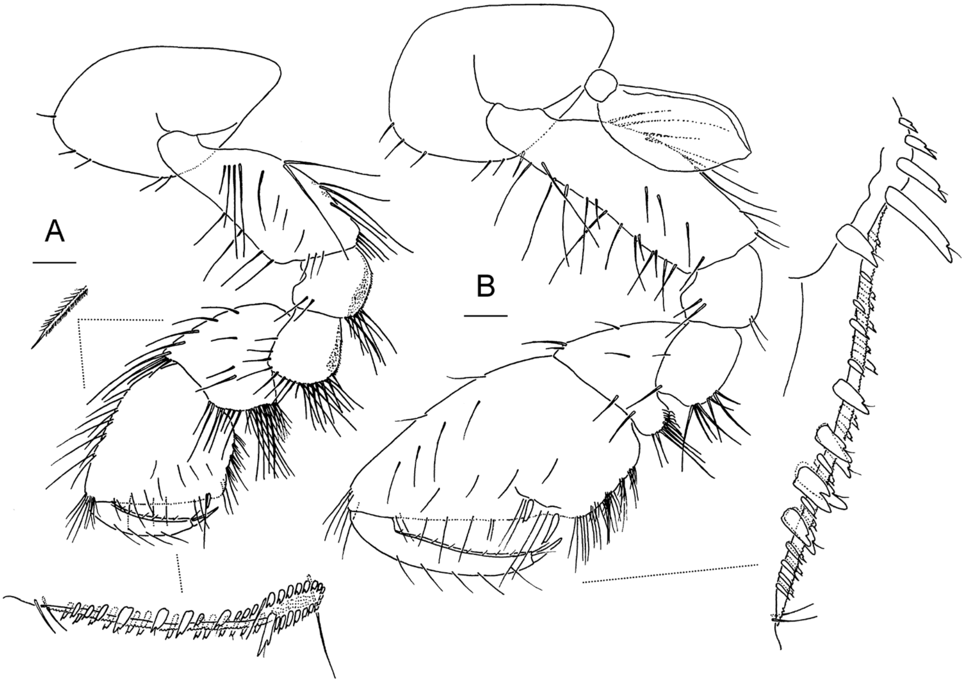

Figure 4. *Synurella odessana* sp. n.: male, 11.5 mm, holotype X42024/Cr-1541-FEFU: **A** gnathopod 1 **B** gnathopod 2. Scale bars 0.2 mm.

ventral margin, *coxa 4* roundly convex distally, posterior margin without excavation, ventral margin with 9 short setae; *coxal plates 5–6* (Figures 6C, D) bilobate, posterior lobe of *coxa 6* larger than anterior ones and armed with 4 short setae on posterior margin; *coxal plate 7* small, semilunar (Figure 6E) with 5 short setae on posterior margin. *Gnathopod 1* (Figure 4A) smaller than gnathopod 2; basis stout with 4 long setae on anterior margin, some setae on inner face, 6 long thread-like setae (some in pairs) on posterior margin; carpus 0.6x as long as propodus, carpal lobe broad, bearing numerous setae; propodus smaller than propodus of gnathopod 2, sub-quadrate, weak, subchelate, palm slightly convex with cutting margin acanthaceous and armed with row of 7 distally notched robust spines on inside and 10 on outside, 18 short (1 very long) distally notched robust spines at defining angle arranged in a semicircle, anterior margin densely setose with paired setae, posterior margin short with 5 sets of simple setae; dactylus short with 7 minute setules on inner and 4 setae on outer margins, nail short with 2 setules at hinge. *Gnathopod 2* (Figure 4B): basis stout with 11 long and 3 short setae on anterior margin, 3 setae on inner face and with 7 long thread-like setae (some in pairs) on posterior margin; carpus 0.35x as long as propodus, carpal lobe narrow and tapered bearing short serrate setae; propodus larger than propodus of gnathopod 1, sub-triangular, stout, subchelate, palm somewhat sinusoidal with cutting margin acanthaceous, armed with row of 13 distally notched robust spines on inside and 15 on outside (middle spines very strong), deep recess (or pouch) armed with 1 strong lateral

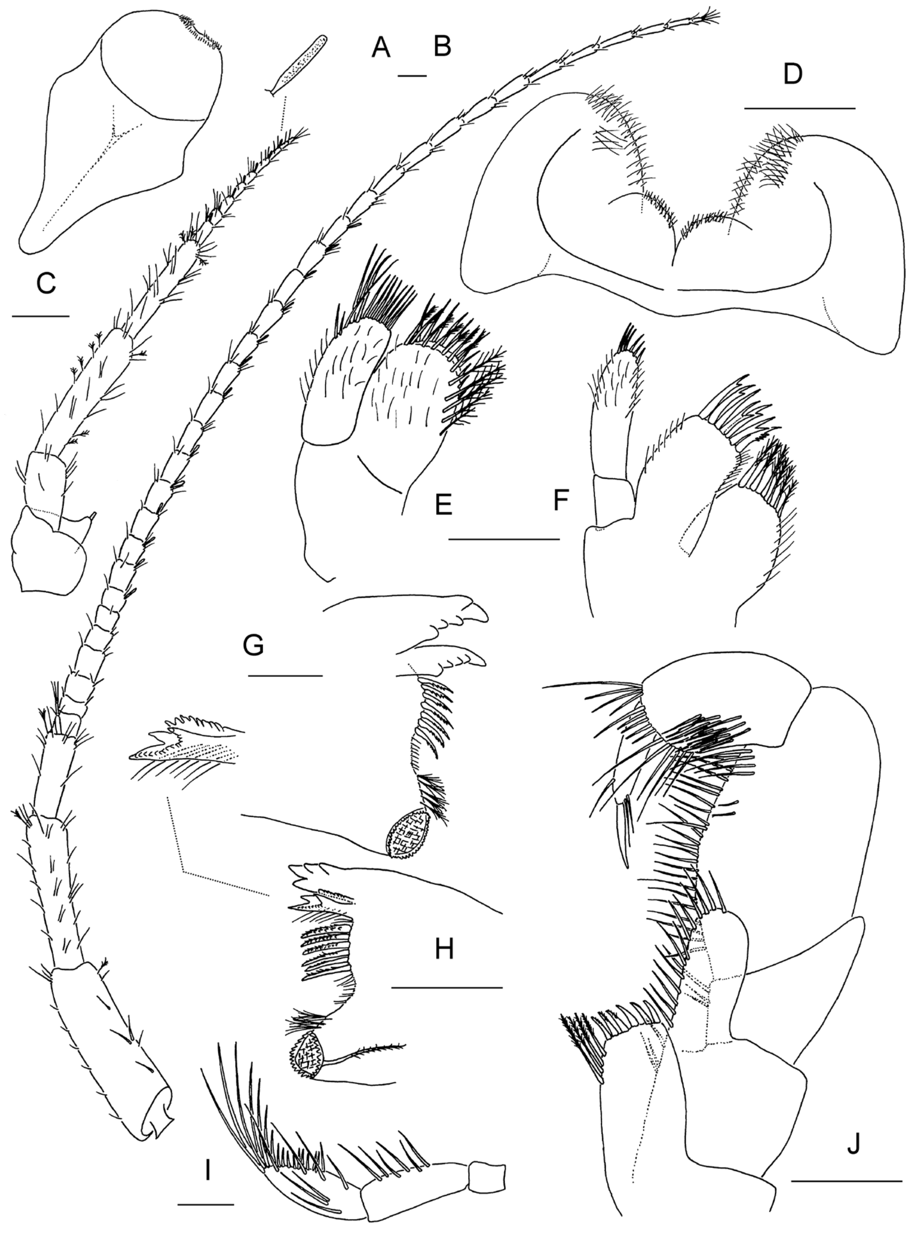

Figure 5. *Synurella odessana* sp. n.: male, 11.5 mm, holotype X42024/Cr-1541-FEFU: **A** antenna 2 **B** antenna 1 **C** upper lip **D** lower lip **E** maxilla 2 **F** maxilla 1 **G** mandible, left **H** mandible, right **I** mandible, palp **J** maxilliped. Scale bars 0.2 mm.

distally notched robust spine on inner face and 4 spines (one of them long) near defining angle, posterior margin about 3 times as long as palm with 5 sets of setae; dactylus long, with 8 minute setules on inner and 5 setae on outer margins, nail short with 2

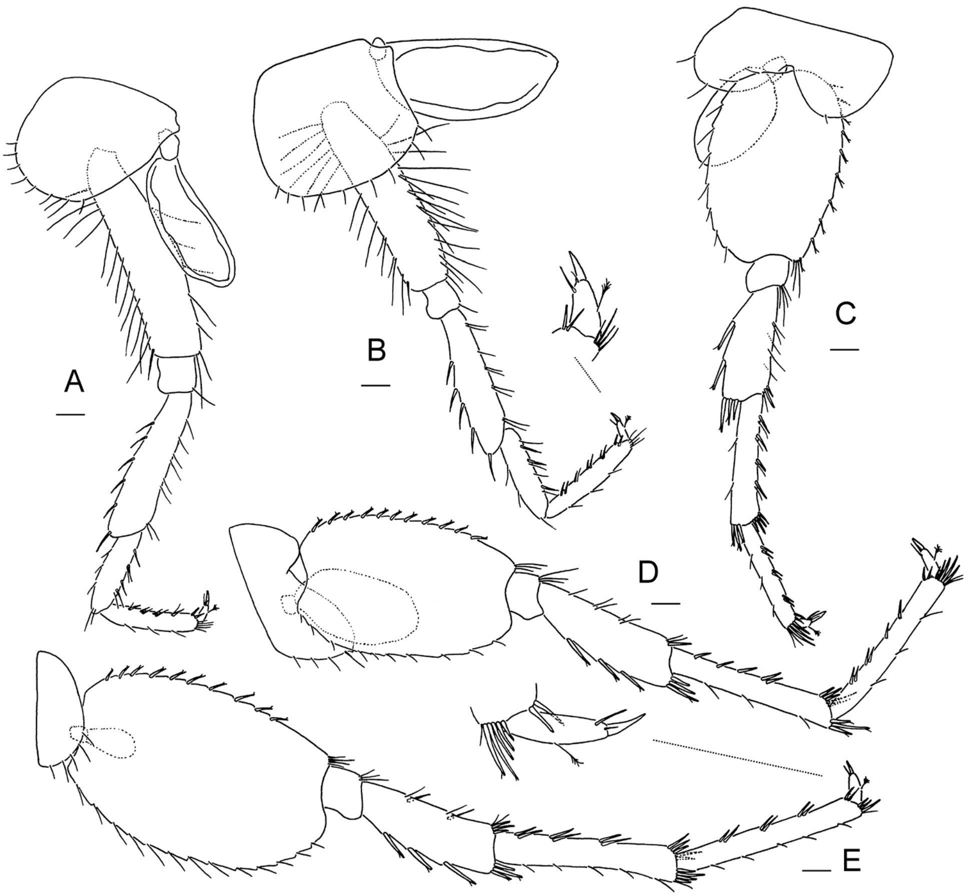

Figure 6. *Synurella odessana* sp. n.: male, 11.5 mm, holotype X42024/Cr-1541-FEFU: **A** pereopod 3 **B** pereopod 4 **C** pereopod 5 **D** pereopod 6 **E** pereopod 7. Scale bars 0.2 mm.

setules at hinge. *Pereopods 3* and *4* (Figures 6A, B) sub-equal in length; bases sub-linear bearing short thread-like setae on both margins; dactyli short, about 33% length of corresponding propodi, inner margin with 1 long seta and 1 minute setula at hinge. *Pereopods 5-7* (Figures 6C–E): pereopod 6 88% length of pereopod 7; basis 7 20% longer than basis 6; bases of pereopods 5 and 6 slightly broader proximally than distally, margins serrated with setules, distoposterior lobes poorly developed, basis 7 oblong with distoposterior lobe distinct; dactyli short about 25–30% length of corresponding propodi, inner margin with 1 long seta and 1 minute setula at hinge. *Coxal gills 2–7* (Figures 4B, 6A–E) stalked and sub-ovate, coxal gill 7 very small. Simple, very small medial *sternal gill* on pereonite 2; simple, large, lateral sternal gills present on pereonites 6, 7 and pleonite 1. *Genital papillae* on ventral surface of pereonite 7 (smaller than, and located posterior to sternal gill). **Pleon**. *Epimera 1–3* (pleonal plates) (Figures 2, 3B): posterior margins of plates convex with 3–4 stiff setae; distoposterior corners acute; ventral margin of plate 1 nearly straight with 3 strongly notched spines; plates

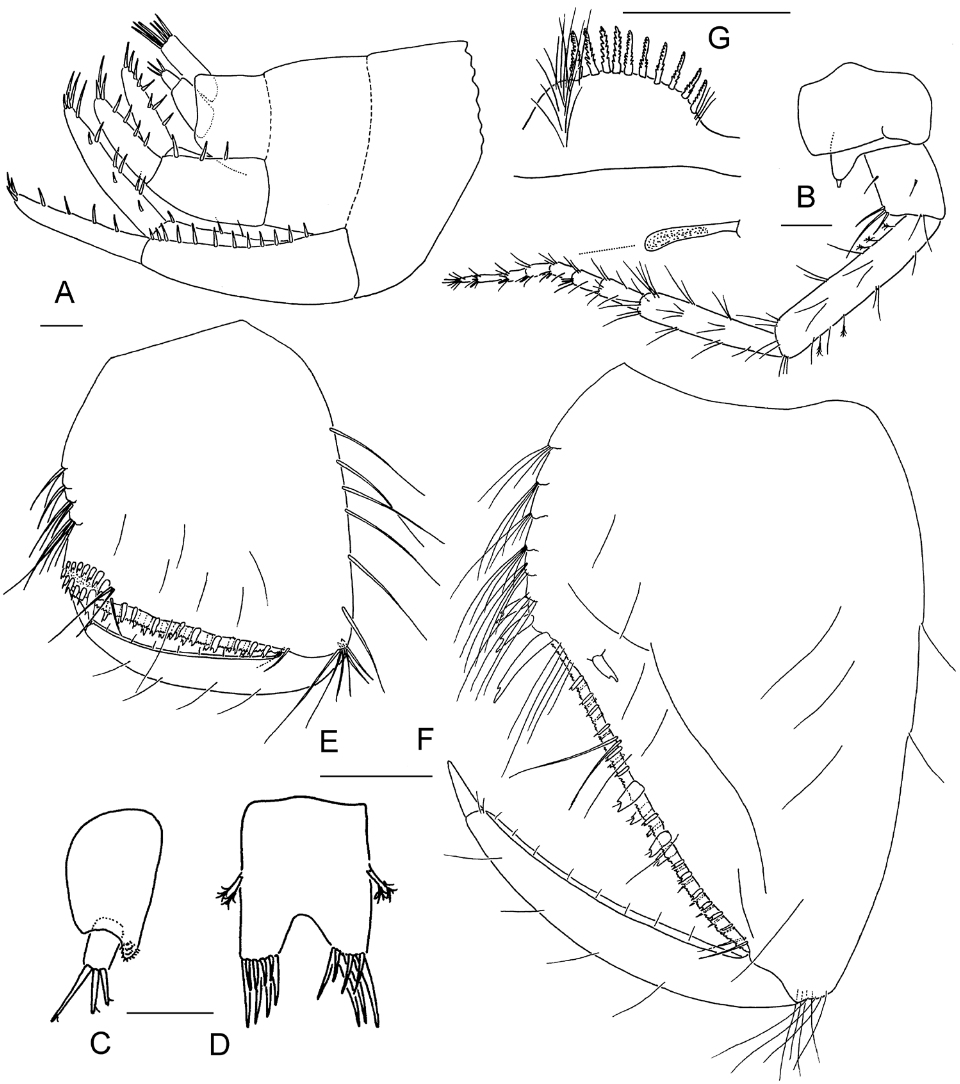

Figure 7. *Synurella odessana* sp. n.: female, 9.0 mm, paratype X42025/Cr-1542-FEFU: **A** urosome **B** antenna 2 **C** uropod 3 **D** telson **E** gnathopod 1, propodus **F** gnathopod 2, propodus **G** lateralia. Scale bars 0.2 mm.

2 and 3 convex, bearing 7 and 9 strong notched sub-marginal spines; plates 2 and 3 with 1 long upward-directed seta above posterolateral angle. *Pleopods 1–3* (Figure 3C): sub-equal, peduncular articles each with 6 retinacula (coupling setae), 3 simple setae on distal margin; proximal article of inner ramus on inner face naked or bearing 1 seta; inner rami slightly longer with 10 articles, outer rami with 12 articles, both rami fringed with plumose setae. *Urosome* (Figure 2): urosomites completely fused but sutures visible, lacking dorsal armament. *Uropod 1* (Figures 2, 3D): peduncle with 13

setae on outer margin, 2 setae on inner margin; outer ramus as long as inner ramus, 77% length of peduncle; both rami armed with 10 weak spines on both margins, inner ramus with 4 spines and outer ramus with 5 spines on apices. *Uropod 2* (Figures 2, 3E): peduncle with 5 setae on outer margin and 1 distal bifid and 1 simple (corner) setae on inner margin; outer ramus shorter than inner ramus, 80% length of peduncle; both rami armed with 4–8 weak spines and setae on both margins, inner ramus with 5 spines and outer ramus with 4 spines on apices. *Uropod 3* (Figure 3F) uniramous, peduncle cone-shaped, about 1.3x as long as endopodite, with a terminal "squamous knob" and 1 weak spine on distal margin; lateral and apical margin of ramus armed with 1 and 3 weak spines correspondingly. *Telson* (Figure 3G) not tapered distally, elongate, 0.7x as long as broad, as long as uropod 3; apical margin cleft, about 1/3 of total length, with mix of short and long 10–11 curved spines on each lobe.

Female, 9.0 mm long, [X42025/Cr-1542-FEFU], sexually dimorphic characters. Smaller than male, with more slender body. *Antenna 1* 50% of total body length; almost twice as long as antenna 2. *Gnathopods 1* and *2* (Figures 7E, F) propodi poorly setose and palmar margins weakly armed with spines. *Oöstegites 2–5* on gnathopod 2 and pereopods 3–5 broad, expanded distally, with long marginal setae. *Telson* (Figure 7D) bearing 7–8 spines on each lobe.

Variability. Examined specimens have variations in setation of peduncular articles of pleopods, which can be naked or with single thin seta and bearing 5–6 retinacula (coupling setae) each. The ventral margin of epimera varies slightly in number of spines according to age and body size.

Taxonomic comments. Among the eight known species of *Synurella* of the Volga-Black Sea area, *S. odessana* sp. n. has a number of unique features: (1) developed spines at defining angle of gnathopod 1 forming a semicircle; (2) inner face of gnathopod 2 propodus with a deep "recess" fitted with 1 strong, lateral spine; (3) pleonal plates 1 and 2 each with an erect, long seta at corner, (4) uropod 3 with small squamous projection (rudiment of exopod).

Within the genus *Synurella*, *S. odessana* sp. n. is clearly related to three species (*S. donensis* Martynov, 1919, *S. dershavini* Behning, 1928, *S. osellai* Ruffo, 1972) known from springs of the Volga-Black Sea basin. Along with these species, the new species is appointed in a new group, the *dershavini*-group. This group is characterized by the largest set of plesiomorphic states of selected morphological features (see Table 1). *S. odessana* sp. n. resembles *S. donensis* and *S. osellai* in the shape of the lower lip. The densely setose anterior margin of carpus and propodus of gnathopod 1 are similar to feature of *S. osellai*, from which it differs by the 6-dentate pars incisiva of the left mandible. For some species that belong to the *dershavini*-group the defining features have been insufficiently described in earlier publications, thus it is difficult to identify which species within the group resembles most closely to *S. odessana* sp. n. The incisor of the right mandible of *S. odessana* sp. n. is 4-dentate, typical for both species in the genus *Lyurella*.

Type locality. Ukraine, catacombs under Odessa, Slobodka District [approx. 46.480593, 30.700242].

Table 1. Comparison of the morphological and ecological characteristics of defined groups of *Synurella* occurring in the Volga-Black Sea basin.

Character	Character states		
	***dershavini*-gr.**	***ambulans*-gr.**	***wachuschtii*-gr.**
[1]Eyes	ommatidia reduced	well developed	entirely lost
Antenna 1 / Body length ratio (males)	0.60–0.90	0.45–0.60	up to 0.30
Antenna 1 / Antenna 2 length ratio (males)	>2.0	>1.33	<=2.0
Calceoli	absent	present	?
Inferior antennal sinus	distinct	indistinct	indistinct
Lower lip, inner lobes	broad	vestigial	vestigial
Gnathopod 2 type, (palmar margin)	crangonyctid type (bevelled)	synurellid type (sub-transverse)	synurellid type (sub-transverse)
Gnathopod 2, carpal lobe	narrow	broad	broad
Number of pleopod retinacula	4–6	2	2
Coxal plates 1-4	shallow or deep	deep	deep
Sexual dimorphism	Males larger than females	Females larger than males	?
Body length, mm	up to 13	up to 10	up to 6
Species	*S. dershavini*, *S. donensis*, *S. osellai*, *S. odessana*, sp. nov.	*S. ambulans*, *S. behningi*, *S. lepida*, *S. philareti*	*S. wachuschtii*, *Synurella* sp. (Sidorov et al. in prep.)
Ecology	hypogean or spring inhabitants of karstic regions (preadapted stygobionts)	epigean inhabitants of coastal lowlands, stygophiles (crenobionts)	minute inhabitants of interstitial waters (stygobionts)

1 Subspecific status has been assigned to blind and unpigmented subterranean populations of *S. ambulans* (see *S. ambulans subterranea* S. Karaman, 1929).

Etymology. The epithet *odessana* (lat.) refers to the city name, Odessa, where species was collected.

Distribution and ecology. *S. odessana*, is known only from the type locality. The specimens were collected in various flooded parts of the catacombs, at a fairly remote distance from each other. In areas where karst sinkholes were present, where the water contains large amount of organics (earth, rotten wood, etc.), the species was abundant, reaching about 50 individuals/m^2. In areas with relatively oligotrophic water, animals were rare or absent. The epimeral plates and pleopods of almost all specimens were densely parasitized by the suctorial infusoria *Dendrocometes* (Protozoa: Ciliata) (Dovgal and Mayén-Estrada 2013). Unidentified stygobiontic Copepoda (Crustacea) were also collected from the same locality. Physical parameters of the water at the collecting site included: temperature 12.5 °C, hardness 3.74 ‰ (Kovtun and Sidorov 2014).

All females of *S. odessana*, were mature and characterized by developed brood plates (oöstegites) with a long marginal setae, but without eggs or youngs. As all specimens were collected on a single date and a fairly large series of females was available, these data suggest that this species has a seasonal cycle of reproduction.

Discussion

The discovery of a new *Synurella* species in Odessa has shed light on the evolution of the genus in the Volga-Black Sea basin. *S. odessana*, clearly exhibits close relationship with *S. osellai* (Tirebolu District near Giresun) from the south-eastern area of the Black Sea coast of Turkey, and undoubtedly resembles *S. dershavini* from the southern tip of the Volga Uplands near Saratov (Burkin Buerak), as well as *S. donensis* described from the karst spring in Nakhichevan-na-Donu (Rostov Region of Russia). A number of features, such as length of antenna and absence of calceoli, distinct inferior antennal sinus of head, armature of both gnathopods and more than two retinacula on pleopods clearly distinguish this group from the other *Synurella*.

The genus *Synurella* is heterogeneous in the Caucasus-Black Sea region. In addition to the *dershavini*-group, two other species groups are present. The *ambulans*-group inhabitants of the coastal lowlands attracted to the outputs of spring waters, while the *wachuschtii*-group is comprised of small, narrowly distributed endemics known from interstitial waters of the Armenian Highland (see Table 1). Sidorov and Palatov (2012) pointed out that the subgenus *Eosynurella*, proposed by Martynov (1931), apparently represents a distinct group with a number of features in common with *dershavini*-group (viz., pear-shaped gnathopod 2 propodi, structure of uropod 3 with a strongly reduced terminal segment, etc.). *Eosynurella* differs from the *dershavini*-group by the following characters: inferior antennal sinus indistinct, antenna 1 slightly longer then antenna 2, calceoli presence on antenna 2, but the representatives of the Far East-Alaskan group need a further investigation, as number of important features are unclear.

According to Charygin and Vasiliev (1968) and the RGRI (1983), the species in the *dershavini*-group occur in unrelated geologic formations: *S. donensis*–is found at the boundary of the north-eastern platform, the eastern edge of the Ukrainian Shield, karst spring (47.231390, 39.756940) ([1]Pliocene); *S. dershavini*–occurs in the Ryazan-Saratov flexure of the north-eastern platform, wells, springs and spring-brooks, seeps (51.411803, 45.757709) (Lower Cretaceous). Nothing can be said about the geology of the habitat of *S. osellai*, because the exact type locality of the species is unknown. The catacombs, inhabited by *S. odessana*, are located in the Black Sea basin, in karstic Pontian limestone. This limestone was deposited at the bottom of the Pontic Sea. The desalinated Pontian Sea-Lake appeared about 6–7 Mya, in the Upper Miocene of the Neogene system (Pontian stage / Messinian for S. Europe) and lasted about 1.2 million years. The Pontic Sea covered a much of the current Odessa region (Muratov 1978). *S. odessana*, is relatively abundant but spatially heterogeneous in the catacombs, the eyes are not lost, whereas *E. catacumbae*, described from a similar habitat, is blind (Karaman and Ruffo 1977). The presence of pigmented eyes in *S. odessana*, might suggests that groundwater colonization of this species is relatively recent from a geological perspective. Additionally, it is possible that there are epigean, spring-associated populations of this species in the vicinity of the city of Odessa.

1 Age determined by the outcropped stratified layers at localities with reference to RGRI (1983).

While we are able to identify species groups within *Synurella* based on morphological and/or ecological similarity (see Table 1), interpreting evolutionary relationships among these groups remains challenging. The absence of fossils limits our understanding of evolution within the Crangonyctidae. Available data from the Caucasus region are only limited by disparate findings of the gammaridean Upper Sarmatian amphipods (Petunnikov 1914; Lednev 1926; Derzhavin 1927, 1941; Karaman 1984). *Synurella* from the Oligocene-Eocene amber (Coleman 2004, 2006; Jażdżewski et al. 2014) have not much shed light on the problem, but morphological characters from the fossil *Synurella* in Baltic amber seem to suggest a relationship to the *ambulans*-group, though this relationship is not clear.

Characters of the *dershavini*-group (Table 1) show clear affinities to certain species of the genera *Crangonyx* (*C. chlebnikovi* Borutzky, 1928, *C. richmondensis*-group sensu Holsinger 1972), *Stygobromus* (*S. gracilipes* (Holsinger, 1967)), *Amurocrangonyx* and *Bactrurus*, exhibiting some or all of a common set of plesiomorphies. This "plesiomorphic aggregation of species" possibly indicates a common ancestor (or group of locally similar ancestors), while other species could have secondary origins through diversification (Hou et al. 2011). The preadapted species of the spring-associated *dershavini*-group are apparently phyletically older than the relatively young *wachuschtii*-group, which has only recently moved into underground habitats as a narrowly regional derivative of the *ambulans*-group (Sidorov et al., in prep.). A recent study of the other spring-associated and endemic Transcaucasian genus *Lyurella* Derzhavin supports this view, revealing a number of features (e.g., rudimentary squamiform uropod 3, uropod 1 with distal marginally serrate process in male) in common with the rejected genus *Apocrangonyx* Stebbing from the North America (Sidorov 2015). These data strongly suggest the presence of a historical assemblage of these now disparate groups.

Considering the present distribution of the *dershavini*-group in the Volga-Black Sea basin the group seems related to the formation of the paleo-basins of the Don and Volga rivers of the European part of Russia. The geographic distribution of the group was significantly changed after the reconfiguration of the river network over the ages. These relationships, like many others associated with riverine paleodynamics, await the results of further studies.

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References

Birstein JA, Ljovuschkin SI (1967) Some results and problem in studying of the subterranean fauna of the USSR. Zoologicheskii Zhurnal 46: 1509–1535. [in Russian, with English abstract]

Charygin MM, Vasiliev YM (1968) Obŝaâ i istoričeskaâ geologiâ. Nedra, Moscow, 448 pp. [in Russian]

Coleman CO (2004) Aquatic amphipods (Crustacea: Amphipoda: Crangonyctidae) found in three pieces of Baltic amber. Organisms, Diversity & Evolution 4: 119–122. doi: 10.1016/j.ode.2004.01.003

Coleman CO (2006) An amphipod of the genus *Synurella* Wrzesniowski, 1877 (Crustacea, Amphipoda, Crangonyctidae) found in Baltic amber. Organisms, Diversity & Evolution 6: 103–108. doi: 10.1016/j.ode.2005.06.002

Derzhavin AN (1927) Notes on the Upper Sarmatian amphipods of the Ponto-Caspian region. Bulletin de la Societe des Naturalistes de Moscou, section geologique, nouvelle serie 35, 5: 183–196. [in Russian, with English abstract]

Derzhavin AN (1927) Iskopaemye bokoplavy Èl'dara. Izvestia Azerbaidjanskogo filiala Akademii Nauk SSSR 2: 65–69. [in Russian]

Dovgal IV, Mayén-Estrada R (2013) Comparative morphology of *Dendrocometes paradoxus* (Ciliophora, Suctorea) from two distant regions (Ukraine and Mexico) and different host species. Vestnik Zoologii, Kiev 47: 47–53. doi: 10.2478/vzoo-2013-0025

Russian Geological Research Institute (1983) Geological map of the USSR. Soviet 1:1M geological maps (first series). Scale 1:1,000,000. Russian Geological Research Institute, Moscow. [in Russian]

Gorodkov KB (1961) The simplest microprojector for drawing insects. Entomological Review 40: 936–939. [in Russian, with English abstract]

Holsinger JR (1972) The freshwater amphipod crustaceans (Gammaridae) of North America. Biota of freshwater ecosystems, Identification manual 5. US Environmental protection agency, Cincinnati, 89 pp.

Holsinger JR (1974) Systematics of the subterranean amphipod genus *Stygobromus* (Gammaridae), Part I: Species of the western United States. Smithsonian Contributions to Zoology 160: 1–63. doi: 10.5479/si.00810282.160

Hou Z, Sket B, Fišer C, Li S (2011) Eocene habitat shift from saline to freshwater promoted Tethyan amphipod diversification. Proceedings of the National Academy of Sciences, USA 108: 14533–14538. doi: 10.1073/pnas.1104636108

Jażdżewski K, Grabowski M, Kupryjanowicz J (2014) Further records of Amphipoda from Baltic Eocene amber with first evidence of prae-copulatory behaviour in a fossil amphipod and remarks on the taxonomic position of *Palaeogammarus* Zaddach, 1864. Zootaxa 3765: 401–417. doi: 10.11646/zootaxa.3765.5.1

Jordana R, Baquero E, Reboleira S, Sendra A (2012) Reviews of the genera *Schaefferia* Absolon, 1900, *Deuteraphorura* Absolon, 1901, *Plutomurus* Yosii, 1956 and the *Anurida* Laboulbène, 1865 species group without eyes, with the description of four new species of cave springtails

(Collembola) from Krubera-Voronya cave, Arabika Massif, Abkhazia. Terrestrial Arthropod Reviews 5: 35–85. doi: 10.1163/187498312X622430

Karaman GS (1974) Genus *Synurella* Wrzes. in Yugoslavia with remarks on its all world known species, their synonymy, bibliography and distribution (fam. Gammaridae). Poljoprivreda i Šumarstvo, Titograd 20: 83–133.

Karaman GS (1984) Critical remarks to the fossil Amphipoda with description of some new taxa. Poljoprivreda i Šumarstvo (Titograd) 30: 87–104.

Karaman GS, Ruffo S (1977) Ricerche faunistiche ed ecologiche sulle grotte di Sicilia. IV. On some interesting *Echinogammarus* species from the Mediterranean basin with description of a new species, *E. catacumbae* n. sp. (Amphipoda, Gammaridae). Animalia, Catania 4: 163–182.

Klimchouk AB, Pronin KK, Timokhina EI (2010) Speleogenesis in the Pontian limestones of Odessa. Speleology and Karstology, Simferopol 5: 76–93. [in Russian]

Kovtun OA, Sidorov DA (2014) Finding of a new species of subterranean crustacean amphipod of the genus *Synurella* (Crustacea: Amphipoda, Crangonyctidae) from water flooded catacombs of Odessa (Ukraine). Marine Ecological Journal, Simferopol 2: 1. [in Russian]

Lednev HM (1926) Geologičeskie issledovaniâ v okrestnostâh g. Mahač-Kala (Petrovsk) s priloženiem opisaniâ obnaženij i razrezov, sostavlennogo gornym inž. N.B. Vassoevičem. Oil Industry, suppl. 11/12: 1–40. [in Russian]

Marin I, Sokolova A (2014) Redescription of the stygobitic shrimp *Troglocaris* (*Xiphocaridinella*) *jusbaschjani* Birštein, 1948 (Decapoda: Caridea: Atyidae) from Agura River, Sochi, Russia, with remarks on other representatives of the genus from Caucasus. Zootaxa 3754: 277–298. doi: 10.11646/zootaxa.3754.3.3

Martynov A (1931) Note on the fresh-water Amphipoda and Isopoda of northern Yakutia. Annuaire du Musée Zoologique de l'Academie des Sciences de l'USSR 32: 523–543.

Muratov MV (1978) Neogenovaâ sistema (period). In: Prokhorov AM (Ed.) Great Soviet Encyclopedia. Soviet Encyclopedia, Moscow. CD-ROM. [in Russian]

Orlov YA (1989) V mire drevnih životnyh. Nauka, Moscow, 213 pp. [in Russian]

Petunnikov GA (1914) Rakoobraznye nižnemiocenovyh sloev bliz seleniâ Binagady. Ežegodnik po geologii i mineralogii Rossii 16: 148–154. [in Russian]

Pronin KK (1989) Istoriâ vozniknoveniâ odesskih katakomb i ih geologičeskoe stroenie. Balta printing house, Balta, 28 pp. [in Russian]

Pronin KK (2009) Estestvennye peŝery Pričernomorsko-Azovskoj i Moldavsko-Podol'skoj karstovyh oblastej. SONAT, Simferopol-Odessa, 130 pp. [in Russian]

Sidorov DA (2014) Towards the systematics of the subterranean amphipod genus *Niphargus* (Crustacea: Amphipoda: Niphargidae) of Transcaucasia: new record of *N. inermis* and *N. iniochus* in Abkhazia. Arthropoda Selecta 23: 363–377.

Sidorov DA (2015) The spring-dwelling amphipod genus *Lyurella* (Peracarida, Amphipoda): Systematics, distribution, and affinity, with description of the second representative from the Black Sea coast region. Crustaceana 88.

Sidorov DA, Palatov DM (2012) Taxonomy of the spring dwelling amphipod *Synurella ambulans* (Crustacea: Crangonyctidae) in West Russia: with notes on its distribution and ecology. European Journal of Taxonomy 23: 1–19. doi: 10.5852/ejt.2012.23

Stock JH (1974) The systematics of certain PontoCaspian Gammaridae (Crustacea, Amphipoda). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 70: 75–95.

Vinarski MV, Palatov DM, Glöer P (2014) Revision of '*Horatia*' snails (Mollusca: Gastropoda: Hydrobiidae sensu lato) from South Caucasus with description of two new genera. Journal of Natural History 48: 2237–2253. doi: 10.1080/00222933.2014.917210

Zaitsev Y, Mamaev V (1997) Marine biological diversity in the Black Sea: a study of change and decline. Black Sea Environmental Series No. 3. United Nations Publications, New York, 208 pp.