

Taxonomic, ecological and morphological diversity of Ponto-Caspian gammaridean amphipods: a review

Denis Copilaş-Ciocianu^{1*} (ORCID: 0000-0002-6374-2365), Dmitry Sidorov² (ORCID: 0000-0003-2635-9129)

¹Laboratory of Evolutionary Ecology of Hydrobionts, Nature Research Centre, Vilnius, Lithuania; ²Federal Scientific Centre of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russian Federation

*Corresponding author: denis.copilas-ciocianu@gamtc.lt

Abstract Thanks to its dynamic geological history the Ponto-Caspian region harbors a unique and unusually adaptable fauna, notorious for its invasive species. Gammarid amphipods attained considerable diversity, becoming the world's second most speciose ancient-lake amphipod radiation. Nonetheless, apart from a few invasive species, this group remains poorly studied. Herein, we review and quantify the taxonomic, morphological and ecological diversity, as well as phylogenetic context of Ponto-Caspian gammarids within the adaptive radiation framework. Published molecular phylogenies indicate that this radiation has a monophyletic mid-Miocene Paratethyan origin, and is nested within the morphologically-conserved Atlanto-Mediterranean genus *Echinogammarus*. We find extensive disparity in body shape, size, ornamentation and appendage length, along a broad ecological gradient from mountain springs to depths exceeding 500 m, on virtually all substrate types (including symbiosis). We propose four putative ecomorphs that appear convergent with distantly related oceanic and Baikal Lake taxa. Thus, the identified patterns support the adaptive radiation model, although extensive further research is needed. A checklist and provisional key to all known endemic species are provided to facilitate taxonomic research. Ponto-Caspian gammarids could be a potentially powerful model for studying adaptive radiations and invasive species evolution.

Keywords: ancient lake, crustacean, evolution, radiation, systematics

Acknowledgements This study was financed by the Lithuanian Research Council (contract no. 09.3.3-LMT-K-712-19-0149). We thank Nadezhda Berezina for providing important literature.

Introduction

Ancient lakes are evolutionary cradles, harboring a rich endemic fauna that fascinated biologists for centuries (M. E. Cristescu et al. 2010; Martens 1997). Their confined nature coupled with large size and relative stability over geological time scales promoted lineage accumulation, diversification and ecological specialization. Many of these lineages probably arose through adaptive radiation, an evolutionary process wherein species rapidly evolve from a common ancestor and diversify to occupy various ecological niches (Schluter 2000). Classical examples of adaptive radiations in ancient lakes are cichlid species flocks in African Rift Valley lakes (Salzburger et al. 2014), or the gammarid amphipods inhabiting Lake Baikal (Naumenko et al. 2017).

Situated in the Ponto-Caspian region, the Caspian Sea is the world's largest ancient lake (M. E. Cristescu et al. 2010). The Azov, Aral and Black seas are also part of this system. These water bodies are remnants of the once widespread epicontinental Paratethys Sea, which stretched from the foothills of the Alps to the Himalayas (Popov et al. 2004). The Paratethys had a turbulent geological history with numerous regression-transgression phases causing drastic salinity fluctuations and repeated episodes of isolation and reconnection with the world ocean (Audzijonyte et al. 2015; Palcu et al. 2019; Popov et al. 2004; Rögl 1999). The uplift of the Caucasus range during the late Miocene triggered the formation and separation of the Black and Caspian seas. During the last two million

51 years these two basins experienced recurrent phases of mutual isolation and reconnection
52 (Krijgsman et al. 2019).

53

54 It is thought that this tumultuous geological past drove the evolution of the unusually euryhaline
55 fauna that inhabits the region today (Reid and Orlova 2002). This plasticity has enabled many Ponto-
56 Caspian species to spread across the Northern Hemisphere and become invasive due to human
57 interference (Adrian-Kalchhauser et al. 2020; Cuthbert et al. 2020; Vanderploeg et al. 2002).
58 Nevertheless, many Ponto-Caspian endemics face severe conservation challenges due to climate
59 change, invasive species and multifarious anthropogenic disturbances (Dumont 1995; Gogaladze et
60 al. 2020; Lattuada et al. 2019; Prange et al. 2020). The Ponto-Caspian region is a hot-spot of
61 endemism and biodiversity with hundreds of species from various animal phyla, but particularly rich
62 in crustaceans (Birstein et al. 1968; Chertoprud et al. 2018; M. E. A. Cristescu and Hebert 2005;
63 Mordukhai-Boltovskoi 1979; Naseka and Bogutskaya 2009; Wesselingh et al. 2019).

64

65 Amphipod crustaceans radiated multiple times in the world's temperate ancient lakes. Several
66 radiations occurred in Lake Titicaca (Hyalellidae) (Adamowicz et al. 2018; Jurado-Rivera et al. 2020),
67 two in Lake Baikal (Gammaridae) (Macdonald et al. 2005; Naumenko et al. 2017), probably two in the
68 Ponto-Caspian basin (Gammaroidea, Corophiidae) (M. E. A. Cristescu and Hebert 2005; Hou et al.
69 2014), and apparently one radiation in other lakes such as Ohrid (Gammaridae) (Wysocka et al. 2013,
70 2014), and Fuxian Hu (Anisogammaridae) (Sket and Fišer 2009). Other lakes throughout Asia also
71 harbor endemic species, although their monophyly has yet to be proven. These are Lake Issyk-Kul in
72 Kyrgyzstan (Gammaridae) (Karaman and Pinkster 1977) and Lake Teletskoye (Gammaridae) in Russia
73 (Martynov 1930). In most of these lakes amphipods display a bewildering diversity in form and
74 ecology, with remarkable convergence in body armature among evolutionary and geographically
75 distant groups (Martens 1997).

76

77 The endemic amphipod fauna of the Ponto-Caspian basin is one of the world's most diverse, second
78 only to Lake Baikal (Barnard and Barnard 1983; Väinölä et al. 2008). Among all endemic Ponto-
79 Caspian organisms, amphipods seem to be the most species-rich and successful group, attaining
80 significant ecological and morphological disparity, akin to an adaptive radiation (Derzhavin 1948;
81 Pjatakova and Tarasov 1996; Sars 1895). However, despite these appealing features for evolutionary
82 and ecological studies, Ponto-Caspian amphipods are obscure and poorly known, even ignored in
83 some relatively recent reviews (Martens and Schön 1999). Most attention has been focused on the
84 invasive species that are spreading throughout European freshwaters (e.g. Cristescu et al., 2004;
85 Grabowski et al., 2007; Arbačiauskas et al., 2013; Rewicz et al., 2015), while the non-invasive ones
86 were largely ignored in the last two decades. The taxonomy of the group is rather chaotic due to old
87 and incomplete species descriptions, which led to fuzzy generic diagnoses and lack of a formal
88 system. Even online databases such as World Amphipoda Database
89 (<http://www.marinespecies.org/amphipoda/>) are incomplete (Horton et al. 2020). Furthermore, a
90 significant part of the literature predates the digital era and is published in Russian, thus not readily
91 available for the international community. As such, to date, there is no comprehensive overview of
92 the Ponto-Caspian amphipod diversity in terms of taxa, ecology and morphology. Some attempts
93 have been made in the past, but these either focused on taxonomy or ecology and never considered
94 the amphipods from all of the Ponto-Caspian basins (Birstein and Romanova 1968; Mordukhai-
95 Boltovskoi 1964, 1979; Pjatakova and Tarasov 1996).

96

97 In this study we aim to provide a first comprehensive overview of endemic Ponto-Caspian
98 gammaridean amphipods (taxonomy, morphology and ecology) by examining all of the original
99 species descriptions and relevant literature. Furthermore, by integrating the results of this study with
100 previous phylogenetic research, we strived to identify to which extent the current knowledge on
101 Ponto-Caspian amphipods satisfies the adaptive radiation model (Schluter 2000; Simões et al. 2016).

102 Specifically, we looked for evidence pointing to: I) monophyly of endemic Ponto-Caspian gammarids,
103 II) an increase in their diversification rates, and III) ecomorphological divergence.

104

105 This overview is intended to serve as a foundation and to encourage future eco-evolutionary and
106 taxonomic studies on Ponto-Caspian amphipods. To this end, we also provide a complete checklist
107 and a provisional key to all known endemic species in the hopes of reviving taxonomic interest and to
108 stabilize the systematics of the group.

109

110 Taxonomic diversity

111 Our study focuses on the Ponto-Caspian amphipod taxa that belong to the superfamily
112 Gammaroidea. Specifically, we included the endemic genera of the family Gammaridae, as well as
113 the fully endemic families Behningiellidae, Caspicolidae, Iphigenellidae, and Pontogammaridae.
114 These taxa form the bulk of the endemic diversity and are most likely a monophyletic group (Hou et
115 al. 2014; Sket and Hou 2018), which is a necessary prerequisite for the adaptive radiation model
116 (Schluter 2000). The remaining Ponto-Caspian endemic amphipods such as *Chelicorophium* (9 spp.,
117 Corophiidae), *Gammaracanthus* (1 sp., Gammaracanthidae), *Niphargus* (1 sp.), *Onisimus* (2 spp.,
118 Uristidae), and *Monoporeia* (1 sp.) were excluded since they are unrelated to the focal gammarids
119 (Copilaş-Ciocianu et al. 2020; Lowry and Myers 2017; Väinölä et al. 2001). However, we include the
120 monotypic family Caspicolidae because it is very likely a highly derived gammarid (Derzhavin 1944).
121 Although this family is currently included in the infraorder Talitridira by Lowry & Myers (2013), we
122 consider this placement erroneous due to a character coding mistake (see Discussion for further
123 details).

124

125 We compiled a checklist of all known Ponto-Caspian gammaroids by reviewing all of the original
126 species descriptions, including re-descriptions. It is presented in Table 1 along with species
127 systematics, native distribution and short taxonomic remarks where necessary. A total of 82 valid
128 extant species are known, belonging to 34 genera and five families: Behningiellidae (3 genera, 4
129 spp.), Caspicolidae (monotypic), Gammaridae (18 genera, 39 spp.), Iphigenellidae (monotypic) and
130 Pontogammaridae (11 genera, 37 spp.) (Fig. 1a). Five species are doubtful since they may be junior
131 synonyms and further study is needed (Table 1). The most diverse genus is *Pontogammarus* (8 spp.),
132 followed by *Dikerogammarus* and *Obesogammarus* (7 spp. each), *Stenogammarus* (6 spp.),
133 *Chaetogammarus* and *Amathillina* (5 spp. each). Eighteen genera (53%) are monotypic (Fig. 1a). The
134 extinct fossil genera *Andrussovia* (3 spp.) and *Praegmelina* (2 spp.) are currently placed in the
135 Pontogammaridae (Table 1).

136

137 The trend of species description through time reveals little taxonomic activity from the 18th to late
138 19th centuries, a sudden increase with Sars' monographs in the late 19th century, followed by a more
139 or less steady increase towards the present day with peaks of activity in the middle 20th century by
140 Russian and Romanian authors (Fig. 1b). A noticeable stagnation can be observed in the last two
141 decades. By far the most prolific author was G. O. Sars (37 spp.), followed by A. N. Derzhavin (9 spp.)
142 and S. Cărăușu (8 spp.) (Fig. 1b inset).

143

144 A provisional key to all known endemic families, genera and species (including non-Gammaroidea) is
145 provided in the Appendix. We emphasize that some taxa are poorly known and have an uncertain
146 generic placement.

147

148

149

150

151

152 Table 1. Checklist, taxonomy and native distribution of extant and fossil Ponto-Caspian gammaroid
 153 amphipods.
 154

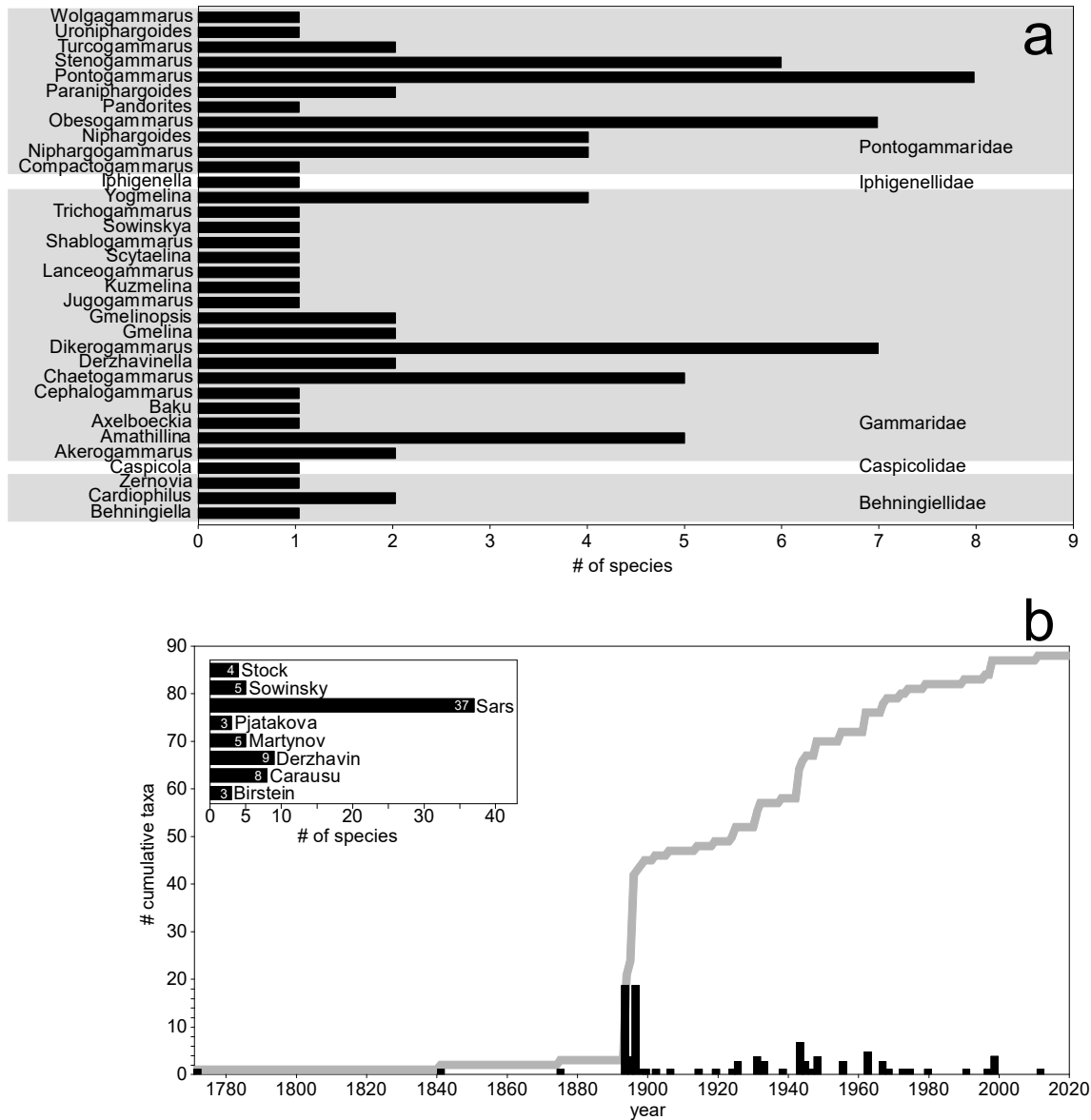
Family	Species	Authority	Distribution basin	Status	Taxonomic remarks
Behningiellidae	<i>Behningiella brachypus</i>	Derzhavin, 1948	Caspian	valid	
Behningiellidae	<i>Cardiophilus baeri</i>	G.O. Sars, 1896	Caspian	valid	
Behningiellidae	<i>Cardiophilus marisnigrae</i>	Miloslavskaja, 1931	Ponto-Azov	valid	Original spelling: <i>C. maris-nigirs</i> Emended by Barnard (1958) according to ICZN article 32.5.2.3 Synonyms: <i>Cardiophilus miloslavskajae</i> Căărăușu, 1955
Behningiellidae	<i>Zernovia volgensis</i>	Derzhavin, 1948	Caspian	valid	
Caspicolidae	<i>Caspicola knipovitschi</i>	Derzhavin, 1944	Caspian	valid	
Gammaridae	<i>Akerogammarus contiguus</i>	(Pjatakova, 1962)	Caspian	valid	
Gammaridae	<i>Akerogammarus knipowitschi</i>	Derzhavin & Pjatakova, 1967	Caspian	valid	
Gammaridae	<i>Amathillina affinis</i>	G.O. Sars, 1894	Caspian	valid	
Gammaridae	<i>Amathillina cristata</i>	G.O. Sars, 1894	Caspian, Ponto-Azov	valid	
Gammaridae	<i>Amathillina maximowiczi</i>	G.O. Sars, 1896	Caspian	valid	
Gammaridae	<i>Amathillina pusilla</i>	G.O. Sars, 1896	Caspian	valid	
Gammaridae	<i>Amathillina spinosa</i>	G.O. Sars, 1896	Caspian	valid	
Gammaridae	<i>Axelboeckia spinosa</i>	(G.O. Sars, 1894)	Caspian	valid	
Gammaridae	<i>Baku paradoxus</i>	(Derzhavin in Derzhavin & Pjatakova, 1967)	Caspian	valid	
Gammaridae	<i>Cephalogammarus macrocephalus</i>	(G.O. Sars, 1896)	Caspian	valid	Possibly a derived <i>Dikerogammarus</i>
Gammaridae	<i>Chaetogammarus hyrcanus</i>	Pjatakova, 1962	Caspian	valid	
Gammaridae	<i>Chaetogammarus ischnus</i>	(Stebbing, 1899)	Caspian, Ponto-Azov	valid	Nom. nov. for <i>Gammarus tennelus</i> Sars 1896; Synonyms: <i>Gammarus sowinskyi</i> (Behning, 1914)
Gammaridae	<i>Chaetogammarus pauxillus</i>	(G.O. Sars, 1896)	Caspian	valid	
Gammaridae	<i>Chaetogammarus placidus</i>	(G.O. Sars, 1896)	Caspian, Ponto-Azov	valid	
Gammaridae	<i>Chaetogammarus warpachowskyi</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	Reassessment of generic status needed. Close morphological affinities with <i>Gmelina</i> group.
Gammaridae	<i>Derzhavinella cava</i>	Stock, Mirzajani, Vonk, Naderi, Kiabi, 1998	Caspian	valid	
Gammaridae	<i>Derzhavinella macrochelata</i>	Birstein, 1938	Caspian	valid	
Gammaridae	<i>Dikerogammarus aralychensis</i>	(Birstein, 1932)	Caucasus	doubtful	Probably junior synonym of <i>Pontogammarus setosus</i> (Schäferna, 1914). Further research needed.
Gammaridae	<i>Dikerogammarus bispinosus</i>	Martynov, 1925	Caspian, Ponto-Azov	valid	
Gammaridae	<i>Dikerogammarus caspius</i>	(Pallas, 1771)	Caspian	valid	
Gammaridae	<i>Dikerogammarus fluviatilis</i>	Martynov, 1919	Caspian, Ponto-Azov	doubtful	Initially described by Martynov 1919 as a morph of <i>D. haemobaphes</i> . Further

					research needed.
Gammaridae	<i>Dikerogammarus gruberi</i>	Mateus & Mateus, 1990	Ponto-Azov	valid	
Gammaridae	<i>Dikerogammarus haemobaphes</i>	(Eichwald, 1841)	Caspian, Ponto-Azov	valid	Synonym: <i>Dikerogammarus balatonicus</i> Pony, 1958
Gammaridae	<i>Dikerogammarus istanbulensis</i>	Özbek and Özkan, 2011	Ponto-Azov	valid	
Gammaridae	<i>Dikerogammarus oskari</i>	Birstein, 1945	Caspian	valid	Nom. nov. for <i>Gammarus grimmi</i> Sars 1896
Gammaridae	<i>Dikerogammarus villosus</i>	(Sowinsky, 1894)	Caspian, Ponto-Azov	valid	
Gammaridae	<i>Gmelina aestuarica</i>	Cărăușu, 1943	Ponto-Azov	valid	
Gammaridae	<i>Gmelina costata</i>	G.O. Sars, 1894	Caspian, Ponto-Azov	valid	
Gammaridae	<i>Gmelinopsis aurita</i>	G.O. Sars, 1896	Caspian	valid	
Gammaridae	<i>Gmelinopsis tuberculata</i>	G.O. Sars, 1896	Caspian, Ponto-Azov	valid	
Gammaridae	<i>Kuzmelina kusnezowi</i>	(Sowinsky, 1894)	Caspian, Ponto-Azov	valid	
Gammaridae	<i>Jugogammarus kusceri</i>	(S. Karaman, 1931)	Balkan	valid	
Gammaridae	<i>Lanceogammarus andrussowi</i>	(G.O. Sars, 1896)	Caspian, Ponto-Azov	valid	
Gammaridae	<i>Scytaelina simplex</i>	Stock, Mirzajani, Vonk, Naderi, Kiabi, 1998	Caspian	valid	
Gammaridae	<i>Shablogammarus shablensis</i>	(Cărăușu, 1943)	Caspian, Ponto-Azov	valid	Original spelling: <i>Gammarus chablensis</i> Emended by Cărăușu et al. (1955)
Gammaridae	<i>Sowinskya macrocera</i>	Derzhavin, 1948	Caspian	Valid	
Gammaridae	<i>Trichogammarus trichiatus</i>	(Martynov, 1932)	Ponto-Azov	Valid	We do not agree that <i>Chaetogammarus tennelus major</i> Cărăușu, 1943 is a junior synonym. Further study is needed.
Gammaridae	<i>Yogmelina brachyura</i>	(Derzhavin & Pjatakova, 1962)	Caspian	valid	
Gammaridae	<i>Yogmelina laeviuscula</i>	(G.O. Sars, 1896)	Caspian	valid	
Gammaridae	<i>Yogmelina limana</i>	G.S. Karaman & Barnard, 1979	Ponto-Azov	valid	
Gammaridae	<i>Yogmelina ovata</i>	(Martynov, 1924)	Ponto-Azov	doubtful	Probably junior synonym of <i>Chaetogammarus warpachowskyi</i> . Further study is needed.
Gammaridae	<i>Yogmelina pusilla</i>	(G.O. Sars, 1896)	Caspian, ?Ponto-Azov	valid	
Iphigenellidae	<i>Iphigenella acanthopoda</i>	G.O. Sars, 1896	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Compactogammarus compactus</i>	(G.O. Sars, 1895)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Niphargogammarus aequimanus</i>	(G.O. Sars, 1895)	Caspian	valid	
Pontogammaridae	<i>Niphargogammarus borodini</i>	(G.O. Sars, 1897)	Caspian	valid	
Pontogammaridae	<i>Niphargogammarus intermedius</i>	(Cărăușu, 1943)	Ponto-Azov	valid	
Pontogammaridae	<i>Niphargogammarus quadrimanus</i>	(G.O. Sars, 1895)	Caspian	valid	
Pontogammaridae	<i>Niphargoides boltovskoyi</i>	Derzhavin & Pjatakova, 1968	Caspian	valid	
Pontogammaridae	<i>Niphargoides caspius</i>	G.O. Sars, 1894	Caspian	valid	
Pontogammaridae	<i>Niphargoides</i>	G.O. Sars, 1894	Caspian,	valid	

	<i>corpulentus</i>		Ponto-Azov		
Pontogammaridae	<i>Niphargoides grimmi</i>	G.O. Sars, 1896	Caspian	valid	
Pontogammaridae	<i>Obesogammarus acuminatus</i>	Stock, Mirzajani, Vonk, Naderi, Kiabi, 1998	Caspian	valid	
Pontogammaridae	<i>Obesogammarus boeoticus</i>	(Schellenberg, 1944)	Balkan	valid	Poorly described, generic status needs revision
Pontogammaridae	<i>Obesogammarus crassus</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	Synonyms: <i>Obesogammarus crassus</i> f. <i>mediodanubialis</i> S. Karaman, 1953
Pontogammaridae	<i>Obesogammarus obesus</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Obesogammarus olvianus</i>	(Sowinsky, 1902)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Obesogammarus platycheir</i>	(G.O. Sars, 1896)	Caspian	valid	
Pontogammaridae	<i>Obesogammarus subnudus</i>	(G.O. Sars, 1896)	Caspian, Ponto-Azov	valid	Provisionally placed in <i>Obesogammarus</i> . Generic status needs revision.
Pontogammaridae	<i>Pandorites podocerooides</i>	(G.O. Sars, 1896)	Caspian	valid	
Pontogammaridae	<i>Paraniphargoides derzhavini</i>	Pjatakova, 1962	Caspian	valid	
Pontogammaridae	<i>Paraniphargoides motasi</i>	(Cărbăușu, 1943)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Pontogammarus abbreviatus</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Pontogammarus aestuarius</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Pontogammarus borceae</i>	Carausu, 1943	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Pontogammarus palmatus</i>	(Martynov, 1925)	Caspian	doubtful	Poor description without illustrations.
Pontogammaridae	<i>Pontogammarus robustoides</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Pontogammarus setosus</i>	(Schäferna, 1914)	Caucasus	valid	
Pontogammaridae	<i>Pontogammarus (=Euxinia) maeoticus</i>	(Sowinsky, 1894)	Caspian, Ponto-Azov	valid	Removed to <i>Pontogammarus</i> since <i>Euxinia</i> Tucolesco, 1933 is preoccupied by the platyhelminth genus <i>Euxinia</i> Graff, 1911. According to ICZN articles 23.1 and 52.4 Synonyms: <i>Euxinia fagei</i> Tucolesco, 1933
Pontogammaridae	<i>Pontogammarus (=Euxinia) sarsi</i>	(Sowinsky, 1898)	Caspian, Ponto-Azov	valid	Removed to <i>Pontogammarus</i> since <i>Euxinia</i> Tucolesco, 1933 is preoccupied by the platyhelminth genus <i>Euxinia</i> Graff, 1911. According to ICZN articles 23.1 and 52.4
Pontogammaridae	<i>Pontogammarus (=Euxinia) weidmanni</i>	(G.O. Sars, 1896)	Caspian, Ponto-Azov	valid	Removed to <i>Pontogammarus</i> since <i>Euxinia</i> Tucolesco, 1933 is preoccupied by the platyhelminth genus <i>Euxinia</i> Graff, 1911. According to ICZN articles 23.1 and 52.4
Pontogammaridae	<i>Stenogammarus compressus</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Stenogammarus compressosimilis</i>	Cărbăușu 1955	Caspian, Ponto-Azov	valid	Original spelling: <i>S. compresso-similis</i> Emended according to ICZN article 32.5.2.3 Synonyms: <i>Stenogammarus</i>

					<i>kereuschi</i> Derzhavin & Pjatakova, 1962 according to ICZN article 23.3.7
Pontogammaridae	<i>Stenogammarus deminutus</i>	(Stebbing, 1906)	Caspian, Ponto-Azov	valid	Nom. nov. for <i>Gammarus minutus</i> G.O. Sars 1894
Pontogammaridae	<i>Stenogammarus macrurus</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Stenogammarus micrurus</i>	Derzhavin & Pjatakova, 1996	Caspian	valid	
Pontogammaridae	<i>Stenogammarus similis</i>	(G.O. Sars, 1894)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Turcogammarus aralensis</i>	(Uljanin, 1875)	Aral, Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Turcogammarus spandli</i>	(Karaman, 1931)	Balkan	valid	
Pontogammaridae	<i>Turcogammarus turcarum</i>	(Stock, 1974)	Caucasus	doubtful	Probably junior synonym of <i>Pontogammarus setosus</i> (Schäferna, 1914). Further research needed.
Pontogammaridae	<i>Uroniphargoides spinicaudatus</i>	(Cărăușu, 1943)	Caspian, Ponto-Azov	valid	
Pontogammaridae	<i>Wolgagammarus dzjubani</i>	(Mordukhai-Boltovskoi & Ljakhov, 1972)	Caspian	valid	
Fossil taxa					
Pontogammaridae	<i>Andrussovia bogacevi</i>	Derzhavin, 1927†	Caspian	valid	
Pontogammaridae	<i>Andrussovia sokolovi</i>	Derzhavin, 1927†	Caspian	valid	
Pontogammaridae	<i>Andrussovia vassoievitschi</i>	Derzhavin, 1941†	Caspian	valid	
Pontogammaridae	<i>Praegmelina andrussovi</i>	Derzhavin, 1927†	Caspian	valid	
Pontogammaridae	<i>Praegmelina archangelskii</i>	Derzhavin, 1927†	Caspian	valid	
Hellenidae	<i>Hellenis saltatorius</i>	Petunnikoff, 1914†	Caspian	valid	Uncertain affiliation with extant Ponto-Caspian taxa

155



156
157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172

Fig. 1 a) Species richness within genera and families. Only valid and extant species were considered. b) Trends in species descriptions through time. The thick gray line indicates the cumulative number of species while black bars indicate the number of species described in that respective year. The inset graph depicts the number of species described by the most prominent authors

Morphology

To explore morphological diversity we extracted data only from those original species descriptions or re-descriptions that provided good quality habitus illustrations (73% of all species) (Cărașu 1943; Cărașu et al. 1955; Derzhavin 1944, 1948; Sars 1894a, 1894b, 1895, 1896). This was necessary because we used the ratios of various body parts and appendages to total body length. In total, we calculated ratios for 53 traits reflecting as much as possible the overall body shape and functional morphology (see Supplementary information Tables S1-S2 and Fig. S1) (Fišer et al. 2009). The ratios were measured using the Digimizer software (<https://www.digimizer.com/>). Whenever possible, both sexes were included. We acknowledge that these illustration obtained ratios do not provide the most exhaustive nor precise morphological detail. However, given that these data have a broad

173 taxonomic coverage, we consider this analysis as a crucial preliminary step in quantifying and
174 understanding the morphological diversity of Ponto-Caspian amphipods.

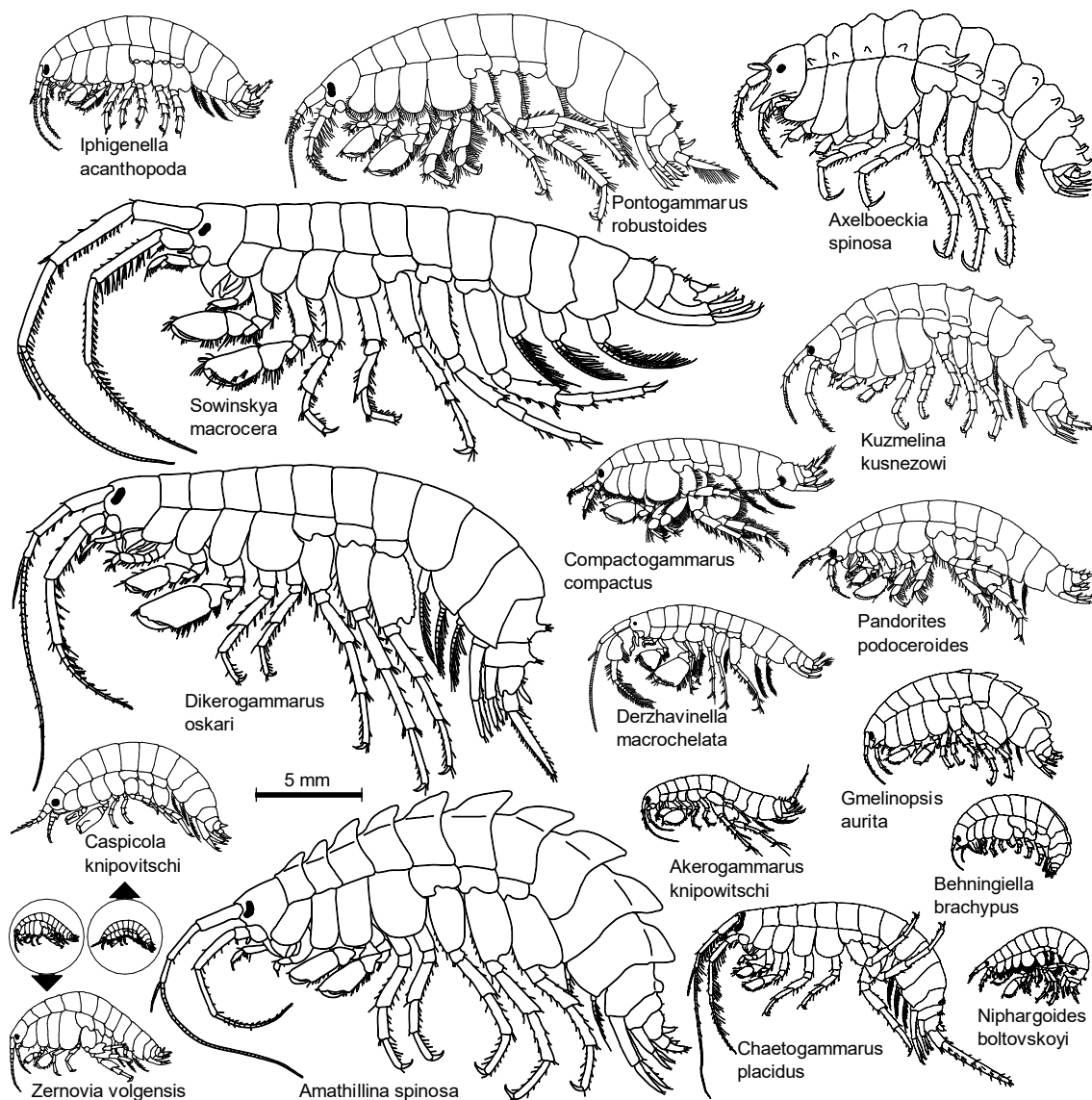
175

176 Apart from ratios, we also extracted body size information from the literature and included it in the
177 analysis as well. The 53 ratio + body-size dataset was subjected to a Principal Component Analysis
178 (PCA) based on a correlation matrix to visualize morphological gradients and similarity among
179 genera. Analysis was performed using Statistica 8.0 (StatSoft, Inc., Tulsa, OK, USA).

180

181 We find substantial diversity in body shape and size. The habitus of representative species is
182 presented in Fig. 2. Body size varies by almost an order of magnitude (3.5 to 27 mm) (Figs. 2, 6). The
183 PCA plot indicates significant morphological disparity (Fig. 3). The first four PCA axes explained 22.76,
184 14.12, 10.17 and 9.28% (56.34%) of the total variation. The first principal component separated
185 species along a gradient from stout bodies with deep coxae and short antennae to slender bodies
186 with shallow coxae and long antennae (Fig. 3a). The second principal component distinguished a
187 gradient along which species were separated by the length of walking appendages and the depth of
188 the tergum (Fig. 3a). The loadings of traits on the PCA axes are presented in Supplementary
189 information Table 3.

190



192

193

Fig. 2 Habitus and morphological diversity of Ponto-Caspian amphipods. *Caspicola knipovitschi* and *Zernovia volgensis* are shown to scale in circles and enlarged outside the circles. All images are redrawn after the original

194

195

196

197

There is significant variation with respect to body armature as well. Although most species are generally smooth, there are diverse patterns of ornamentation with either a medial keel that extends throughout different body regions (e.g. *Amathillina*, *Gmelina* and *Gmelinopsis*) to double dorso-lateral cuspidation (*Kuzmelina*), to lateral spines and dorsal protuberances (*Axelboeckia*) (Fig. 2).

200

201

202

Most genera seem to be relatively well defined in morphospace. However, *Amathillina* and *Obesogammarus* overlap broadly with other genera (Fig. 3a). The monotypic genera (shown with black and white symbols in Fig. 3a) are generally distinct from the more speciose ones, often lying towards the extreme ends of the morphological gradients.

203

204

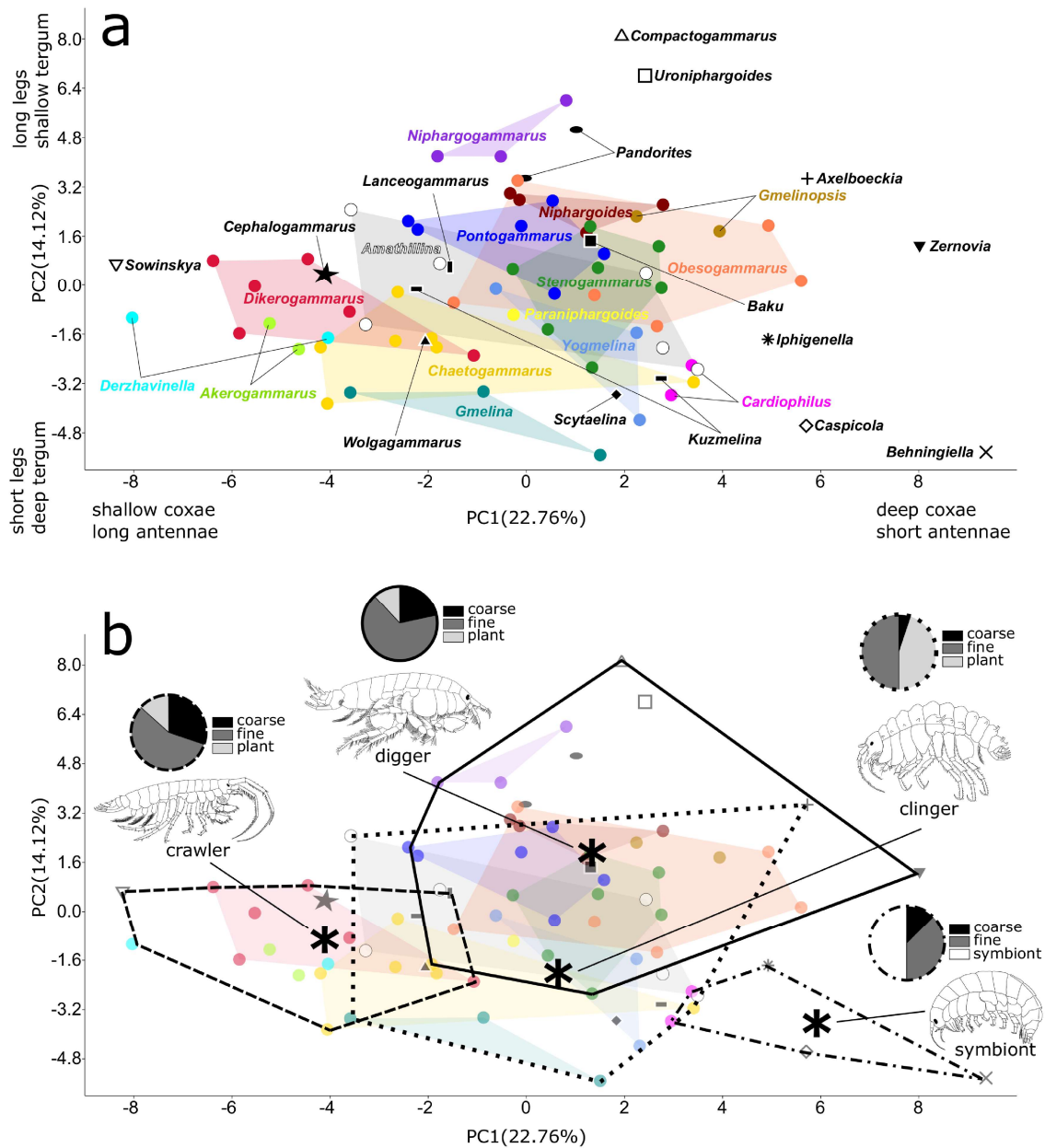
205

206

207

208

209



210
211 **Fig. 3** a) PCA scatterplot depicting the morphological gradients along the first two axes. Genera represented by
212 at least three data points are shown with a uniquely colored convex hull and dots. Monotypic genera are
213 depicted with various black symbols and shapes. b) The same PCA as in a) but with convex hulls delineating
214 putative ecomorphs. Asterisks indicate morph centroid. For each morph a representative species is shown. The
215 pie-charts indicate the proportion of species occurring on various substrates within each ecomorph

216

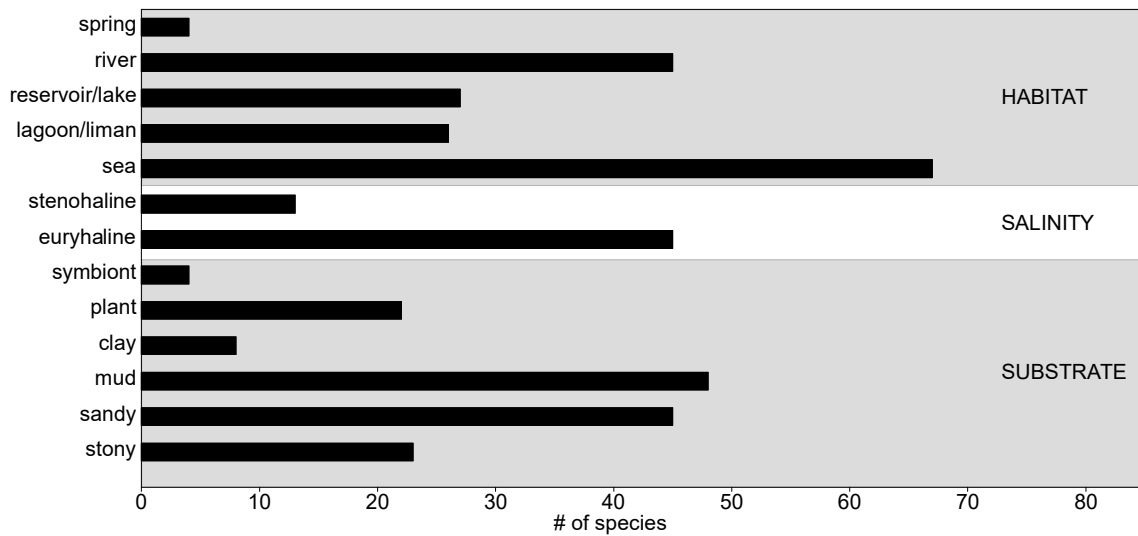
217

218 Ecology

219 To provide a synopsis of ecology we reviewed all the original species descriptions and the relevant
220 literature (Birstein and Romanova 1968; Pjatakova and Tarasov 1996). We gathered data regarding
221 depth (minimum and maximum), habitat (sea, lagoon, lake/reservoir, river and spring), salinity
222 (steno- and/or euryhaline) and substrate type (stone, sand, mud, clay, plant and symbiotic
223 relationships).

224
225
226
227
228
229
230
231
232
233
234
235
236

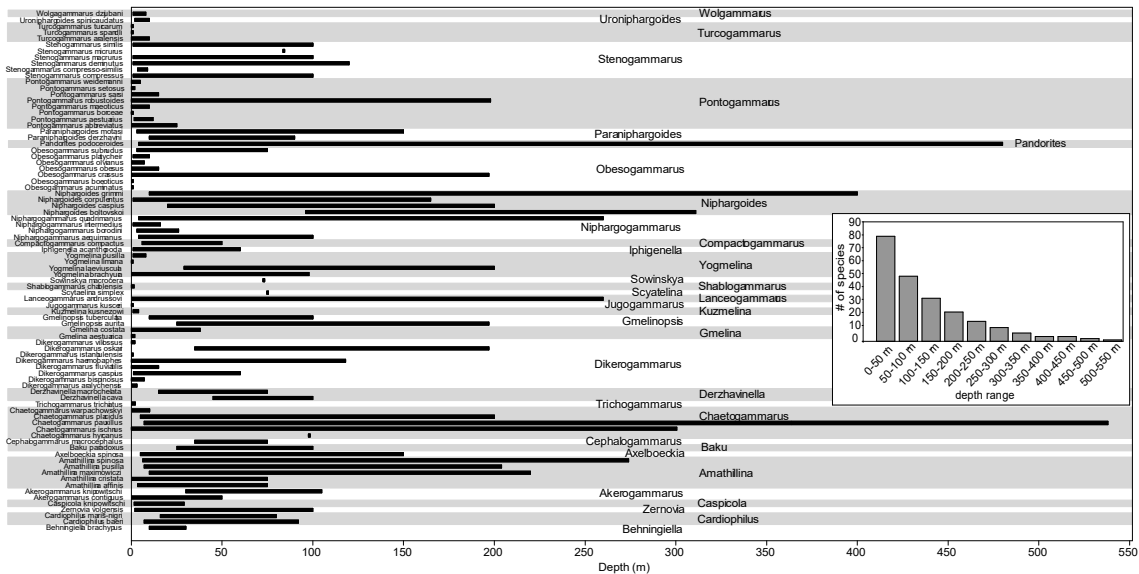
Our review highlights important ecological diversity within the Ponto-Caspian radiation. With respect to habitat, most species live in the sea (67 spp.) and lower courses of rivers (45 spp.), followed by brackish lagoons (26 spp.) and freshwater lakes or reservoirs (27 spp.). Only four species occur exclusively in springs and streams (Table 2, Fig. 4). With respect to salinity, it appears that most species are euryhaline, tolerating both fresh as well as brackish waters. However, salinity preference is not known for many species. With respect to substrate, the great majority of species occur on sandy and muddy substrates, followed by stones and plants. Four species seem to be associated with other organisms such as bivalve mollusks and crayfish (Table 2, Fig. 4). All of the ecological data is summarized in Table 2.



237
238
239
240
241
242
243
244
245
246
247
248
249
250
251
252
253
254
255
256
257
258
259
260

Fig. 4 Number of species occurring on various substrates, habitats and salinities

The depth gradient is broad, ranging from the wet sand of the supra-littoral to more than 500 m depth (Table 2, Fig. 5). Individual species also seem to be quite plastic and can be found from shallow depths (less than 50 m) to more than 200 m. The genera *Amathillina*, *Chaetogammarus*, *Niphargoides* and *Pandorites* have the broadest depth ranges. Species diversity is the highest in the first 50 m (79 species), then rapidly decreases to below 10 species in the 250-550 m interval (Fig. 5). The only species known to occur at depths greater than 500 m is *Chaetogammarus pauxillus*.



261
262 **Fig. 5** Depth ranges structured by taxonomic composition. The inset graph depicts the number of species
263 occurring in 50 m depth intervals

264
265
266
267
268

Table 2. Ecological diversity of Ponto-Caspian gammaroid amphipods.

Species	Min depth	Max depth	Substrate					Salinity	Habitat					Ecomorph	
			sto ¹	san ²	mud	cla ³	pla ⁴		symbiont	sea	lag ⁵	res ⁶	riv ⁷		spr ⁸
<i>Behningiella brachypus</i>	10	30	x	x					?	x					symbiont
<i>Cardiophilus baeri</i>	7	92			?	?		Cardium	?	x					symbiont
<i>Cardiophilus maris-nigri</i>	16	80		x		x		Mytilus	?	x					symbiont
<i>Zernovia volgensis</i>	2	100							?	x			x		digger
<i>Caspicola knipovitschi</i>	1.5	29		x				possibly molluscs	euryh.	x			x		symbiont
<i>Akerogammarus contiguus</i>	0.2	50	x	x	x				?	x					crawler
<i>Akerogammarus knipowitschi</i>	30	105			x				?	x					crawler
<i>Amathillina affinis</i>	3.5	75					x		euryh.	x					clinger
<i>Amathillina cristata</i>	0.5	75					x		euryh.	x	x	x	x		clinger
<i>Amathillina maximowiczi</i>	10	220					?		?	x	x				clinger
<i>Amathillina pusilla</i>	7	204					x		?	x					clinger
<i>Amathillina spinosa</i>	6.4	274		x	x		?		euryh.	x					clinger
<i>Axelboeckia spinosa</i>	5	150			?		x		euryh.	x			x		clinger
<i>Baku paradoxus</i>	25	100			x				?	x					digger
<i>Cephalogammarus macrocephalus</i>	35	75			x				?	x					crawler
<i>Chaetogammarus hyrcanus</i>		98			x				?	x					crawler
<i>Chaetogammarus ischnus</i>	0	300	x	x	x		x		euryh.	x	x	x	x		crawler
<i>Chaetogammarus pauxillus</i>	7	538		x					euryh.	x					crawler

<i>Chaetogammarus placidus</i>	5	200			x				euryh.	x			x		crawler
<i>Chaetogammarus warpachowskyi</i>	0.5	10		x	x		x		euryh.	x	x	x	x		clinger
<i>Derzhavinella cava</i>	45	100							?	x					crawler
<i>Derzhavinella macrochelata</i>	15	75			x				?	x					crawler
<i>Dikerogammarus aralychensis</i>	0.2	3		x	x				stenoh.			x	x		digger
<i>Dikerogammarus bispinosus</i>	0	7	x	x					euryh.	x		x	x		crawler
<i>Dikerogammarus caspius</i>	1.2	60	x						euryh.	x		x	x		crawler
<i>Dikerogammarus fluviatilis</i>	0	15	x	x	x		x		euryh.				x		crawler
<i>Dikerogammarus gruberi</i>									?			x			?
<i>Dikerogammarus haemobaphes</i>	0	118	x	x	x				euryh.	x	x	x	x		crawler
<i>Dikerogammarus istanbulensis</i>	0.2	1			x				?			x			crawler
<i>Dikerogammarus oskari</i>	35	197			x				?	x					crawler
<i>Dikerogammarus villosus</i>	0	2	x				x		euryh.	x	x	x	x		crawler
<i>Gmelina aestuarica</i>	0	2		x	x		x		euryh.		x		x		clinger
<i>Gmelina costata</i>	0	38	x	x			x		euryh.	x			x		clinger
<i>Gmelinopsis aurita</i>	25	197							?	x					digger
<i>Gmelinopsis tuberculata</i>	10	100	x						euryh.	x	x		x		digger
<i>Kuzmelina kusnezowi</i>	1	4			x				euryh.	x	x		x		clinger
<i>Jugogammarus kusceri</i>	0	1	x	x					stenoh.					x	clinger
<i>Lanceogammarus andrussowi</i>	0.5	260		x			x		euryh.	x	x	x			crawler
<i>Scytaelina simplex</i>		75							?	x					clinger
<i>Shablogammarus shablensis</i>	0	1.5			x		x		euryh.		x	x	x		crawler
<i>Sowinskya macrocera</i>		73			x				?	x					crawler
<i>Trichogammarus trichiatus</i>	0	2	x	x					euryh.		x	x	x		crawler
<i>Yogmelina brachyura</i>	0.3	98		x	x		x		?	x					clinger
<i>Yogmelina laeviuscula</i>	29	200			x				?	x					clinger
<i>Yogmelina limana</i>		1		x	x		x		euryh.		x		?		clinger
<i>Yogmelina pusilla</i>	1	8		x	x		x		euryh.	x	x		?		clinger
<i>Iphigenella acanthopoda</i>	1	60						possibly Astacidae	euryh.	x	x	x	x		symbiont
<i>Compactogammarus compactus</i>	6	50		x	x				euryh.	x	x		x		digger
<i>Niphargogammarus aequimanus</i>	4	100							stenoh.	x					digger
<i>Niphargogammarus borodini</i>	3	26							?	x					digger
<i>Niphargogammarus intermedius</i>	1	16		x	x	x			euryh.				x		digger

<i>Niphargogammarus quadrimanus</i>	4	260			x				stenoh.	x					digger	
<i>Niphargoides boltovskoyi</i>	96	311			x				?	x					digger	
<i>Niphargoides caspius</i>	20	200			x				stenoh.	x					digger	
<i>Niphargoides corpulentus</i>	1	165			x				euryh.	x			x		digger	
<i>Niphargoides grimmi</i>	10	400			x				stenoh.	x					digger	
<i>Obesogammarus acuminatus</i>	0.2	1					x		euryh.	x	x				digger	
<i>Obesogammarus boeoticus</i>	0.2	1	x	x					stenoh.				x		digger	
<i>Obesogammarus crassus</i>	0.2	197	x	x	x		x		euryh.	x	x	x	x		digger	
<i>Obesogammarus obesus</i>	0.5	15	x	x			x		euryh.	x	x	x	x		digger	
<i>Obesogammarus olivianus</i>	0.5	7			x				euryh.	x					digger	
<i>Obesogammarus platycheir</i>	1	10		x					euryh.	x			x		digger	
<i>Obesogammarus subnudus</i>	3	75		x					?	x			x		digger	
<i>Pandorites podoceroideus</i>	4	480		x	x				euryh.	x					digger	
<i>Paraniphargoides derzhavini</i>	10	90		x	x				?	x					digger	
<i>Paraniphargoides motasi</i>	3	150		x	x				?				x		digger	
<i>Pontogammarus abbreviatus</i>	0.5	25		x	x	x			euryh.	x			x	x	digger	
<i>Pontogammarus aestuarius</i>	1.5	12	x	x	x				euryh.	x	x			x	digger	
<i>Pontogammarus borcae</i>	0	0.1		x					euryh.	x	x			x	digger	
<i>Pontogammarus maeoticus</i>	0	10		x					euryh.	x	x	x	x		digger	
<i>Pontogammarus robustoides</i>	0	198	x	x	x		x		euryh.	x	x	x	x		digger	
<i>Pontogammarus sarsi</i>	0.5	15		x	x	x			euryh.		x	x	x		digger	
<i>Pontogammarus setosus</i>	0	2	x	x	x		x		stenoh.				x	x	digger	
<i>Pontogammarus weidemanni</i>	0	5		x					euryh.	x	x				digger	
<i>Stenogammarus compressus</i>	1	100			x				euryh.	x			x	x	digger	
<i>Stenogammarus compresso-similis</i>	3.5	9	x	x	x	x			euryh.	x				x	digger	
<i>Stenogammarus deminutus</i>	1	120							euryh.	x			x	x	digger	
<i>Stenogammarus macrurus</i>	1	100	x	x	x	x			euryh.	x			x	x	digger	
<i>Stenogammarus micrurus</i>	84	84			x				?	x					digger	
<i>Stenogammarus similis</i>	1	100	x	x	x	x	x		stenoh.	x			x		digger	
<i>Turcogammarus aralensis</i>	0	10	x	x					euryh.	x			x	x	digger	
<i>Turcogammarus spandii</i>	0	0.5	x						stenoh.					x	x	crawler

<i>Turcogammarus turcarum</i>	0	1	x	x					stenoh.					x	crawler
<i>Uroniphargoides spinicaudatus</i>	2	10		x	x				stenoh.		x		x		digger
<i>Wolgagammarus dzjubani</i>	1	8		x					stenoh.			x	x		digger

269 ¹–stony, ²–sandy, ³–clay, ⁴–plant, ⁵–lagoon, ⁶–reservoir/lake, ⁷–river, ⁸–spring

270

271

272 Proposed ecomorphs

273 By integrating morphology and substrate type we aimed to classify the species into putative
 274 ecomorphs. Specifically, we looked for common morphological characteristics among taxa, while
 275 taking into account their similarity in PCA morphospace. We also took into account previous informal
 276 groupings of genera (Barnard and Barnard 1983). Once these groups were identified, their substrate
 277 preference was established by estimating the proportion of species occurring on a particular
 278 substrate. The substrate classification was simplified and divided into four groups: coarse
 279 (corresponding to stones and gravel), fine (corresponding to sand, mud and clay), plant and
 280 symbiotic. We acknowledge that this is a somewhat arbitrary approach. However, more
 281 sophisticated analyses could not be performed given the scarce data at hand. Quantitative data
 282 regarding ecology (substrate or trophic niche) are only limited to a few invasive species. Likewise,
 283 morphology is incompletely known in many species (especially mouthparts). We emphasize that our
 284 goal here was to provide a first exploratory step into understanding the connection between
 285 morphology and ecology.

286

287 We tentatively defined four ecomorphs: clingers, crawlers, diggers and symbionts. Loosely, these
 288 ecomorphs correspond with the currently recognized families and informal groupings of Barnard &
 289 Barnard (1983): crawlers with Gammaridae or “Echinogammarids” + “Dikerogammarids” (*sensu*
 290 Barnard & Barnard, 1983), clingers with Gammaridae or “Gmelinids” (*sensu* Barnard & Barnard,
 291 1983), diggers with Pontogammaridae or “Pontogammarids” + “Compactogammarids” (*sensu*
 292 Barnard & Barnard, 1983), and symbionts with Behningiellidae, Caspicolidae and Iphigeniellidae or
 293 “Cardiophilids” (*sensu* Barnard & Barnard, 1983). Below we describe the morphological and
 294 ecological peculiarities of each ecomorph.

295

296 1) Clinger. Stout body often keeled and/or ornamented with spines and tubercles, antennae are
 297 slender, short to medium length, coxal plates medium to deep, gnathopods weak, and pereopods
 298 short to medium length with pairs 3-4 strongly opposable to pairs 5-7 (Fig. 6). Clingers are
 299 intermediate in morphospace between crawlers and diggers, although there is significant overlap
 300 significantly with the latter group (Fig. 3b). Most species are associated with plants and fine substrate
 301 (Fig. 3b). Around 19% of all species belong to this ecomorph. Taxonomic composition is given in Table
 302 2. Representative genera: *Axelboeckia* and *Gmelina*.

303

304 2) Crawler. Body is slender and generally smooth, antennae are long and slender, coxal plates
 305 shallow, pereopods slender, short to medium, gnathopods generally strong, and uropods long (Fig.
 306 6). It is generally well-defined in morphospace having little overlap with clingers and diggers (Fig. 3b).
 307 Species are mainly associated with fine and coarse substrates (Fig. 3b). Around 26% of species belong
 308 to this ecomorph. Taxonomic composition is given in Table 2. Representative genera:
 309 *Chaetogammarus* and *Dikerogammarus*.

310

311 3) Digger. Stout body and almost exclusively smooth, antennae very short and thick, with 1st article of
 312 antenna 1 often swollen, coxal plates deep, gnathopods generally strong, pereopods medium to long,
 313 with broadened articles often fringed with long and dense setae (Fig. 6). Diggers are very distinct in
 314 morphospace from crawlers and symbionts, but overlap noticeably with clingers (Fig. 3b). Species of

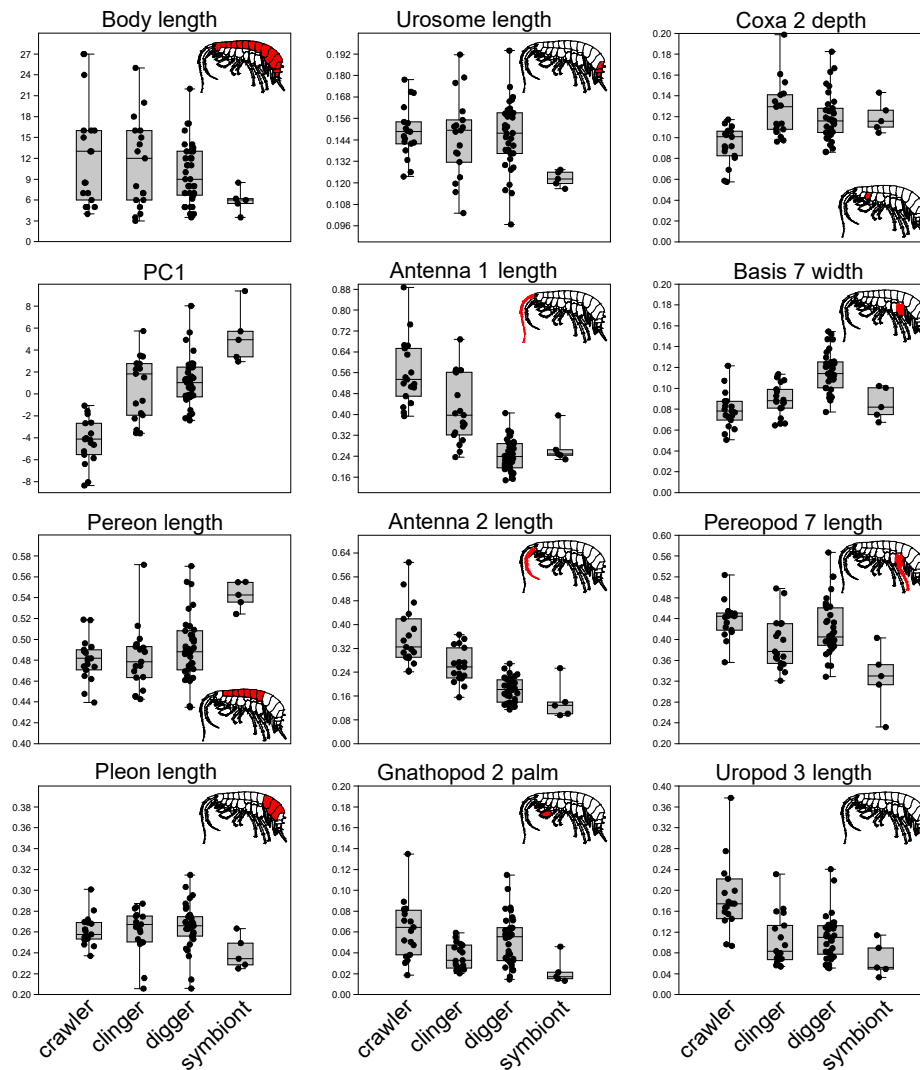
315 this ecomorph predominantly occur on fine substrates and are characterized by a fossorial behavior
316 (Fig. 3b). This appears to be the most common ecomorph since almost half of the Ponto-Caspian
317 species are classified as diggers (49%). Taxonomic composition is given in Table 2. Representative
318 genera: *Pontogammarus* and *Niphargoides*.

319

320 4) Symbiont. Very stout and generally minute bodies, with well-developed coxal plates and pereopod
321 bases, usually characterized by diminished mouthparts (palps of maxilla 2 and maxilliped), pleon,
322 urosome, antennae and pereopods (Fig. 6). The gnathopods can be very specialized (*Caspicola* and
323 *Iphigenella*), or rudimentary (*Behningiella* and *Cardiophilus*). This ecomorph is the most distinct in
324 morphospace, with hardly any overlap (Fig. 3b). Its species are known to live on or inside bivalve
325 mollusks (*Cardiophilus* and *Caspicola*), or commensals with crayfish (*Iphigenella*). This ecomorph is
326 the rarest and accounts for 6 % of all species. Taxonomic composition is given in Table 2.

327 Representative genera: *Cardiophilus* and *Iphigenella*.

328



329

330

331 **Fig. 6** Boxplots comparing selected traits among the four proposed ecomorphs. PC1 refers to the first principal
332 component resulting from the PCA analysis. It mainly describes the gradient from slender bodies with long
333 antennae (negative values) to stout bodies with short antennae (positive values). All traits except body length
334 and PC1 values are presented relative to total body length

335

336 **Discussion**

337 Our study reviewed and quantified for the first time the rich taxonomic, ecological and morphological
338 diversity of Ponto-Caspian amphipods. Although we consider these findings preliminary, our synopsis
339 will serve as a foundation for future eco-evolutionary and systematic studies. Below we discuss the
340 evidence accrued so far that point towards a remarkable, yet unrecognized adaptive radiation.
341 Within each of the following sub-sections we also highlight the gaps in existing knowledge and
342 recommend further research.

343

344 ***Ponto-Caspian gammarid amphipods – an adaptive radiation?***

345 The main prerequisites that define an adaptive radiation are: monophyly, species sympatry,
346 speciation rate increase, and ecomorphological divergence (Schluter 2000; Simões et al. 2016). With
347 respect to Ponto-Caspian amphipods the sympatry criterion is the most readily fulfilled since most of
348 the species co-occur in the Caspian Sea and Lower Volga (Table 1). Furthermore, most species seem
349 to be widespread in the Caspian Sea, occurring in all of its main areas (north, middle and southern)
350 (Pjatakova and Tarasov 1996). A significant number of species are also found in sympatry in the
351 Ponto-Azov region (Cărbăuşu et al. 1955).

352

353 The monophyly condition is supported by recent molecular phylogenies which indicate that several
354 morphologically disparate Ponto-Caspian genera form a well-supported clade (Copilaş-Ciocianu,
355 Borko, et al. 2020; Hou et al. 2014; Hou and Sket 2016; Sket and Hou 2018). Although relatively few
356 taxa have been sequenced so far, it is likely that the remaining species would fall within the same
357 clade. The Ponto-Caspian amphipod radiation also satisfies the requirement of speciation rate
358 increase since it experienced a higher diversification rate in comparison to its sister clades (Hou et al.
359 2014).

360

361 We consider that our current study fulfills, at least partially, the criterion of ecomorphological
362 divergence, which is perhaps the most relevant to the adaptive radiation model. We highlight
363 significant ecological and morphological disparity within the Ponto-Caspian amphipod radiation.
364 Along an order of magnitude body-size gradient, morphology ranges from minute (several
365 millimeters), stout-bodied symbiotic species with attenuated appendages, to large and slender
366 (several centimeters), stocky and setose, or heavily armored species. Likewise, ecological diversity is
367 also remarkable, with species being encountered along a >500 m depth gradient on virtually all types
368 of substrates and water bodies (mountain springs to deep sea). By integrating morphology and
369 ecology, we propose a provisional classification into four main ecomorphs: clingers, crawlers, diggers
370 and symbionts. Although this classification is only tentative, we consider it a necessary first step
371 towards understanding the evolution of Ponto-Caspian amphipods. We highlight that these
372 ecomorphs have potential analogues in distantly related marine or Lake Baikal taxa that occupy
373 similar habitats (see Morphological evolution section below), further strengthening the environment-
374 phenotype association.

375

376 Overall, it appears that Ponto-Caspian amphipods fulfill, at least to some extent, the main
377 prerequisites of the adaptive radiation model. However, our findings provide only a first glimpse.
378 Extensive further research is needed to corroborate the patterns highlighted herein. Specifically, the
379 criteria of monophyly and speciation rate increase have to be tested on larger multilocus phylogenies
380 with a greater taxonomic coverage. The morphology-environment association needs to be refined
381 with newly collected field data. Specifically, fine-scale morphometry of functionally relevant traits
382 coupled with trophic niche (gut content DNA metabarcoding and stable isotopes) and ecology
383 (depth, substrate and salinity) in a phylogenetic context will provide a more comprehensive
384 ecomorphological understanding. Furthermore, it is important to test whether these ecomorphs
385 have a common ancestor or evolved several times independently (Trontelj et al. 2012). It is likely that
386 upon more detailed investigation they could be split into more specialized forms. Comparative

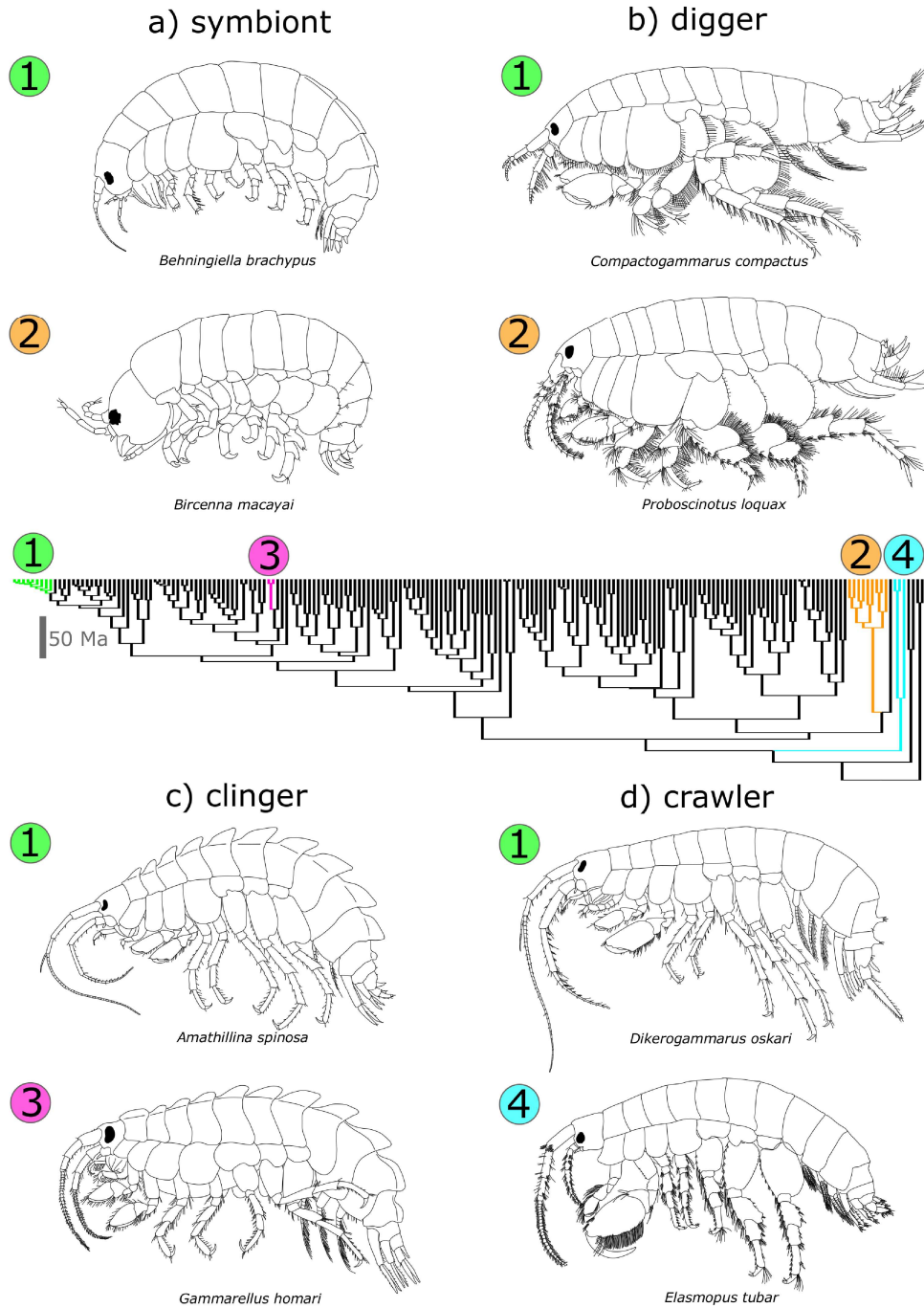
387 transcriptomics and genomics could provide important insight into adaptation and selection at the
388 molecular level. A well-sampled time-calibrated molecular phylogeny could also prove invaluable for
389 understanding the historical circumstances that promote the evolution of invasive species.

390

391 ***Morphological evolution***

392 Recent molecular phylogenies revealed that the morphologically diverse Ponto-Caspian amphipod
393 radiation is nested within the genus *Echinogammarus* (Hou and Sket 2016; Sket and Hou 2018),
394 which is characterized by morphological conservatism (Pinkster 1993). This is in good agreement with
395 previous hypotheses that postulated a close relationship between these two groups (Barnard and
396 Barnard 1983). A similar pattern is also encountered in the two highly diverse Baikal amphipod
397 radiations which are classified into several families (Hou and Sket 2016; Lowry and Myers 2013), yet
398 they are both nested within the genus *Gammarus* (Hou et al. 2011, 2014; Macdonald et al. 2005;
399 Naumenko et al. 2017), notorious for its low morphological diversity, morphological crypsis (Copilaş-
400 Ciocianu and Petrusek 2015; Katouzian et al. 2016; Mamos et al. 2014) and generalist ecology
401 (MacNeil et al. 1997; Piscart et al. 2011). And yet again the same pattern appears in the distantly
402 related American genus *Hyalella* where morphologically conserved riverine species (Witt et al. 2006)
403 colonized the ancient Titicaca Lake multiple times, giving rise to a remarkable array of forms
404 (Adamowicz et al. 2018; González and Coleman 2002; Jurado-Rivera et al. 2020). These compelling
405 patterns indicate that species living in ephemeral, highly fluctuating and ecologically limited
406 environments (springs, streams, rivers and shallow lakes/ponds) are under stabilizing selection for
407 maintaining a generalist life-style and a conserved, non-specialized morphology (Wellborn and
408 Broughton 2008). On the other hand, species inhabiting stable ancient lakes with broad niche space
409 are probably under disruptive selective pressures which in turn promote specialization and ecological
410 speciation (Seehausen 2015; Wellborn and Langerhans 2015). Thus, it would seem that the ecological
411 transition from ephemeral habitats to long-lived ancient lakes promotes adaptive radiations in some
412 freshwater amphipod groups. These intriguing patterns are worth pursuing further and could shed
413 more light on the role of ecological opportunity in driving adaptive radiations.

414



415
416
417
418
419
420
421
422
423
424
425

Fig. 7 Putative examples of ecomorphological convergence of Ponto-Caspian and distantly related oceanic taxa. Ponto-Caspian species are shown with green. a) Symbiotic ecomorph adapted to piercing various organic substrates (redrawn from Derzhavin (1948) and Loerz et al. (2010)), b) digger ecomorph adapted for digging and burrowing in fine substrates (redrawn from Sars (1895) and Barnard (1967)), c) clinger ecomorph adapted to cling on algal and vegetal substrates (redrawn from Sars (1896)), and d) crawler ecomorph adapted to a generalist life-style, usually hiding in coarse stony substrates (redrawn from (Sars (1896) and Garcia-Madrigal (2010))). The phylogenetic tree is a time-calibrated molecular phylogeny of Amphipoda modified after Copilaş-Ciocianu et al. (2020)

426

427 We propose that the ecological and morphological diversity of Ponto-Caspian gammarids can be
428 distilled into four ecomorphs. Remarkably, all of them apparently have analogues in distantly related
429 lineages inhabiting oceanic waters or other ancient lakes (Figs. 7-8). The Ponto-Caspian symbiotic
430 ecomorph is the most specialized and morphologically distinct due to its reduced mouthparts,
431 antennae, pereopods and urosome, presumably due to a semi-parasitic life-style. We highlight a
432 striking resemblance between the Ponto-Caspian genus *Behningiella* and the oceanic algae-boring
433 genus *Bircenna* Chilton, 1884 (Fig. 7a). Both exhibit typical features for substrate boring such as a
434 large head with protruding mandibles adapted to cutting into tough material, and extremely short
435 antennae and pereopods due to living in narrow self-constructed tunnels (Mejaes et al. 2015). Within
436 the Baikal Lake Acanthogammaride radiation, the symbiotic ecomorph is probably represented by
437 the parasitic genus *Pachyschysis* (Naumenko et al. 2017; Takhteev 2019).

438

439 The fossorial ecomorph seems to be the most common among Ponto-Caspian amphipods. These
440 species are generally adapted for digging in fine substrates and have stout, strong bodies with very
441 short yet powerful and thick antennae, and broadened pereopods usually fringed with dense rows of
442 setae. This ecomorph is widely encountered among amphipods in general, albeit under slightly
443 different iterations (Bousfield 1970). Morphologically, most fossorial amphipods are classified within
444 the superfamily Haustorioidea (Lowry and Myers 2017). However, molecular phylogenies indicate
445 that the fossorial body-type evolved multiple times independently (Copilaş-Ciocianu, Borko, et al.
446 2020; Hancock et al. 2020). A noticeable resemblance can be observed between the Ponto-Caspian
447 genus *Compactogammarus* and the hyaloidean *Probosciniotus* Barnard, 1967 (Fig. 7b). Additionally, in
448 Lake Baikal this ecomorph is possibly represented by the Micruropodidae radiation, comprising
449 fossorial species living on fine substrate (Naumenko et al. 2017; Takhteev 2019).

450

451 The clinger ecomorph characterizes species with elaborate body armature/ornamentation and
452 preference for living (plant) substrate. These species often have elongated and curved dactyls for
453 improved grasping of the substrate. Given the exposed nature of their life-style, the armature might
454 serve as protection against predators (Bollache et al. 2006; Copilaş-Ciocianu, Borza, et al. 2020) or, in
455 combination with variegated coloration (as is often the case with armored taxa), may act as
456 camouflage by disrupting the body contour (d'Udekem d'Acoz and Verheye 2017). We point out the
457 high similarity among the Ponto-Caspian genus *Amathillina* and the oceanic algae-clinging
458 *Gammarellus* Herbst, 1793 (Fig. 7c). Although the Ponto-Caspian clingers are diverse in
459 ornamentation and armature, some striking resemblance can be observed with Baikal Lake taxa. For
460 example *Amathillina* and *Eucarinogammarus* (Baikal), *Axelboeckia* and *Acanthogammarus* (Baikal),
461 and *Kuzmelina* and *Propachygammarus* (Baikal) (Naumenko et al. 2017; Takhteev 2019).

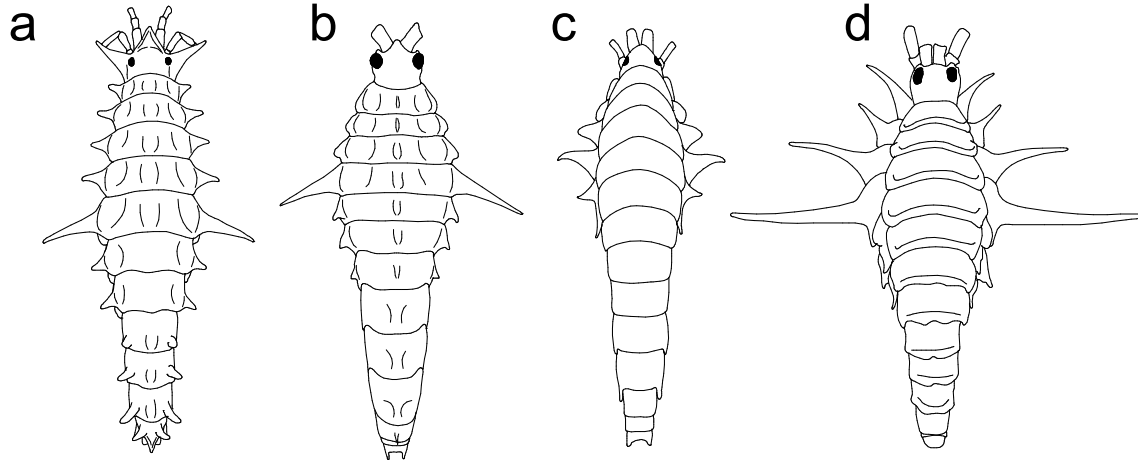
462

463 The crawler ecomorph is the second-most encountered in Ponto-Caspian amphipods, characterizing
464 species living on coarse or fine substrate, often in shallow water. Typically, these taxa are strongly
465 sexually dimorphic, males possessing very large second gnathopods, relatively long antennae and
466 slender bodies with shallow coxal plates. Morphologically, this morph is probably the most
467 plesiomorphic, being widespread among the amphipod evolutionary tree, especially in some basal
468 branches (Copilaş-Ciocianu, Borko, et al. 2020; Lowry and Myers 2017) as well as in the oldest known
469 fossils (Jarzembowski et al. 2020). As an example, we emphasize the similarity among the Ponto-
470 Caspian genus *Dikerogammarus* and the widespread littoral genus *Elasmopus* Costa, 1853 (Fig.
471 7d). The Baikalian analogues of this ecomorph could be envisioned in *Eulimnogammarus* and
472 *Corophiomorphus* (Naumenko et al. 2017; Takhteev 2019).

473

474 Body armature is extremely diverse in amphipods, with similar phenotypes having evolved
475 independently multiple times (Copilaş-Ciocianu, Borko, et al. 2020; Lowry and Myers 2017;
476 Naumenko et al. 2017). We highlight a remarkably convergent evolution of body armature in some
477 ancient lake radiations where strong lateral spines appear on the pereonites, the longest one being

478 located on the 4th or 5th segment (Fig. 8). In some cases the spine is an outgrowth of the tergum,
479 while in others an outgrowth of the coxal plate. These analogous convergent structures point
480 towards a strong selective pressure. Most likely these spines function as a mechanism for deterring
481 ingestion by predatory fish (Bollache et al. 2006; Copilaş-Ciocianu, Borza, et al. 2020), although the
482 exact mechanical interactions are unknown.
483



484

485

486

487 **Fig. 8** Examples of evolutionary convergent patterns in body armature of species inhabiting different ancient

488

489

490

491

492

Spatio-temporal origin

493

494

495

496

497

498

499

500

501

502

503

504

505

506

507

508

509

510

511

512

513

514

515

The phylogenetic position of Ponto-Caspian amphipods within the Atlanto-Mediterranean *Echinogammarus* clade (*sensu* Hou et al., 2014; Sket & Hou, 2018) indicates that this radiation likely has a Mediterranean origin. Specifically, its sister clade is represented by the genus *Dinarogammarus*, which is endemic to freshwaters of the Western Balkans (Sket and Hou 2018). Regarding the temporal time-frame, several recent studies proposed a Middle Miocene origin (ca.12-14 Ma) (Copilaş-Ciocianu, Borko, et al. 2020; Hou and Sket 2016), coeval with the final closure of the Paratethys, which caused a switch from marine to brackish conditions and promoted the evolution of endemic faunas after initial mass extinctions (Popov et al. 2004; Rögl 1999). This time frame is also supported by Late Miocene (ca. 9-10 Ma) Caucasian fossil taxa (two genera and five species) that have clear affinities with extant Ponto-Caspian genera *Axelboeckia*, *Gmelina*, *Kuzmelina* and *Yogmelina* (Derzhavin 1927, 1941). Alternatively, an earlier study suggested an origin dating back to the Eocene (30-40 Ma) (Hou et al. 2014). However, this analysis was based on biogeographical calibration of the molecular clock rather than fossils, thus possibly resulting in biased inferences (Hou et al. 2015). Furthermore, a Late Eocene origin does not correspond with an isolation of the Paratethys realm from the world ocean (Popov et al. 2004). As such, we consider that a middle Miocene origin is more plausible considering the data at hand.

A densely sampled, multilocus and time-calibrated phylogeny will be of critical importance in understanding the historical biogeography and evolution of Ponto-Caspian gammarids. Furthermore, such a phylogeny could complement geological studies regarding the palaeogeographic history of the Paratethyan region, as seen with other freshwater gammarids (Copilaş-Ciocianu et al. 2019; Copilaş-Ciocianu and Petrussek 2017; Hou et al. 2011; Mamos et al. 2016). It could provide additional time constraints on some important palaeogeographic events such as the final Paratethys closure, the

516 isolation of the Pannonian, Pontic and Caspian basins, the emergence of the Caucasus, as well as the
517 recurrent episodic connections of the Pontic and Caspian basins during the Plio-Pleistocene.

518

519 ***Taxonomic and systematic remarks***

520 The Ponto-Caspian gammaroid amphipods as defined in this study are formally split into 5 families:
521 Behningiellidae, Caspicolidae, Gammaridae, Iphigeniellidae and Pontogammaridae. However,
522 molecular research has revealed that Pontogammaridae is nested within Gammaridae, and also
523 harbors the gammarid genus *Dikerogammarus* (Copilaş-Ciocianu, Borko, et al. 2020; Hou et al. 2014).
524 Members of this family correspond to the digger ecomorph, which probably evolved on more than
525 one occasion. Moreover, the Ponto-Caspian “Gammaridae” form a paraphyletic grade at the base of
526 Pontogammaridae (Sket and Hou 2018). A taxonomically more inclusive morphological and molecular
527 study will clarify this issue, but most likely will not recover Pontogammaridae as monophyletic.
528 However, for the sake of stability we do not propose any taxonomic changes until this issue is firmly
529 resolved.

530

531 The remaining families Behningiellidae, Caspicolidae and Iphigeniellidae are poorly known and have
532 not yet been sequenced. Behningiellidae and Iphigeniellidae have been classified into Gammaroidea
533 based on a morphological cladistic analysis (Lowry and Myers 2013). However, the monotypic
534 Caspicolidae is currently not recognized as part of Gammaroidea, but as a distinct superfamily
535 (Caspicoloidea) within the infraorder Talitrida (Lowry and Myers 2013). This classification is
536 erroneous because the authors mistakenly considered that the antenna I lacks an accessory flagellum
537 (a defining character state of the infraorder Talitrida). Derzhavin’s (1944) original description clearly
538 indicates the presence of the accessory flagellum, although it is reduced and unarticulate. Another
539 issue with assigning Caspicolidae to Talitrida is the presence of a well-developed mandibular palp,
540 whereas an absent/vestigial palp is another defining character state of the Talitrida (Lowry and
541 Myers 2013). Behningiellidae, Caspicolidae and Iphigeniellidae belong to the symbiotic ecomorph and
542 represent highly specialized taxa which are difficult to classify using external morphology alone. It is
543 very likely that these small families are nothing but highly derived Ponto-Caspian gammarids,
544 possibly related to the various genera of the gmelinid facies (*Gmelina*, *Kuzmelina* and *Yogmelina*)
545 (Barnard and Barnard 1983; Bousfield 1977; Derzhavin 1944). Thus, the systematic position of these
546 families will be clarified only with additional morphological and molecular study.

547

548 We argue that most, if not all Ponto-Caspian amphipod species are in need of thorough, modern
549 revision using morphology, multilocus DNA sequences and ecology. Many species are only partially
550 illustrated and intraspecific variability has been studied in only a handful of taxa (Cărăușu 1936;
551 Nahavandi et al. 2013). Moreover, cryptic lineages of potential specific status have been recently
552 discovered (Jażdżewska et al. 2020). As such, a first step towards a modern taxonomic revision could
553 be the generation of a well-sampled DNA barcode reference library.

554

555 Lastly, the Late-Miocene (Upper Sarmatian, ca. 9 Ma) fossil genera *Andrussovia* and *Praegmelina*
556 have long been considered ancestral to extant Ponto-Caspian genera such as *Gmelina* and
557 *Amathillina*, albeit without a formal analysis (Barnard and Barnard 1983; Derzhavin 1927, 1941). The
558 fossils were discovered in calcareous clay deposits at the foothills of the Caucasus near Grozny,
559 Solenaya balka (Chechnya, Russian Federation) and from Eldar Oyugu Ridge (Azerbaijan). We agree
560 that there are rather clear affinities with extant Ponto-Caspian species in general, mainly in the
561 combination of the following traits: shape of the basis of pereopod 7, ornamentation and armature,
562 short and thick antennae, and deep coxal plates. Some traits are considered plesiomorphic, such as
563 the lack of a postero-ventral lobe on the basis of pereopod 7, and the long endopod of uropod 3. A
564 cladistic analysis is necessary to confidently assess evolutionary relationships with extant taxa. Until
565 then, these species should be conservatively treated as stem Ponto-Caspian amphipods (Copilaş-
566 Ciocianu, Borko, et al. 2020).

567

568 Two more Miocene fossil taxa have been reported from the Caucasus that have less clear affinity
569 with extant Ponto-Caspian taxa. These are *Gammarus praecyrius*, Derzhavin, 1941 and *Hellenis*
570 *saltatorius*, Petunnikoff, 1914. The former is indistinguishable from a typical *Gammarus* and it is thus
571 not considered a Ponto-Caspian taxon. The affinities of the latter taxon are less straightforward to
572 interpret due to its high degree of morphological specialization (very short antennae, large raptorial
573 gnathopods and unusually long pereopods). Such a combination of traits is not present in the extant
574 Ponto-Caspian fauna. Furthermore, Petunnikoff's illustrations are also not detailed enough to draw a
575 conclusion. At the moment we consider that it is possible that *H. saltatorius* could be related to
576 Ponto-Caspian amphipods but further detailed studies are needed.

577

578

579 **Conclusion**

580 The Ponto-Caspian gammarid radiation fulfills, at least partially, the most important criteria of an
581 adaptive radiation: 1) apparent monophyly, 2) sympatric occurrence within a constrained area, 3)
582 accelerated diversification and 4) ecomorphological disparity. Nevertheless, these literature-based
583 results are only preliminary and a lot of in depth eco-evolutionary study is further needed. Moreover,
584 most species need a modern taxonomic revision within an evolutionary context. Nevertheless, we
585 consider that Ponto-Caspian amphipods could be an excellent future model for the study of adaptive
586 radiation, origin of invasive species, and could even help illuminate the region's dynamic
587 palaeogeographic history.

588

589 **References**

- 590 Adamowicz, S. J., Marinone, M. C., Menu-Marque, S., Martin, J. W., Allen, D. C., Pyle, M. N., et al.
591 (2018). The Hyalella (Crustacea: Amphipoda) species cloud of the ancient Lake Titicaca
592 originated from multiple colonizations. *Molecular Phylogenetics and Evolution*, 125, 232–242.
593 doi:10.1016/j.ympev.2018.03.004
- 594 Adrian-Kalchhauser, I., Blomberg, A., Larsson, T., Musilova, Z., Peart, C. R., Pippel, M., et al. (2020).
595 The round goby genome provides insights into mechanisms that may facilitate biological
596 invasions. *BMC Biology*, 18(1), 1–33. doi:10.1186/s12915-019-0731-8
- 597 Arbačiauskas, K., Lesutiene, J., & Gasiunaite, Z. R. (2013). Feeding strategies and elemental
598 composition in Ponto-Caspian peracaridans from contrasting environments: Can stoichiometric
599 plasticity promote invasion success? *Freshwater Biology*, 58(5), 1052–1068.
600 doi:10.1111/fwb.12108
- 601 Audzijonyte, A., Baltrunaite, L., Väinölä, R., & Arbačiauskas, K. (2015). Migration and isolation during
602 the turbulent Ponto-Caspian Pleistocene create high diversity in the crustacean *Paramysis*
603 *lacustris*. *Molecular Ecology*, 24(17), 4537–4555. doi:10.1111/mec.13333
- 604 Barnard, J. L. (1958). Index to the families, genera and species of the gammaridean Amphipoda
605 (Crustacea). *Occasional Papers of the Allan Hancock Foundation*, 19, 1–145.
- 606 Barnard, J. L. (1967). New and old dogielinotid marine Amphipoda. *Crustaceana*, 13, 281–291.
- 607 Barnard, J. L., & Barnard, C. M. (1983). *Freshwater Amphipoda of the World*. Mt. Vernon, Virginia:
608 Hayfield Associates.
- 609 Birstein, J. A., & Romanova, N. N. (1968). Amphipoda. In J. A. Birstein, L. G. Vinogradova, & N. N.
610 Kondakova (Eds.), *Atlas bespozvonochnykh Kaspiiskogo morya* (pp. 241–289). Moscow:
611 Pishhevaya Promyshlennost Publ.
- 612 Birstein, J. A., Vinogradov, L. G., Kondakov, N. N., Kun, M. . ., Astakhova, T. V., & Romanova, N. N.
613 (1968). *Atlas bespozvonochnykh Kaspiiskogo morya (Atlas of Invertebrates of the Caspian Sea)*.
614 Moscow: Pishhevaya Promyshlennost Publ.
- 615 Bollache, L. Ī., Kaldonski, N., Troussard, J. P., Lagrue, C., & Rigaud, T. (2006). Spines and behaviour as
616 defences against fish predators in an invasive freshwater amphipod. *Animal Behaviour*, 72(3),
617 627–633. doi:10.1016/j.anbehav.2005.11.020
- 618 Bousfield, E. L. (1970). Adaptive Radiation in Sand-burrowing Amphipod Crustaceans. *Chesapeake*

- 619 *Science*, 11(3), 143–154.
- 620 Bousfield, E. L. (1977). A New Look at the Systematics of Gammaroidean Amphipods of the World.
- 621 *Crustaceana*, 4(4), 282–316. doi:10.2307/25027471
- 622 Cărauşu, S. (1936). Etude sur le *Pontogammarus maeoticus* (Sow.) Mart. *Annales Scientifique de*
- 623 *l'Universite de Jassy*, 13(1–4), 133–156.
- 624 Cărauşu, S. (1943). *Amphipodes de Roumanie I. Gammarides de type Caspian*. Bucharest: Institutul de
- 625 Cercetari Piscicole al Romaniei.
- 626 Cărauşu, S., Dobreanu, E., & Manolache, C. (1955). *Fauna Republicii Populare Romîne. Crustacea.*
- 627 *Amphipoda Forme Salmastre și de Apă Dulce*. Bucharest: Editura Academiei RPR.
- 628 Chertoprud, E. S., Sokolova, A. M., & Garlitska, L. A. (2018). Harpacticoida (Copepoda) of the Caspian
- 629 Sea: Faunistics, ecology and biogeography. *Journal of Experimental Marine Biology and Ecology*,
- 630 502, 63–70. doi:10.1016/j.jembe.2017.03.011
- 631 Chevreux, E. (1908). Études sur la faune du Turkestan basées sur les matériaux recueillis par D.D.
- 632 Pedaschenko (1904–1906). In *II. Crustacés Amphipodes* (pp. 91–110).
- 633 Copilaş-Ciocianu, D., Borko, Š., & Fišer, C. (2020). The late blooming amphipods: Global change
- 634 promoted post-Jurassic ecological radiation despite Palaeozoic origin. *Molecular Phylogenetics*
- 635 *and Evolution*, 143(October 2019), 106664. doi:10.1016/j.ympev.2019.106664
- 636 Copilaş-Ciocianu, D., Borza, P., & Petrusek, A. (2020). Extensive variation in the morphological anti-
- 637 predator defense mechanism of *Gammarus roeselii* Gervais, 1835 (Crustacea:Amphipoda).
- 638 *Freshwater Science*, 39(1), 47–55. doi:10.1086/707259
- 639 Copilaş-Ciocianu, D., & Petrusek, A. (2015). The southwestern Carpathians as an ancient centre of
- 640 diversity of freshwater gammarid amphipods: Insights from the *Gammarus fossarum* species
- 641 complex. *Molecular Ecology*, 24(15), 3980–3992. doi:10.1111/mec.13286
- 642 Copilaş-Ciocianu, D., & Petrusek, A. (2017). Phylogeography of a freshwater crustacean species
- 643 complex reflects a long-gone archipelago. *Journal of Biogeography*, 44, 421–432.
- 644 doi:10.1111/jbi.12853
- 645 Copilaş-Ciocianu, D., Sidorov, D. A., & Gontcharov, A. A. (2019). Adrift across tectonic plates:
- 646 molecular phylogenetics supports the ancient Laurasian origin of old limnic crangonyctid
- 647 amphipods. *Organisms Diversity & Evolution*, 19, 191–207. doi:10.1007/s13127-019-00401-7
- 648 Cristescu, M. E. A., & Hebert, P. D. N. (2005). The “Crustacean Seas” — an evolutionary perspective
- 649 on the Ponto-Caspian peracarids. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(3),
- 650 505–517. doi:10.1139/f04-210
- 651 Cristescu, M. E. A., Witt, J. D. S., Grigorovich, I. A., Hebert, P. D. N., & MacIsaac, H. J. (2004). Dispersal
- 652 of the Ponto-Caspian amphipod *Echinogammarus ischnus*: invasion waves from the Pleistocene
- 653 to the present. *Heredity*, 92(3), 197–203. doi:10.1038/sj.hdy.6800395
- 654 Cristescu, M. E., Adamowicz, S. J., Vaillant, J. J., & Haffner, D. G. (2010). Ancient lakes revisited: From
- 655 the ecology to the genetics of speciation. *Molecular Ecology*, 19(22), 4837–4851.
- 656 doi:10.1111/j.1365-294X.2010.04832.x
- 657 Cuthbert, R. N., Kotronaki, S. G., Dick, J. T. A., & Briski, E. (2020). Salinity tolerance and geographical
- 658 origin predict global alien amphipod invasions. *Biology Letters*, 16(9), 2–7.
- 659 doi:10.1098/rsbl.2020.0354
- 660 d’Udekem d’Acoz, C., & Verheyen, M. L. (2017). Epimeria of the Southern Ocean with notes on their
- 661 relatives (Crustacea, Amphipoda, Eusiroidea). *European Journal of Taxonomy*, 359, 1–553.
- 662 doi:10.5852/ejt.2017.359
- 663 Daneliya, M. E., Kamaltynov, R. M., & Väinölä, R. (2011). Phylogeography and systematics of
- 664 *Acanthogammarus* s. str., giant amphipod crustaceans from Lake Baikal. *Zoologica Scripta*,
- 665 40(6), 623–637. doi:10.1111/j.1463-6409.2011.00490.x
- 666 Derzhavin, A. N. (1927). Notes on the Upper Sarmatian Amphipods of the Ponto-Caspian region.
- 667 *Bulletin de la Societe des Naturalistes de Moscou*, 2, 183–196.
- 668 Derzhavin, A. N. (1941). Iskolaemye bokoplavii Eldara. *Izvestiya Azerbaidzhanskogo Filiala Akademii*
- 669 *nauk SSSR*, (2), 65–69.
- 670 Derzhavin, A. N. (1944). A new family Caspiellidae from the Caspian Sea. *Bulletin of the Azerbaijan*

- 671 *Filiation of the Academy of Sciences of the USSR*, 8, 20–24.
- 672 Derzhavin, A. N. (1948). Novye formy gammarid iz Kaspiiskogo Morya. In *Pamiaty akademika Sergeia*
673 *Aleksandrovicha Zernova* (pp. 280–286). Moscow: USSR Academy of Sciences Publishing House.
- 674 Dumont, H. (1995). Ecocide in the Caspian sea. *Nature*, 377(6551), 673–674. doi:10.1038/377673a0
- 675 Fišer, C., Trontelj, P., Luštrik, R., & Sket, B. (2009). Toward a unified taxonomy of *Niphargus*
676 (Crustacea: Amphipoda): a review of morphological variability. *Zootaxa*, 2061, 1–22.
- 677 Garcia-Madrugal, M. S. (2010). Littoral Maeridae and Melitidae (Amphipoda: Gammaridea) from the
678 Gulf of Tehuantepec, Mexico. *Zootaxa*, 2623, 1–51.
- 679 Gogaladze, A., Raes, N., Biesmeijer, J. C., Ionescu, C., Pavel, A. B., Son, M. O., et al. (2020). Social
680 network analysis and the implications for Pontocaspian biodiversity conservation in Romania
681 and Ukraine: A comparative study. *PLoS ONE*, 15(10 October), 1–20.
682 doi:10.1371/journal.pone.0221833
- 683 González, E. R., & Coleman, C. O. (2002). *Hyaella armata* (Crustacea, Amphipoda, Hyaellidae) and
684 the description of a related new species from Lake Titicaca. *Organisms Diversity and Evolution*,
685 2(3), 271–273. doi:10.1078/1439-6092-00047
- 686 Grabowski, M., Bacela, K., & Konopacka, A. (2007). How to be an invasive gammarid (Amphipoda:
687 Gammaroidea) - Comparison of life history traits. *Hydrobiologia*, 590(1), 75–84.
688 doi:10.1007/s10750-007-0759-6
- 689 Hancock, Z. B., Ogawa, H., Light, J. E., & Wicksten, M. K. (2020). Origin and evolution of the
690 Haustoriidae (Amphipoda): A eulogy for the Haustoriidira. *bioRxiv*.
691 doi:10.1101/2020.10.24.353664
- 692 Ho, S. Y. W., Tong, K. J., Foster, C. S. P., Ritchie, A. M., Lo, N., & Crisp, M. D. (2015). Biogeographic
693 calibrations for the molecular clock. *Biology Letters*, 11(9). doi:10.1098/rsbl.2015.0194
- 694 Horton, T., Lowry, J., De Broyer, C., Bellan-Santini, D., Coleman, C. O., Corbari, L., Costello, M. J.,
695 Daneliya, M., et al. (2020). World Amphipoda Database. Accessed at
696 <http://www.marinespecies.org/amphipoda> on 2020-11-10. doi:10.14284/368.
697 <http://www.marinespecies.org/amphipoda>. Accessed 29 March 2019
- 698 Hou, Z., & Sket, B. (2016). A review of Gammaridae (Crustacea: Amphipoda): The family extent, its
699 evolutionary history, and taxonomic redefinition of genera. *Zoological Journal of the Linnean*
700 *Society*, 176(2), 323–348. doi:10.1111/zoj.12318
- 701 Hou, Z., Sket, B., Fišer, C., & Li, S. (2011). Eocene habitat shift from saline to freshwater promoted
702 Tethyan amphipod diversification. *Proceedings of the National Academy of Sciences of the*
703 *United States of America*, 108(35), 14533–14538. doi:10.1073/pnas.1104636108
- 704 Hou, Z., Sket, B., & Li, S. (2014). Phylogenetic analyses of Gammaridae crustacean reveal different
705 diversification patterns among sister lineages in the Tethyan region. *Cladistics*, 30(4), 352–365.
706 doi:10.1111/cla.12055
- 707 Jarzembowski, E. A., Chény, C., Fang, Y., & Wang, B. (2020). First Mesozoic amphipod crustacean
708 from the Lower Cretaceous of SE England. *Cretaceous Research*, 112, 104429.
709 doi:10.1016/j.cretres.2020.104429
- 710 Jażdżewska, A. M., Rewicz, T., Mamos, T., Wattier, R., Baćela-Spychalska, K., & Grabowski, M. (2020).
711 Cryptic diversity and mtDNA phylogeography of the invasive demon shrimp, *Dikerogammarus*
712 *haemobaphes* (Eichwald, 1841), in Europe. *NeoBiota*, 57, 53–86.
713 doi:10.3897/neobiota.57.46699
- 714 Jurado-Rivera, J. A., Zapelloni, F., Pons, J., Juan, C., & Jaume, D. (2020). Morphological and molecular
715 species boundaries in the *Hyaella* species flock of Lake Titicaca (Crustacea: Amphipoda).
716 *Contributions to Zoology*, 89(4), 353–372. doi:10.1163/18759866-bja10004
- 717 Karaman, G. S., & Pinkster, S. (1977). Freshwater *Gammarus* species from Europe, North Africa and
718 adjacent regions of Asia (Crustacea-Amphipoda). Part I *Gammarus pulex*-group and related
719 species. *Bijdragen Tot De Dierkunde*, 47, 1–97.
- 720 Katouzian, A.-R., Sari, A., Macher, J. N., Weiss, M., Saboori, A., Leese, F., & Weigand, A. M. (2016).
721 Drastic underestimation of amphipod biodiversity in the endangered Irano-Anatolian and
722 Caucasus biodiversity hotspots. *Scientific Reports*, 6(1), 22507. doi:10.1038/srep22507

- 723 Krijgsman, W., Tesakov, A., Yanina, T., Lazarev, S., Danukalova, G., Van Baak, C. G. C., et al. (2019).
724 Quaternary time scales for the Pontocaspian domain: Interbasinal connectivity and faunal
725 evolution. *Earth-Science Reviews*, 188(October 2018), 1–40.
726 doi:10.1016/j.earscirev.2018.10.013
- 727 Lattuada, M., Albrecht, C., & Wilke, T. (2019). Differential impact of anthropogenic pressures on
728 Caspian Sea ecoregions. *Marine Pollution Bulletin*, 142, 274–281.
729 doi:10.1016/j.marpolbul.2019.03.046
- 730 Loerz, A. N., Kilgallen, N. M., & Thiel, M. (2010). Algal-dwelling Eophliantidae (Amphipoda):
731 description of a new species and key to the world species, with notes on their biogeography.
732 *Journal of the Marine Biological Association of the United Kingdom*, 90(5), 1055–1063.
- 733 Lowry, J. K., & Myers, A. A. (2013). A Phylogeny and Classification of the Senticaudata subord. nov.
734 (Crustacea: Amphipoda). *Zootaxa*, 3610(1), 1–80. doi:10.11646/zootaxa.3610.1.1
- 735 Lowry, J. K., & Myers, A. A. (2017). A Phylogeny and Classification of the Amphipoda with the
736 establishment of the new order Ingolfiellida (Crustacea: Peracarida). *Zootaxa*, 4265(1), 1–89.
737 doi:10.11646/zootaxa.4265.1.1
- 738 Macdonald, K. S., Yampolsky, L., & Duffy, J. E. (2005). Molecular and morphological evolution of the
739 amphipod radiation of Lake Baikal. *Molecular Phylogenetics and Evolution*, 35(2), 323–343.
740 doi:10.1016/j.ympev.2005.01.013
- 741 MacNeil, C., Dick, J., & Elwood, R. (1997). The trophic ecology of freshwater *Gammarus* spp.
742 (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group
743 concept. *Biological Reviews*, 72, 349–364. <https://www.cambridge.org/core/journals/biological-reviews/article/trophic-ecology-of-freshwater-gammarus-spp-crustacea-amphipoda-problems-and-perspectives-concerning-the-functional-feeding-group-concept/20499173A4878B0DF607A797CBE32671>
- 744
745
746
- 747 Mamos, T., Wattier, R., Burzynski, A., & Grabowski, M. (2016). The legacy of a vanished sea: A high
748 level of diversification within a European freshwater amphipod species complex driven by 15
749 My of Paratethys regression. *Molecular Ecology*, 25(3), 795–810. doi:10.1111/mec.13499
- 750 Mamos, T., Wattier, R., Majda, A., Sket, B., & Grabowski, M. (2014). Morphological vs. molecular
751 delineation of taxa across montane regions in Europe: The case study of *Gammarus balcanicus*
752 Schaferna, (Crustacea: Amphipoda). *Journal of Zoological Systematics and Evolutionary*
753 *Research*, 52(3), 237–248. doi:10.1111/jzs.12062
- 754 Martens, K. (1997). Speciation in ancient lakes. *Trends in Ecology and Evolution*, 12(5), 177–182.
755 doi:10.1016/S0169-5347(97)01039-2
- 756 Martens, K., & Schön, I. (1999). Crustacean Biodiversity in Ancient Lakes : A Review. *Crustaceana*,
757 72(8), 899–910.
- 758 Martynov, A. V. (1930). Fauna Amphipoda Teletskogo ozera I ee proiskhozhdenie. *Izv. Gosud. Gidrob.*
759 *Inst.*, 29, 95–128.
- 760 Mejaes, A. B., Poore, A. G. B., & Thiel, M. (2015). Crustaceans inhabiting domiciles excavated from
761 macrophytes and stone. In *The Natural History of the Crustacea, Volume 2. Lifestyles and*
762 *Feeding Biology* (pp. 118–144). New York: Oxford University Press.
- 763 Mordukhai-Boltovskoi. (1964). Caspian Fauna Beyond the Caspian Sea. *Internationale Revue der*
764 *gesamten Hydrobiologie und Hydrographie*, 49(1), 139–176. doi:10.1002/iroh.19640490105
- 765 Mordukhai-Boltovskoi, P. D. (1979). Composition and Distribution of Caspian Fauna in the Light of
766 Modern Data. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 64(1), 1–38.
767 doi:10.1002/iroh.19790640102
- 768 Nahavandi, N., Ketmaier, V., Plath, M., & Tiedemann, R. (2013). Diversification of Ponto-Caspian
769 aquatic fauna: Morphology and molecules retrieve congruent evolutionary relationships in
770 *Pontogammarus maeoticus* (Amphipoda: Pontogammaridae). *Molecular Phylogenetics and*
771 *Evolution*, 69(3), 1063–1076. doi:10.1016/j.ympev.2013.05.021
- 772 Naseka, A. M., & Bogutskaya, N. G. (2009). Fishes of the Caspian Sea: zoogeography and updated
773 check-list. *Zoosystematica Rossica*, 18(2), 295–317. doi:10.31610/zsr/2009.18.2.295
- 774 Naumenko, S. A., Logacheva, M. D., Popova, N. V., Klepikova, A. V., Penin, A. A., Bazykin, G. A., et al.

- 775 (2017). Transcriptome-based phylogeny of endemic Lake Baikal amphipod species flock: fast
776 speciation accompanied by frequent episodes of positive selection. *Molecular Ecology*, 26(2),
777 536–553. doi:10.1111/mec.13927
- 778 Palcu, D. V., Popov, S. V., Golovina, L. A., Kuiper, K. F., Liu, S., & Krijgsman, W. (2019). The shutdown
779 of an anoxic giant: Magnetostratigraphic dating of the end of the Maikop Sea. *Gondwana*
780 *Research*, 67, 82–100. doi:10.1016/j.gr.2018.09.011
- 781 Pinkster, S. (1993). A revision of the genus *Echinogammarus* Stebbing, 1899 with some notes on
782 related genera (Crustacea, Amphipoda). *Memorie del Museo Civico di Storia Naturale*, 10, 1–
783 185.
- 784 Piscart, C., Navel, S., Maazouzi, C., Montuelle, B., Cornut, J., Mermillod-Blondin, F., et al. (2011). Leaf
785 litter recycling in benthic and hyporheic layers in agricultural streams with different types of
786 land use. *Science of the Total Environment*, 409(20), 4373–4380.
787 doi:10.1016/j.scitotenv.2011.06.060
- 788 Pjatakova, G. M., & Tarasov, A. G. (1996). Caspian Sea amphipods: biodiversity, systematic position
789 and ecological peculiarities of some species. *International Journal of Salt Lake Research*, 5(1),
790 63–79. doi:10.1007/BF01996036
- 791 Popov, S. V., Rögl, F., Rozanov, A. Y., Steininger, F. F., Shcherba, I. G., & Kovac, M. (2004). Lithological-
792 paleogeographic maps of Paratethys. *CFS Courier Forschungsinstitut Senckenberg*, 250, 1–46.
- 793 Prange, M., Wilke, T., & Wesselingh, F. P. (2020). The other side of sea level change. *Communications*
794 *Earth & Environment*, 1, 69. doi:10.1038/s43247-020-00075-6
- 795 Reid, D. F., & Orlova, M. I. (2002). Geological and evolutionary underpinnings for the success of
796 Ponto-Caspian species invasions in the Baltic Sea and North American Great Lakes. *Canadian*
797 *Journal of Fisheries and Aquatic Sciences*, 59(7), 1144–1158. doi:10.1139/f02-099
- 798 Rewicz, T., Wattier, R., Grabowski, M., Rigaud, T., & Bacela-Spychalska, K. (2015). Out of the Black
799 sea: Phylogeography of the invasive killer shrimp *Dikerogammarus villosus* across Europe. *PLoS*
800 *ONE*, 10(2), 1–20. doi:10.1371/journal.pone.0118121
- 801 Rögl, F. (1999). Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene
802 paleogeography (short overview). *Geologica Carpathica*, 50(4), 339–349. [http://www.nhm-](http://www.nhm-wien.ac.at/jart/prj3/nhm/data/uploads/mitarbeiter_dokumente/roegl/1999_Roegl_Palgeo_GeolCarp.pdf)
803 [wien.ac.at/jart/prj3/nhm/data/uploads/mitarbeiter_dokumente/roegl/1999_Roegl_Palgeo_Ge](http://www.nhm-wien.ac.at/jart/prj3/nhm/data/uploads/mitarbeiter_dokumente/roegl/1999_Roegl_Palgeo_GeolCarp.pdf)
804 [olCarp.pdf](http://www.nhm-wien.ac.at/jart/prj3/nhm/data/uploads/mitarbeiter_dokumente/roegl/1999_Roegl_Palgeo_GeolCarp.pdf)
- 805 Salzburger, W., Bocxlaer, B. Van, & Cohen, A. S. (2014). Ecology and evolution of the African great
806 lakes and their faunas. *Annual Review of Ecology, Evolution, and Systematics*, 45, 519–545.
807 doi:10.1146/annurev-ecolsys-120213-091804
- 808 Sars, G. O. (1894a). Crustacea caspia. Contributions to the knowledge of the Carcinological Fauna of
809 the Caspian Sea. Part III. Amphipoda. *Bulletin de l'Academie Imperiale des Sciences de St.-*
810 *Petersbourg*, 1(2), 179–223.
- 811 Sars, G. O. (1894b). Crustacea caspia. Contributions to the knowledge of the Carcinological Fauna of
812 the Caspian Sea. Part III. Amphipoda. *Bulletin de l'Academie Imperiale des Sciences de St.-*
813 *Petersbourg*, 1(4), 343–378.
- 814 Sars, G. O. (1895). Crustacea caspia. Contributions to the knowledge of the Carcinological Fauna of
815 the Caspian Sea. Part III. Amphipoda. *Bulletin de l'Academie Imperiale des Sciences de St.-*
816 *Petersbourg*, 3(3), 275–314.
- 817 Sars, G. O. (1896). Crustacea caspia. Contributions to the knowledge of the Carcinological Fauna of
818 the Caspian Sea. *Bulletin de l'Academie Imperiale des Sciences de St.-Petersbourg*, 4(5), 421–
819 489.
- 820 Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford: Oxford University Press.
- 821 Seehausen, O. (2015). Process and pattern in cichlid radiations – inferences for understanding
822 unusually high rates of evolutionary diversification. *New Phytologist*, 207(2), 304–312.
823 doi:10.1111/nph.13450
- 824 Simões, M., Breikreuz, L., Alvarado, M., Baca, S., Cooper, J. C., Heins, L., et al. (2016). The Evolving
825 Theory of Evolutionary Radiations. *Trends in Ecology and Evolution*, 31(1), 27–34.
826 doi:10.1016/j.tree.2015.10.007

- 827 Sket, B., & Fišer, C. (2009). A new case of intralacustrine radiation in amphipoda. a new genus and
828 three new species of Anisogammaridae (Crustacea, Amphipoda) from the ancient lake Fuxian
829 Hu in Yunnan, China. *Journal of Zoological Systematics and Evolutionary Research*, 47(2), 115–
830 123. doi:10.1111/j.1439-0469.2008.00477.x
- 831 Sket, B., & Hou, Z. (2018). Family Gammaridae (Crustacea: Amphipoda), mainly its *Echinogammarus*
832 clade in SW Europe. Further elucidation of its phylogeny and taxonomy. *Acta Biologica*
833 *Slovenica*, 61(1), 93–102.
- 834 Takhteev, V. V. (2019). On the current state of taxonomy of the Baikal Lake amphipods (Crustacea:
835 Amphipoda) and the typological ways of constructing their system. *Arthropoda Selecta*, 28(3),
836 374–402. doi:10.15298/arthscl.28.3.03
- 837 Trontelj, P., Blejec, A., & Fišer, C. (2012). Ecomorphological convergence of cave communities.
838 *Evolution*, 66(12), 3852–3865. doi:10.1111/j.1558-5646.2012.01734.x
- 839 Väinölä, R., Vainio, J. K., & Palo, J. U. (2001). Phylogeography of “glacial relict” *Gammaracanthus*
840 (Crustacea, Amphipoda) from boreal lakes and the Caspian and White seas. *Canadian Journal of*
841 *Fisheries and Aquatic Sciences*, 58, 2247–2257.
- 842 Väinölä, R., Witt, J. D. S., Grabowski, M., Bradbury, J. H., Jazdzewski, K., & Sket, B. (2008). Global
843 diversity of amphipods (Amphipoda; Crustacea) in freshwater. *Hydrobiologia*, 595(1), 241–255.
844 doi:10.1007/s10750-007-9020-6
- 845 Vanderploeg, H. A., Nalepa, T. F., Jude, D. J., Mills, E. L., Holeck, K. T., Liebig, J. R., et al. (2002).
846 Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great
847 Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(7), 1209–1228. doi:10.1139/f02-
848 087
- 849 Wellborn, G. A., & Broughton, R. E. (2008). Diversification on an ecologically constrained adaptive
850 landscape. *Molecular Ecology*, 17(12), 2927–2936. doi:10.1111/j.1365-294X.2008.03805.x
- 851 Wellborn, G. A., & Langerhans, R. B. (2015). Ecological opportunity and the adaptive diversification of
852 lineages. *Ecology and Evolution*, 5(1), 176–195. doi:10.1002/ece3.1347
- 853 Wesselingh, F. P., Neubauer, T. A., Anistratenko, V. V., Vinarski, M. V., Yanina, T., ter Poorten, J. J., et
854 al. (2019). Mollusc species from the Pontocaspian region - an expert opinion list. *ZooKeys*,
855 2019(827), 31–124. doi:10.3897/zookeys.827.31365
- 856 Witt, J. D. S., Threlloff, D. L., & Hebert, P. D. N. (2006). DNA barcoding reveals extraordinary cryptic
857 diversity in an amphipod genus: Implications for desert spring conservation. *Molecular Ecology*,
858 15(10), 3073–3082. doi:10.1111/j.1365-294X.2006.02999.x
- 859 Wysocka, A., Grabowski, M., Sworobowicz, L., Burzyński, A., Kilikowska, A., Kostoski, G., & Sell, J.
860 (2013). A tale of time and depth: Intralacustrine radiation in endemic *Gammarus* species flock
861 from the ancient Lake Ohrid. *Zoological Journal of the Linnean Society*, 167(3), 345–359.
862 doi:10.1111/j.1096-3642.2012.00878.x
- 863 Wysocka, A., Grabowski, M., Sworobowicz, L., Mamos, T., Burzyński, A., & Sell, J. (2014). Origin of the
864 Lake Ohrid gammarid species flock: Ancient local phylogenetic lineage diversification. *Journal of*
865 *Biogeography*, 41(9), 1758–1768. doi:10.1111/jbi.12335
- 866
867
868
869
870
871
872
873
874
875
876
877
878

879

880

881 **Appendix**

882 Key to endemic families, genera and species of Ponto-Caspian amphipods (including non-
883 Gammaroidea).

884

885 **Key to families** (parentheses indicate non-Gammaroid genera that contain more than one
886 species; their species are keyed in the “Key to species” below)

- 887 1. Eyes absent **Niphargidae**
888 - Eyes present 2
889 2. Body dorso-ventrally compressed, coxal plates rudimentary, antenna 2 greatly developed
890 **Corophiidae (Chelicorophium)**
891 - Body laterally compressed, coxal plates developed, antenna 2 normally developed 3
892 3. Head rostrum long and narrow, uropod 3 rami foliaceous of equal length **Gammaracanthidae**
893 - Head rostrum absent or rudimentary, uropod 3 rami slender, subequal 4
894 4. Telson uncleft **Uristidae (Onisimus)**
895 - Telson cleft 5
896 5. Pereopod 6 much longer than pereopods 5 and 6 **Pontoporeiidae**
897 - Pereopod as long as or slightly longer than pereopods 5 and 6 6
898 6. Gnathopods chelate **Caspicolidae**
899 - Gnathopods subchelate 7
900 7. Pereopods 5-7 prehensile **Iphigenellidae**
901 - Pereopods 5-7 not prehensile 8
902 8. Maxilliped and mandibular palp reduced, and/or meral articles of pereopod 5-7 with postero-distal
903 lobe **Behningiellidae**
904 - Maxilliped and mandibular palp normal, meral articles of pereopod 5-7 without postero-distal lobe
905 9
906 9. Antenna 1 peduncle article 1 slender, as long as or shorter than articles 2 and 3 combined
907 **Gammaridae**
908 - Antenna 1 peduncle article 1 swollen, longer than articles 2 and 3 combined **Pontogammaridae**
909

910 **Key to genera (only Gammaroidea)**

- 911 1. Gnathopods chelate **Caspicola**
912 (monotypic: *Caspicola knipovitschi* Derzhavin, 1945)
913 - Gnathopods subchelate 2
914 2. Head with lateral projections 3
915 - Head without lateral projections 5
916 3. Strong lateral-pointing spine on pereonite 5 **Axelboeckia**
917 (monotypic: *Axelboeckia spinosa* (G.O. Sars, 1894))
918 - No spines, only blunt knobs on pereonite 5 4
919 4. Body with two dorso-lateral rows of knobs **Kuzmelina**
920 (monotypic: *Kuzmelina kusnezowi* (Sowinsky, 1894))
921 - Body with a central dorsal a keel on pereonal segments 6-7 and pleosome **Gmelinopsis**
922 5. Antenna 1 accessory flagellum uniarticulate 6
923 - Antenna 1 accessory flagellum two- or multiarticulated 10
924 6. Lateral head lobes form a characteristic “hood” **Scytaelina**
925 (monotypic: *Scytaelina simplex* Stock et al., 1998)
926 - Lateral head lobes normal 7
927 7. Bases of pereopods 5-6 lobed, uropod 3 reduced **Behningiella**
928 (monotypic: *Behningiella brachypus* Derzhavin, 1948)
929 - Bases of pereopods 5-6 not lobed, uropod 3 normal 8
930 8. Body with an obvious central dorsal keel, more pronounced on the pleosome **Gmelina**
931 - Body with a weak or absent central dorsal keel 9

932	9. Pereopod 7 basis with a large downward pointing postero-distal lobe	Jugogammarus
933	(monotypic: <i>Jugogammarus kusceri</i> (S. Karaman, 1931))	
934	- Pereopod 7 basis with minute/without a downward pointing postero-distal lobe	Yogmelina
935	10. Gnathopod 1 broader and larger than gnathopod 2	11
936	- Gnathopod 1 equal or smaller than gnathopod 2	13
937	11. Uropod 3 reduced, exopod shorter than twice the peduncle length	Baku
938	(one species: <i>Baku paradoxus</i> (Derzhavin in Derzhavin & Pjatakova, 1967))	
939	- Uropod 3 normal, exopod at least twice the peduncle length	12
940	12. Dactyli of pereopods 3-7 prehensile	Iphigenella
941	(monotypic: <i>Iphigenella acanthopoda</i> G.O. Sars, 1896)	
942	- Dactyli of pereopods 3-7 not prehensile	Lanceogammarus
943	(monotypic: <i>Lanceogammarus andrussowi</i> (G.O. Sars, 1896))	
944	13. Pereopod 7 basis not lobed	14
945	- Pereopod 7 basis lobed	18
946	14. Antenna 1 accessory flagellum bi-articulated	Cardiophilus
947	- Antenna 1 accessory flagellum tri- or more articulated	15
948	15. Antenna 2 peduncle greatly expanded, article 3 with a downward projection	Derzhavinella
949	- Antenna 2 peduncle normal, article 3 without a downward projection	16
950	16. Antenna 1 peduncle article 3 longer or equal with article 1	Sowinskya
951	(monotypic: <i>Sowinskya macrocera</i> Derzhavin, 1948)	
952	- Antenna 1 peduncle article 3 shorter than article 1	17
953	17. Uropod 3 setae curled, longer than spines	Trichogammarus
954	(monotypic: <i>Trichogammarus trichiatus</i> (Martynov, 1932))	
955	- Uropod 3 setae straight, shorter than spines	Chaetogammarus
956	18. Pereopod 6 basis lobed	19
957	- Pereopod 6 basis not lobed	20
958	19. Pereopod 5-7 meral articles with a postero-distal lobe	Zernovia
959	(monotypic: <i>Zernovia volgensis</i> Derzhavin, 1948)	
960	- Pereopod 5-7 meral articles without a postero-distal lobe	Shablogammarus
961	(monotypic: <i>Shablogammarus shablensis</i> (Cărăușu, 1943))	
962	20. Antenna 1 flagellum shorter than peduncle	21
963	- Antenna 1 flagellum equal/longer than peduncle	25
964	21. Epimeron 3 with postero-ventral setal fan	22
965	- Epimeron 3 without postero-ventral setal fan	24
966	22. Uropod 3 endopod longer than half of exopod	Uroniphargoides
967	(monotypic: <i>Uroniphargoides spinicaudatus</i> (Cărăușu, 1943))	
968	- Uropod 3 endopod shorter than half of exopod	23
969	23. Gnathopod 2 propodus palm longer than posterior margin	Compactogammarus
970	(monotypic: <i>Compactogammarus compactus</i> (G.O. Sars, 1895))	
971	- Gnathopod 2 propodus palm shorter than posterior margin	Niphargoides
972	24. Uropod 3 exopod 2 nd article well developed, bearing lateral setae	Niphargogammarus
973	- Uropod 3 exopod 2 nd article minute/absent, bearing no lateral setae	Paraniphargoides
974	25. Eyes round to ovoid, gnathopod 2 propodus large and triangular, armed with a palmar spine as	
975	long as 1/3 of dactylus	Pandorites
976	(monotypic: <i>Pandorites podocerooides</i> (G.O. Sars, 1896))	
977	- Eyes reniform, gnathopod 2 propodus armed with a palmar spine(s) shorter than 1/3 of dactylus	
978	26
979	26. Antenna 1 peduncular article 1 slender, width not exceeding 1/3 of length, pereopods 3-4 with	
980	sparse setae shorter than the width of underlying segment	27
981	- Antenna 1 peduncular article 1 robust, width exceeding 1/3 of length, pereopods 3-4 with dense	
982	setae as long as/longer than the width of underlying segment (except <i>O. subnudus</i>)	30
983	27. Body with a central dorsal a keel	Amathillina
984	- Body without a keel	28

985	28. Head swollen and enlarged	Cephalogammarus
986		(monotypic: <i>Cephalogammarus macrocephalus</i> (G.O. Sars, 1896))
987	- Head normal	29
988	29. Urosomites 1-2 with columnar tubercles	Dikerogammarus
989	- Urosomites 1-2 without columnar tubercles	Akerogammarus
990	30. Uropod 3 exopod 2 nd article at least 1/5 the length of 1 st article	31
991	- Uropod 3 exopod 2 nd article much shorter than 1/5 the length of 1 st article	32
992	31. Uropod 3 exopod outer margin armed with few simple setae	Stenogammarus
993	- Uropod 3 exopod outer margin armed with many plumose setae	Wolgagammarus
994		(monotypic: <i>Wolgagammarus dzjubani</i> (Mordukhai-Boltovskoi & Ljakhov, 1972))
995	32. Setae on posterior margin of carpal articles of pereopods 3-4 arranged in a continuous fan	
996	Pontogammarus
997	- Setae on posterior margin of carpal articles of pereopods 3-4 arranged in clusters	33
998	33. Urosomites 1-2 with noticeable dorsal knobs	Turcogammarus
999	- Urosomites 1-2 flat or humped	Obesogammarus

1000
1001

Key to species

Doubtful species are indicated with an asterisk (*).

1003
1004

Key to species of *Akerogammarus*

- 1005
1006 1. Propodi of gnathopods 1 and 2 similar in size, telson with short apical setae *A. contiguous*
1007 - Propodus of gnathopod 2 larger than gnathopod 1, telson with long apical setae *A. knipowitschi*

1008

Key to species of *Amathillina*

- 1009
1010 1. Body keel starts from the first pereonite 2
1011 - Body keel starts from the sixth pereonite or later 3
1012 2. Pereonites 1-2 with well-developed dorsal spines, urosomite 1 humped *A. spinosa*
1013 - Pereonites 1-2 with barely visible crest, urosomite 1 not humped *A. cristata*
1014 3. Body keel present only on pleosome *A. maximowiczi*
1015 - Body keel present on pereonites 6-7 and pleosome 4
1016 4. Antenna 1 accessory flagellum bi-articulated, last pleonal projection rounded *A. pussila*
1017 - Antenna 1 accessory flagellum tri-articulated, last pleonal projection triangular *A. affinis*

1018

Key to species of *Cardiophilus*

- 1019
1020 1. Uropod 3 exopod less than twice the length of peduncle, 2nd article present *C. baeri*
1021 - Uropod 3 exopod twice the length of peduncle, 2nd article absent *C. maris-nigri*

1022

Key to species of *Chaetogammarus*

- 1023
1024 1. Antenna 1 accessory flagellum bi-articulated *C. warpachowskyi*
1025 - Antenna 1 accessory flagellum at least three articles 2
1026 2. Pleosome covered with small spines *C. hyrcanus*
1027 - Pleosome bare 3
1028 3. Eyes very elongated and constricted in the middle *C. placidus*
1029 - Eyes regular (reniform) 4
1030 4. Antenna 1 and 2 set with dense setae longer than the underlying segment *C. ischnus*
1031 - Antenna 1 and 2 set with sparse setae shorter/equal with the underlying segment *C. pauxillus*

1032

Key to species of *Chelicorophium*

- 1033
1034 1. Antenna 2 peduncular article 4 distal tooth simple *C. monodon*
1035 - Antenna 2 peduncular article 4 distal tooth with an additional simple or bidentate tooth 2

1036	2. Antenna 2 peduncular article 4 distal tooth with an additional simple tooth	3
1037	- Antenna 2 peduncular article 4 distal tooth with an additional bidentate tooth	6
1038	3. Pereopods 3-4 meral articles stout, length is less than twice the width	<i>C. mucronatum</i>
1039	- Pereopods 3-4 meral articles slender, length is twice the width	4
1040	4. Antenna 2 peduncular article 5 with a proximal and distal tooth	<i>C. chelicorne</i>
1041	- Antenna 2 peduncular article 5 with either a proximal or distal tooth	5
1042	5. Antenna 2 peduncular article 5 with a small proximal tooth, distal tooth missing	<i>C. nobile</i>
1043	- Antenna 2 peduncular article 5 with a strong distal tooth, proximal tooth missing	<i>C. spinulosum</i>
1044	6. Antenna 2 peduncular article 5 with a proximal and distal tooth	7
1045	- Antenna 2 peduncular article 5 with a proximal tooth only	8
1046	7. Antenna 2 peduncular article 5 proximal tooth situated in the distal half of the article, inner side of	
1047	uropod 3 peduncle without spines	<i>C. maeoticum</i>
1048	- Antenna 2 peduncular article 5 proximal tooth situated in the proximal half of the article, inner side	
1049	of uropod 3 peduncle with spines	<i>C. robustum</i>
1050	8. Antenna 1 flagellum as long as peduncle	<i>C. sowinskyi</i>
1051	- Antenna 1 flagellum half as long as peduncle	<i>C. curvispinum</i>
1052		
1053	Key to species of <i>Derzhavinella</i>	
1054	1. Anterior margin of pereopod 7 with long setae	<i>D. macrochelata</i>
1055	- Anterior margin of pereopod 7 with short setae	<i>D. cava</i>
1056		
1057	Key to species of <i>Dikerogammarus</i>	
1058	1. Pleosome segments keeled	<i>D. caspius</i>
1059	- Pleosome segments flat	2
1060	2. Urosomal tubercles low	<i>D. fluviatilis*</i>
1061	- Urosomal tubercles columnar, well developed	3
1062	3. Antenna 1 accessory flagellum bi-articulated	<i>D. gruberi</i>
1063	- Antenna 1 accessory flagellum 4 or more articles	4
1064	4. Propodi of gnathopods 1 & 2 with mid-palmar spine	<i>D. aralychensis*</i>
1065	- Propodi of gnathopods 1 & 2 without mid-palmar spine	5
1066	5. Medial surface of pereopod 7 basis with setae	6
1067	- Medial surface of pereopod 7 basis without setae	7
1068	6. Antenna 2 peduncular segments with numerous clusters of setae longer than the underlying	
1069	segment	<i>D. bispinosus</i>
1070	- Antenna 2 peduncular segments with few clusters of setae shorter than the underlying segment	
1071	<i>D. istanbulensis</i>
1072	7. Propodi of gnathopods 1 & 2 with setae as long as propodus width	<i>D. villosus</i>
1073	- Propodi of gnathopods 1 & 2 with setae much shorter than propodus width	8
1074	8. Uropod 3 exopod with spines on inner and outer margins	<i>D. haemobaphes</i>
1075	- Uropod 3 exopod without spines	<i>D. oskari</i>
1076		
1077	Key to species of <i>Gmelina</i>	
1078	1. Pleonal humps high and triangular	<i>G. costata</i>
1079	- Pleonal humps low and rounded	<i>G. aestuarica</i>
1080		
1081	Key to species of <i>Gmelinopsis</i>	
1082	1. Head lateral projections blunt, tubercle-like	<i>G. tuberculata</i>
1083	- Head lateral projections pointed, spear-like	<i>G. aurita</i>
1084		
1085	Key to species of <i>Niphargogammarus</i>	
1086	1. Antenna 1 main flagellum as long as the first peduncular article	2
1087	- Antenna 1 main flagellum shorter than the first peduncular article	3

1088	2. Body size ca. 10 mm, gnathopod 2 propodus larger than gnathopod 1, telson lobes diverging and	
1089	armed with 1 apical spine	<i>N. quadrimanus</i>
1090	- Body size ca. 5 mm, propodi of both gnathopods similar in size, telson lobes not diverging and	
1091	armed apically with 2 spines	<i>N. aequimanus</i>
1092	3. Body size ca. 13 mm, urosomite 1 bare, uropod 3 exopod external margin armed with many setae	
1093	<i>N. borodini</i>
1094	- Body size ca. 7 mm, urosomite 1 armed with small setae, uropod 3 exopod external margin armed	
1095	with few distal setae	<i>N. intermedius</i>
1096		
1097	Key to species of <i>Niphargoides</i>	
1098	1. Posterior margin of pereopod 6 basis armed with a few short setae proximally	<i>N. grimmi</i>
1099	- Posterior margin of pereopod 6 basis armed with long setae along its entire length	2
1100	2. Ventral margin of coxal plate 4 armed with setae shorter than 1/2 of its length	<i>N. corpulentus</i>
1101	- Ventral margin of coxal plate 4 armed with setae longer than 1/2 of its length	3
1102	3. Uropod 3 exopod bares a well-developed setal fan	<i>N. caspius</i>
1103	- Uropod 3 exopod lacks setal fan, armed with strong spines	<i>N. boltovskoyi</i>
1104		
1105	Key to species of <i>Obesogammarus</i>	
1106	1. Posterior margin of pereopods 3-4 with few sparse setae shorter than the underlying segment	
1107	<i>O. subnudus</i>
1108	- Posterior margin of pereopods 3-4 with numerous setae as long as/longer than the underlying	
1109	segment	2
1110	2. Uropod 3 exopod less than twice peduncle length	3
1111	- Uropod 3 exopod at least twice as long as peduncle	4
1112	3. Posterior margin of basis of pereopods 5-7 with short setae	<i>O. olvianus</i>
1113	- Posterior margin of basis of pereopods 5-7 with long setae	<i>O. obesus</i>
1114	4. Coxae 1-2 tapering towards distal end, propodus of gnathopod 2 triangular	<i>O. platycheir</i>
1115	- Coxae 1-2 not tapering, propodus of gnathopod 2 roughly rectangular	5
1116	5. Medial surface of pereopod 7 basis without setae	<i>O. crassus</i>
1117	- Medial surface of pereopod 7 basis armed with clusters of setae	6
1118	6. Urosomites with dorsal elevations	<i>O. acuminatus</i>
1119	- Urosomites without dorsal elevations	<i>O. boeoticus</i>
1120		
1121	Key to species of <i>Onisimus</i>	
1122	1. Antenna 1 peduncle article 1 longer than head, accessory flagellum 6-segmented, postero-ventral	
1123	corner of 3 rd epimere almost straight	<i>O. platyceras</i>
1124	2. Antenna 1 peduncle article 1 shorter than head, accessory flagellum 4-segmented, postero-ventral	
1125	corner of 3 rd epimere sharp	<i>O. caspius</i>
1126		
1127	Key to species of <i>Paraniphargoides</i>	
1128	1. Uropod 3 exopod without terminal article, plumose setae absent	<i>P. derzhavini</i>
1129	- Uropod 3 exopod with minute terminal article, plumose setae present	<i>P. motasi</i>
1130		
1131	Key to species of <i>Pontogammarus</i>	
1132	1. Uropod 3 endopod reaches half the length of the exopod 1 st article	2
1133	- Uropod 3 endopod shorter than half the length of the exopod 1 st article	4
1134	2. Dactylus nail of pereopods 5-7 hook-like	<i>P. sarsi</i>
1135	- Dactylus nail of pereopods 5-7 straight	3
1136	3. Mandibular palp very large, plumose D-setae present, last article of antenna 2 bares continuous	
1137	setal fan	<i>P. maeoticus</i>
1138	- Mandibular palp normal, D-setae absent, last article of antenna 2 bares several setal clusters	
1139	<i>P. weidemanni</i>

1140	4. Urosome with dorsal elevations	5
1141	- Urosome flat	7
1142	5. Dorsal elevations tall, pillar-like	<i>P. setosus</i>
1143	- Dorsal elevations low, hump like	6
1144	6. Urosomite 1 armed with a crown of spines	<i>P. robustoides</i>
1145	- Urosomite 1 armed with setae only	<i>P. aestuarius</i>
1146	7. Uropod 3 exopod 2 nd article as long as broad, uropod 2 exopod devoid of spines	<i>P. borceae</i>
1147	- Uropod 3 exopod 2 nd article longer than broad, uropod 2 exopod with 1 spine	<i>P. abbreviatus</i>
1148		
1149	Key to species of <i>Stenogammarus</i>	
1150	1. Uropod 3 reduced, 1 st exopod article as long as peduncle	<i>S. micrurus</i>
1151	- Uropod 3 not reduced, 1 st exopod article longer than peduncle	2
1152	2. Uropod 3 exopod inner margin bare/with 1 long seta	3
1153	- Uropod 3 exopod inner margin with multiple long setae	4
1154	3. Pereopods 6-7 basis medial surface with clusters of setae, basis 6 with long setae on posterior margin, basis 7 with long setae on anterior margin	<i>S. compresso-similis</i>
1155	- Pereopods 6-7 basis medial surface bare, basis 6 with short setae on posterior margin, basis 7 with short setae on anterior margin	<i>S. deminutus</i>
1156	4. Uropod 3 exopod 2 nd article shorter than half of 1 st article	<i>S. similis</i>
1157	- Uropod 3 exopod 2 nd article as long/longer than half of 1 st article	5
1158	5. Uropod 3 endopod longer than 2 nd exopod article and is 1/2 of 1 st article	<i>S. compressus</i>
1159	- Uropod 3 endopod shorter than 2 nd exopod article and is 1/3 1 st article	<i>S. macrurus</i>
1160		
1161		
1162		
1163	Key to species of <i>Turcogammarus</i>	
1164	1. Pleosome segments keeled	<i>T. spandli</i>
1165	- Pleosome segments flat	2
1166	2. Urosomal tubercles low	<i>T. aralensis</i>
1167	- Urosomal tubercles tall and columnar	<i>T. turcarum*</i>
1168		
1169	Key to species of <i>Yogmelina</i>	
1170	1. Uropod 3 reduced, 1 st article of exopod as long as peduncle	<i>Y. brachyura</i>
1171	- Uropod 3 not reduced, 1 st article of exopod longer than peduncle	2
1172	2. Basis of pereopod 7 truncated, abruptly tapering towards the distal edge	<i>Y. ovata*</i>
1173	- Basis of pereopod 7 not truncated, gradually tapering towards the distal edge	3
1174	3. Coxal plate 1 slightly bent forwards, fringed with short setae	<i>Y. laeviuscula</i>
1175	- Coxal plate 1 strongly bent forwards fringed with long setae	4
1176	4. Urosomites without setae, epimeral plates 2-3 with short distal setae	<i>Y. pusilla</i>
1177	- Urosomites with setae, epimeral plates 2-3 with long distal setae	<i>Y. limana</i>
1178		
1179		
1180		
1181		