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

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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

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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

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

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

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

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

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

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

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

Taxonomic diversity

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

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

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

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

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

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> Cărașu, 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 fluvialilis</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>	Cărașu, 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>	(Cărașu, 1943)	Caspian, Ponto-Azov	valid	Original spelling: <i>Gammarus chablensis</i> Emended by Cărașu et al. (1955)
Gammaridae	<i>Sowinskyia 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> Cărașu, 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>	(Cărașu, 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 olivianus</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 podoceroideis</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 boraceae</i>	Caraus, 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> Tuculesco, 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> Tuculesco, 1933
Pontogammaridae	<i>Pontogammarus (=Euxinia) sarsi</i>	(Sowinsky, 1898)	Caspian, Ponto-Azov	valid	Removed to <i>Pontogammarus</i> since <i>Euxinia</i> Tuculesco, 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> Tuculesco, 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>	(Cărbăușu, 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

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

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

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

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

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

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).

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.

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

Ecology

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

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.

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*.

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

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		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 fluvialilis</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 boraceae</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 weidmanni</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 spandli</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

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

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

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

Discussion

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

Ponto-Caspian gammarid amphipods – an adaptive radiation?

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

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

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

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

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

Morphological evolution

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

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 Copilaș-Ciocianu et al. (2020)

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

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

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

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

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

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

Fig. 8 Examples of evolutionary convergent patterns in body armature of species inhabiting different ancient lakes. a) *Axelboeckia spinosa* (Caspian Sea, redrawn after Sars (1894b)), b) *Acanthogammarus lappaceus* (Lake Baikal, redrawn after Daneliya et al. (2011)), c) *Issykogammarus hamatus* (Lake Issyk-Kul, redrawn after Chevreux (1908)), and d) *Hyaella armata* (Lake Titicaca, redrawn after González & Coleman (2002))

Spatio-temporal origin

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 Petrusek 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

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

Taxonomic and systematic remarks

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

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

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

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

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

Conclusion

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

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Appendix

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

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

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

Key to genera (only Gammaroidea)

1. Gnathopods chelate **Caspicola**
(monotypic: *Caspicola knipovitschi* Derzhavin, 1945)
- Gnathopods subchelate 2
2. Head with lateral projections 3
- Head without lateral projections 5
3. Strong lateral-pointing spine on pereonite 5 **Axelboeckia**
(monotypic: *Axelboeckia spinosa* (G.O. Sars, 1894))
- No spines, only blunt knobs on pereonite 5 4
4. Body with two dorso-lateral rows of knobs **Kuzmelina**
(monotypic: *Kuzmelina kusnezowi* (Sowinsky, 1894))
- Body with a central dorsal a keel on pereonal segments 6-7 and pleosome **Gmelinopsis**
5. Antenna 1 accessory flagellum uniarticulate 6
- Antenna 1 accessory flagellum two- or multiarticulated 10
6. Lateral head lobes form a characteristic “hood” **Scytaelina**
(monotypic: *Scytaelina simplex* Stock et al., 1998)
- Lateral head lobes normal 7
7. Bases of pereopods 5-6 lobed, uropod 3 reduced **Behningiella**
(monotypic: *Behningiella brachypus* Derzhavin, 1948)
- Bases of pereopods 5-6 not lobed, uropod 3 normal 8
8. Body with an obvious central dorsal keel, more pronounced on the pleosome **Gmelina**
- 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> (Cărbăușu, 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> (Cărbăușu, 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 podoceroideus</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

1002 Key to species

1003 Doubtful species are indicated with an asterisk (*).

1004

1005 Key to species of *Akerogammarus*

- 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

1009 Key to species of *Amathillina*

- 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. maximowiczii*
- 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

1019 Key to species of *Cardiophilus*

- 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

1023 Key to species of *Chaetogammarus*

- 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

1033 Key to species of *Chelicorophium*

- 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 *N. quadrimanus*
 1090 - Body size ca. 5 mm, propodi of both gnathopods similar in size, telson lobes not diverging and
 1091 armed apically with 2 spines *N. aequimanus*
 1092 3. Body size ca. 13 mm, urosomite 1 bare, uropod 3 exopod external margin armed with many setae
 1093 *N. borodini*
 1094 - Body size ca. 7 mm, urosomite 1 armed with small setae, uropod 3 exopod external margin armed
 1095 with few distal setae *N. intermedius*
 1096

1097 **Key to species of *Niphargoides***

- 1098 1. Posterior margin of pereopod 6 basis armed with a few short setae proximally *N. grimmi*
 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 *N. corpulentus*
 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 *N. caspius*
 1103 - Uropod 3 exopod lacks setal fan, armed with strong spines *N. boltovskoyi*
 1104

1105 **Key to species of *Obesogammarus***

- 1106 1. Posterior margin of pereopods 3-4 with few sparse setae shorter than the underlying segment
 1107 *O. subnudus*
 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 *O. olivianus*
 1113 - Posterior margin of basis of pereopods 5-7 with long setae *O. obesus*
 1114 4. Coxae 1-2 tapering towards distal end, propodus of gnathopod 2 triangular *O. platycheir*
 1115 - Coxae 1-2 not tapering, propodus of gnathopod 2 roughly rectangular 5
 1116 5. Medial surface of pereopod 7 basis without setae *O. crassus*
 1117 - Medial surface of pereopod 7 basis armed with clusters of setae 6
 1118 6. Urosomites with dorsal elevations *O. acuminatus*
 1119 - Urosomites without dorsal elevations *O. boeoticus*
 1120

1121 **Key to species of *Onisimus***

- 1122 1. Antenna 1 peduncle article 1 longer than head, accessory flagellum 6-segmented, postero-ventral
 1123 corner of 3rd epimere almost straight *O. platyceras*
 1124 2. Antenna 1 peduncle article 1 shorter than head, accessory flagellum 4-segmented, postero-ventral
 1125 corner of 3rd epimere sharp *O. caspius*
 1126

1127 **Key to species of *Paraniphargoides***

- 1128 1. Uropod 3 exopod without terminal article, plumose setae absent *P. derzhavini*
 1129 - Uropod 3 exopod with minute terminal article, plumose setae present *P. motasi*
 1130

1131 **Key to species of *Pontogammarus***

- 1132 1. Uropod 3 endopod reaches half the length of the exopod 1st article 2
 1133 - Uropod 3 endopod shorter than half the length of the exopod 1st article 4
 1134 2. Dactylus nail of pereopods 5-7 hook-like *P. sarsi*
 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 *P. maeoticus*
 1138 - Mandibular palp normal, D-setae absent, last article of antenna 2 bares several setal clusters
 1139 *P. weidemanni*

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	
1155	margin, basis 7 with long setae on anterior margin	<i>S. compresso-similis</i>
1156	- Pereopods 6-7 basis medial surface bare, basis 6 with short setae on posterior margin, basis 7 with	
1157	short setae on anterior margin	<i>S. deminutus</i>
1158	4. Uropod 3 exopod 2 nd article shorter than half of 1 st article	<i>S. similis</i>
1159	- Uropod 3 exopod 2 nd article as long/longer than half of 1 st article	5
1160	5. Uropod 3 endopod longer than 2 nd exopod article and is 1/2 of 1 st article	<i>S. compressus</i>
1161	- Uropod 3 endopod shorter than 2 nd exopod article and is 1/3 1 st article	<i>S. macrurus</i>
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		