REVIEW

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

Denis Copilaş-Ciocianu[1] · Dmitry Sidorov[2]

Abstract

The dynamic geological history of the Ponto-Caspian region drove the evolution of a highly adaptable endemic fauna that gave rise to notorious aquatic invaders. Amphipod crustaceans of the superfamily Gammaroidea attained considerable diversity, becoming the world's second most speciose ancient lake amphipod radiation. Nonetheless, apart from a few species that became invasive, this group remains poorly studied. Herein, we review and quantify the taxonomic, morphological and ecological diversity, as well as the phylogenetic context of Ponto-Caspian gammaroids within the adaptive radiation framework. Molecular phylogenies indicate that this radiation has a likely monophyletic mid-Miocene Parathethyan origin and is nested within the morphologically conserved Atlanto-Mediterranean *Echinogammarus* clade. 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 hypothesis, although extensive further research is needed. A checklist and provisional key to all known endemic species are provided to facilitate taxonomic research. Ponto-Caspian gammaroids could be a potentially powerful model for studying adaptive radiations and invasive species evolution.

Keywords Ancient lake · Crustacean · Evolution · Radiation · Systematics

Introduction

Ancient lakes are evolutionary cradles, harbouring a rich endemic fauna that fascinated biologists for centuries (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 gammaroid amphipods inhabiting Lake Baikal (Naumenko et al., 2017).

Situated in the Ponto-Caspian region (Fig. 1), the Caspian Sea is the world's largest ancient lake (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 Parathethys Sea, which stretched from the foothills of the Alps to the Himalayas (Fig. 1) (Palcu et al., 2021; Popov et al., 2004). The Parathethys 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 & Orlova, 2002). This plasticity has

✉ Denis Copilaş-Ciocianu
denis.copilas-ciocianu@gamtc.lt

[1] Laboratory of Evolutionary Ecology of Hydrobionts, Nature Research Centre, Vilnius, Lithuania

[2] Far Eastern Branch, Federal Scientific Centre of the East Asia Terrestrial Biodiversity, Russian Academy of Sciences, Vladivostok, Russian Federation
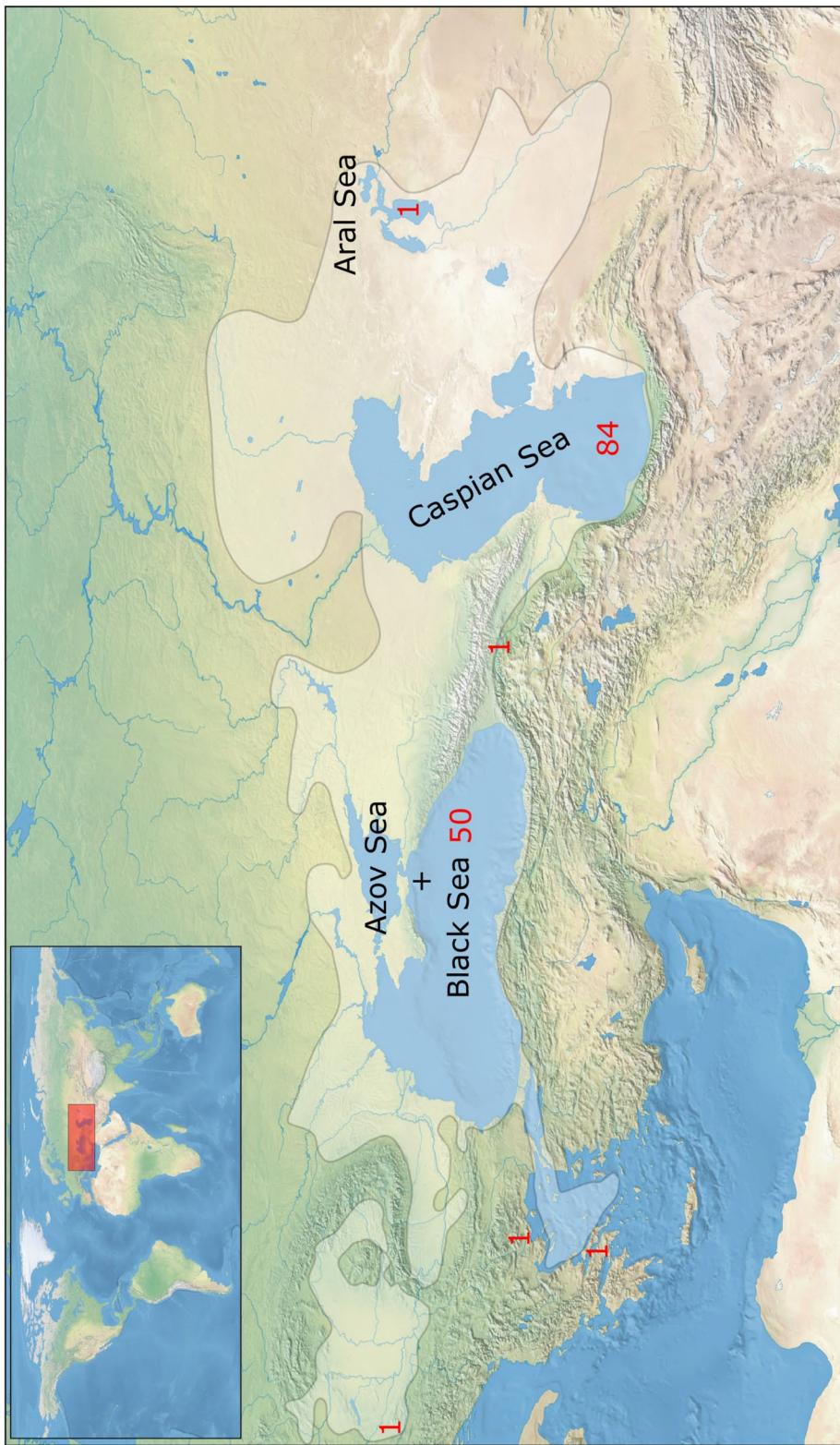
Fig. 1 Overview map of the Ponto-Caspian region, which includes the Black, Azov, Caspian and Aral seas as well as the adjacent lagoons and lower river stretches. Red numerals indicate the number of valid endemic Ponto-Caspian species (including non-Gammaroidea) in various regions (Azov and Black seas shown together). Note that the *Azov/Black Sea region shares 43 species with the Caspian Sea*. The area delimited with transparent white indicates the maximum extent of the Paratethys Sea during the Late Miocene (ca. 11 Ma) (Palcu et al., 2021). All of the contemporary seas are remnants of the Paratethys

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 (from outside the Ponto-Caspian realm) 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 endemicity and biodiversity with hundreds of species from various animal phyla, but particularly rich in crustaceans (Birstein et al., 1968; Chertoprud et al., 2018; Cristescu & Hebert, 2005; Mordukhai-Boltovskoi, 1979; Naseka & Bogutskaya, 2009; Wesselingh et al., 2019).

Amphipod crustaceans radiated multiple times in the world's temperate ancient lakes. Several radiations occurred in Lake Titicaca (Hyalellidae) (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) (Cristescu & 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 & Fišer, 2009). Other lakes throughout Asia also harbour endemic species, although their monophyly has yet to be proven. These are Lake Issyk-Kul in Kyrgyzstan (Gammaridae) (Karaman & 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 (or parallelism) in body armature among evolutionary and geographically distant groups (Martens, 1997; Takhteev, 2000).

The endemic amphipod fauna of the Ponto-Caspian basin is one of the world's most diverse, second only to Lake Baikal (Barnard & 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 & 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 & Schön, 1999). Most attention has been focused on the invasive species of Ponto-Caspian origin that are spreading throughout European freshwaters (e.g. Arbačiauskas et al., 2013; Cristescu et al., 2004; Grabowski et al., 2007; 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 (Cyrillic alphabet), 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 focused either on taxonomy with a brief comparative verbal morphological analysis (Barnard & Barnard, 1983) or on ecology (Pjatakova & Tarasov, 1996). Such analyses rarely, if at all, considered the amphipods from all of the Ponto-Caspian basins (Birstein & Romanova, 1968; Mordukhai-Boltovskoi, 1964, 1979; Pjatakova & Tarasov, 1996). Furthermore, there is no species-level key that encompasses all of the known diversity of the endemic Ponto-Caspian amphipods.

In this study, we aim to provide a first comprehensive overview of endemic Ponto-Caspian gammaroidean 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 criteria for adaptive radiation (Schluter, 2000; Simões et al., 2016). Specifically, we looked for evidence pointing to (I) monophyly of endemic Ponto-Caspian gammaroids, (II) an increase in their diversification rates and (III) ecomorphological divergence.

This overview is intended to serve as a foundation and to encourage future evolutionary, ecological 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.

Phylogenetic context

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, Iphigenellidae and Pontogammaridae. These taxa form the bulk of the endemic diversity and are most likely a monophyletic group (Hou et al., 2014; Sket & Hou, 2018)—a necessary criterion for an adaptive radiation (Schluter, 2000). We added the monotypic family Caspicolidae because it is very likely a highly derived gammarid lineage (Derzhavin, 1944). Although this family is currently included in the infraorder Talitridira by Lowry and Myers (2013), we consider this placement erroneous due to a character coding mistake (see Discussion section for further details). As such, for this presumably monophyletic radiating

species flock, we coin the term "endemic Ponto-Caspian gammaroid radiation", circumscribing the so-called ponto-gammarized amphipods (referring to their apparent fossorial adaptations) (Karaman & Barnard, 1979; Martynov, 1924; Stock, 1974). This group is the focus of the present review.

The remaining endemic Ponto-Caspian taxa such as *Chelicorophium* (9 spp., Corophiidae), *Gammaracanthus* (1 sp., Gammaracanthidae), *Niphargus* (1 sp., Niphargidae), *Onisimus* (2 spp., Uristidae) and *Monoporeia* (1 sp., Pontoporeiidae) were excluded from subsequent analyses since they are unrelated to the focal endemic gammaroids, mainly representing occasional invaders and offshoots of marine genera (Barnard & Barnard, 1983; Copilaş-Ciocianu et al., 2020a; Khusainova, 1959; Lowry & Myers, 2017; Väinölä et al., 2001).

The molecular phylogenetic context of the endemic Ponto-Caspian gammaroid radiation is well known and established. Analyses at the order or family level indicate that the sequenced taxa belonging to this radiation form a highly supported monophyletic lineage, nested within the Atlanto-Mediterranean *Echinogammarus* clade (Fig. 2a) (Copilaş-Ciocianu et al., 2020a; Hou & Sket, 2016; Hou et al., 2014; Sket & Hou, 2018). Specifically, the endemic Ponto-Caspian gammaroid radiation seems to be a sister clade to the narrowly endemic genus *Dinarogammarus*, distributed in the western Balkans (Sket & Hou, 2018). However, around 20 Ponto-Caspian genera (out of 34) have not yet been sequenced. Most of these likely belong to the same clade as the sequenced taxa, given their morphological similarity. However, the phylogenetic position of the small and morphologically advanced families Behningiellidae, Caspicolidae and Iphigenellidae is less straightforward to interpret, especially since they have not yet been sequenced. Thus, it remains to be seen whether

Fig. 2 Phylogenetic context and relationships of the endemic Ponto-Caspian gammaroid radiation. **(a)** Phylogenetic position of the endemic Ponto-Caspian gammaroid radiation (in red) within the superfamily Gammaroidea based on molecular (left) (after Copilaş-Ciocianu et al., 2020a) and morphological (right) (after Lowry & Myers, 2013) analyses. **(b)** Phylogenetic relationships among the currently sequenced taxa belonging to the endemic Ponto-Caspian gammaroid radiation. Genera that have more than one species sequenced are shown with different colors. The tree was modified after Sket and Hou (2018); some taxa were omitted due to misidentifications
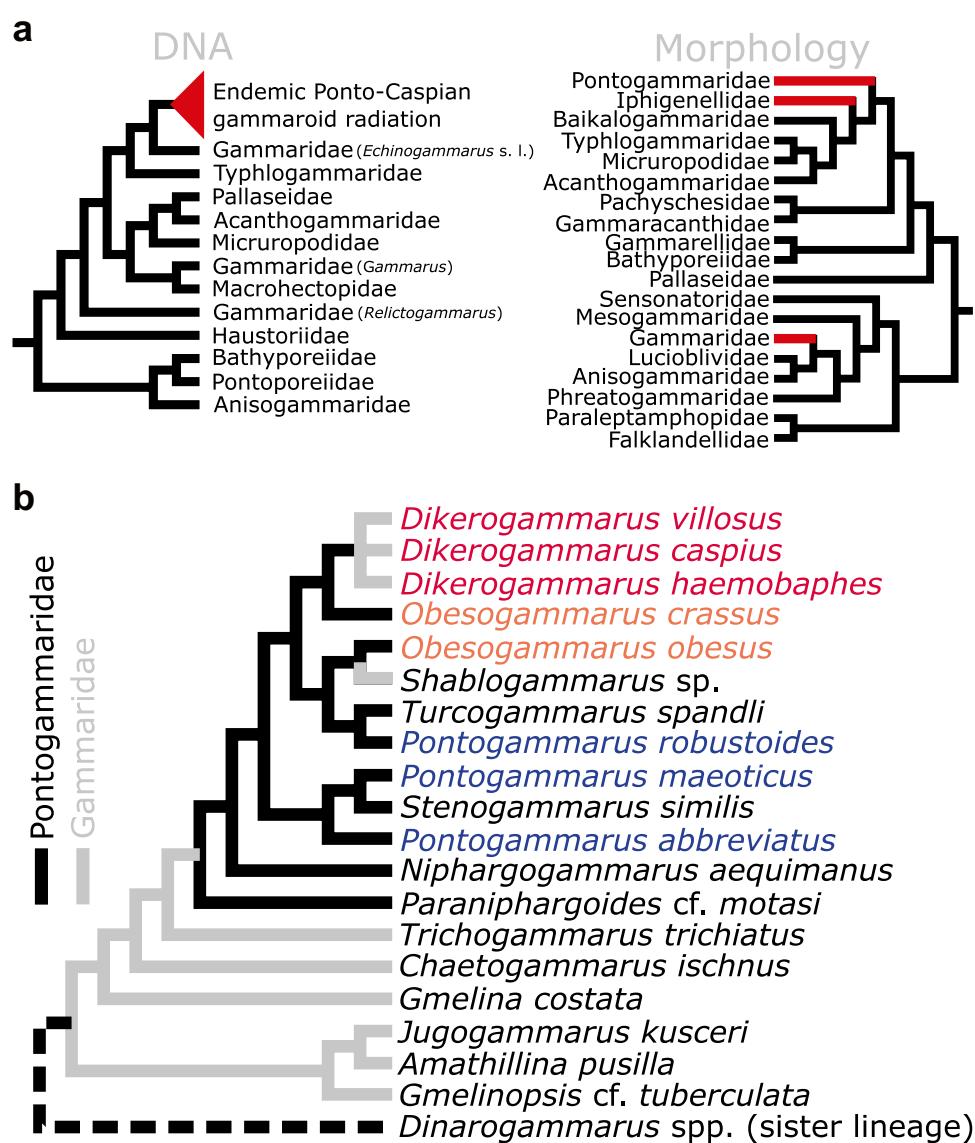
the endemic radiation as defined in this study is indeed monophyletic.

With respect to morphology, however, a recent phylogenetic analysis did not recover the families Pontogammaridae, Iphigenellidae and Gammaridae as a monophylum (Fig. 2a) (Lowry & Myers, 2013). It is important to point out that this analysis was performed only at family level, implicitly assuming family monophyly. It is possible that finer-scale cladistic analyses based on anatomical traits at species/genus level would recover different results. Indeed, the molecular data available thus far does not support the monophyly of the family Pontogammaridae since two nominal gammarid genera (*Dikerogammarus* and *Shablogammarus*) are nested within it (Fig. 2b) (Hou & Sket, 2016; Sket & Hou, 2018).

Apart from issues at the family level, the current molecular data also points out inconsistencies at the generic level. Specifically, the genera *Obesogammarus* and *Pontogammarus* are not monophyletic (Fig. 2b) (Hou et al., 2014; Sket & Hou, 2018), reflecting the morphologically fuzzy borders among these genera (Stock, 1974). The purpose of the current review is not to solve these taxonomic issues, but merely to point them out in order to be tackled in upcoming studies.

Taxonomic diversity

Since the discovery of Ponto-Caspian amphipods, efforts have been made to separate these species from their gammarid counterparts. Initially, Sars classified most of the endemic taxa (except of the marine Lysianassidae, Pontoporeiidae and Corophiidae) in the Gammaridae. Although the morphologically striking taxa were assigned to new genera (*Amathillina*, *Gmelina*, *Iphigenella*, etc.), most species were ascribed to the Holarctic genus *Gammarus* (Sars, 1894a, 1894b, 1895, 1896). However, due to a steady increase of new taxa, two new genera were erected, *Dikerogammarus*, and *Pontogammarus* (Sowinsky, 1904; Stebbing, 1899). Later on, based on a series of significant contributions (Birstein, 1945; Cărăuşu, 1943; Martynov, 1924; Stock, 1974), the *Dikerogammarus-Pontogammarus* complex sensu Stock (1974) was allocated to a separate family, Pontogammaridae, by Bousfield (1977). In addition, in the same study, Bousfield proposed several sub-groups within Pontogammaridae, but neither group has been given formal status (Karaman & Barnard, 1979). Meanwhile, Birstein (1945) created the monotypic Caspicolidae, while Kamaltynov proposed two additional small families, Iphigenellidae and Behningiellidae (Kamaltynov, 2001).

For an overview of taxonomic diversity, we compiled a checklist of all known taxa belonging to the endemic Ponto-Caspian gammaroid radiation 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.), Iphigenellidae (monotypic), and Pontogammaridae (11 genera, 37 spp.) (Fig. 3a). 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. 3a). 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 eighteenth to late nineteenth centuries, a sudden increase with Georg Ossian Sars' monographs in the late nineteenth century, followed by a more or less steady increase towards the present day with peaks of activity in the middle twentieth century by Russian and Romanian authors (Fig. 3b). A noticeable stagnation can be observed in the last two decades. By far, the most prolific author was G. O. Sars (36 spp.), followed by A. N. Derzhavin (10 spp.) and S. Cărăuşu (8 spp.) (Fig. 3b 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. In this key, we do not include the family Melitidae as the recently described Caspian species *Melita mirzajanii* Krapp-Schickel & Sket, 2015 (Krapp-Schickel & Sket, 2015) appears to be a junior synonym of the widespread Atlantic species *Melita nitida* S.I. Smith in Verrill, 1873 (Copilaş-Ciocianu et al., 2020b). The keys are mainly based on original character combinations, but we also drew from other published works (Birstein & Romanova, 1968; Karaman & Barnard, 1979; Stock, 1974).

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) (Cărăuşu, 1943; Cărăuşu 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

Table 1 Checklist, taxonomy and native distribution of the endemic Ponto-Caspian gammaroid radiation (including putative fossil taxa)

Family	Species	Authority	Distribution basin	Status	Taxonomic remarks
Behningiellidae	*Behningiella brachypus*	Derzhavin, 1948	Caspian	Valid	
Behningiellidae	*Cardiophilus baeri*	Sars, 1896	Caspian	Valid	
Behningiellidae	*Cardiophilus marisnigrae*	Miloslavskaja, 1931	Ponto-Azov	Valid	Original spelling: *C. maris-nigirs*. Emended by Barnard (1958) Synonyms: *Cardiophilus miloslavskajae* Cărăuşu, 1955
Behningiellidae	*Zernovia volgensis*	Derzhavin, 1948	Caspian	Valid	
Caspicolidae	*Caspicola knipovitschi*	Derzhavin, 1944	Caspian	Valid	Original spelling: *Caspiella knipovitschi*. Emended by Birstein 1945
Gammaridae	*Akerogammarus contiguus*	(Pjatakova, 1962a)	Caspian	Valid	
Gammaridae	*Akerogammarus knipowitschi*	Derzhavin & Pjatakova, 1967	Caspian	Valid	
Gammaridae	*Amathillina affinis*	Sars, 1894a	Caspian	Valid	
Gammaridae	*Amathillina cristata*	Sars, 1894a	Caspian, Ponto-Azov	Valid	
Gammaridae	*Amathillina maximowiczi*	Sars, 1896	Caspian	Valid	
Gammaridae	*Amathillina pusilla*	Sars, 1896	Caspian	Valid	
Gammaridae	*Amathillina spinosa*	Sars, 1896	Caspian	Valid	
Gammaridae	*Axelboeckia spinosa*	(Sars, 1894a)	Caspian	Valid	Original spelling: *Boeckia spinosa*. Emended by Birstein 1945
Gammaridae	*Baku paradoxus*	(Derzhavin in Derzhavin & Pjatakova, 1967)	Caspian	Valid	
Gammaridae	*Cephalogammarus macrocephalus*	(Sars, 1896)	Caspian	Valid	Possibly a derived *Dikerogammarus*
Gammaridae	*Chaetogammarus hyrcanus*	Pjatakova, 1962a	Caspian	Valid	
Gammaridae	*Chaetogammarus ischnus*	(Stebbing, 1899)	Caspian, Ponto-Azov	Valid	Nom. nov. for *Gammarus tenellus* Sars, 1896; Synonyms: *Gammarus sowinskyi* (Behning, 1914)
Gammaridae	*Chaetogammarus pauxillus*	(Sars, 1896)	Caspian	Valid	
Gammaridae	*Chaetogammarus placidus*	(Sars, 1896)	Caspian, Ponto-Azov	Valid	
Gammaridae	*Chaetogammarus warpachowskyi*	(Sars, 1894b)	Caspian, Ponto-Azov	Valid	Reassessment of generic status needed. Close morphological affinities with *Gmelina/Kuzmelina*
Gammaridae	*Derzhavinella cava*	Stock et al., 1998	Caspian	Valid	
Gammaridae	*Derzhavinella macrochelata*	Birstein, 1938	Caspian	Valid	
Gammaridae	*Dikerogammarus aralychensis*	(Birstein, 1932)	Caucasus	Doubtful	Probably junior synonym of *Pontogammarus setosus* (Schäferna, 1914). Further research needed
Gammaridae	*Dikerogammarus bispinosus*	Martynov, 1925a	Caspian, Ponto-Azov	Valid	
Gammaridae	*Dikerogammarus caspius*	(Pallas, 1771)	Caspian	Valid	

Table 1 (continued)

Family	Species	Authority	Distribution basin	Status	Taxonomic remarks
Gammaridae	*Dikerogammarus fluviatilis*	Martynov, 1919	Caspian, Ponto-Azov	Doubtful	Initially described by Martynov 1919 as a morph of *D. haemobaphes* (Eichwald, 1841). Further research needed
Gammaridae	*Dikerogammarus gruberi*	Mateus & Mateus, 1990	Ponto-Azov	Valid	
Gammaridae	*Dikerogammarus haemobaphes*	(Eichwald, 1841)	Caspian, Ponto-Azov	Valid	Synonym: *Dikerogammarus balatonicus* Pony, 1958
Gammaridae	*Dikerogammarus istanbulensis*	Özbek & Özkan, 2011	Ponto-Azov	Valid	Apparently very similar to *D. haemobaphes* (Eichwald, 1841). Further research needed
Gammaridae	*Dikerogammarus oskari*	Birstein, 1945	Caspian	Valid	Nom. nov. for *Gammarus grimmi* Sars, 1896
Gammaridae	*Dikerogammarus villosus*	(Sowinsky, 1894)	Caspian, Ponto-Azov	Valid	
Gammaridae	*Gmelina aestuarica*	Cărăuşu, 1943	Ponto-Azov	Valid	
Gammaridae	*Gmelina costata*	Sars, 1894a	Caspian, Ponto-Azov	Valid	
Gammaridae	*Gmelinopsis aurita*	Sars, 1896	Caspian	Valid	
Gammaridae	*Gmelinopsis tuberculata*	Sars, 1896	Caspian, Ponto-Azov	Valid	
Gammaridae	*Kuzmelina kusnezowi*	(Sowinsky, 1894)	Caspian, Ponto-Azov	Valid	
Gammaridae	*Jugogammarus kusceri*	(Karaman, 1931)	Balkan	Valid	
Gammaridae	*Lanceogammarus andrussowi*	(Sars, 1896)	Caspian, Ponto-Azov	Valid	
Gammaridae	*Scytaelina simplex*	Stock et al., 1998	Caspian	Valid	
Gammaridae	*Shablogammarus shablensis*	(Cărăuşu, 1943)	Caspian, Ponto-Azov	Valid	Original spelling: *Gammarus chablensis*. Emended by Cărăuşu et al. (1955)
Gammaridae	*Sowinskya macrocera*	Derzhavin, 1948	Caspian	Valid	
Gammaridae	*Trichogammarus trichiatus*	(Martynov, 1932)	Ponto-Azov	Valid	We do not agree that *Chaetogammarus tenellus major* Cărăuşu, 1943 is a junior synonym. Further study is needed
Gammaridae	*Yogmelina brachyura*	(Derzhavin & Pjatakova, 1962)	Caspian	Valid	
Gammaridae	*Yogmelina laeviuscula*	(Sars, 1896)	Caspian	Valid	
Gammaridae	*Yogmelina limana*	Karaman & Barnard, 1979	Ponto-Azov	Valid	
Gammaridae	*Yogmelina ovata*	(Martynov, 1924)	Ponto-Azov	Doubtful	Probably junior synonym of *Chaetogammarus warpachowskyi*. Further study is needed
Gammaridae	*Yogmelina pusilla*	(Sars, 1896)	Caspian, ?Ponto-Azov	Valid	
Iphigenellidae	*Iphigenella acanthopoda*	Sars, 1896	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Compactogammarus compactus*	(Sars, 1895)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Niphargogammarus aequimanus*	(Sars, 1895)	Caspian	Valid	
Pontogammaridae	*Niphargogammarus borodini*	(Sars, 1897)	Caspian	Valid	
Pontogammaridae	*Niphargogammarus intermedius*	(Cărăuşu, 1943)	Ponto-Azov	Valid	
Pontogammaridae	*Niphargogammarus quadrimanus*	(Sars, 1895)	Caspian	Valid	

Table 1 (continued)

Family	Species	Authority	Distribution basin	Status	Taxonomic remarks
Pontogammaridae	*Niphargoides boltovskoyi*	Derzhavin & Pjatakova, 1968	Caspian	Valid	
Pontogammaridae	*Niphargoides caspius*	Sars, 1894b	Caspian	Valid	
Pontogammaridae	*Niphargoides corpulentus*	Sars, 1895	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Niphargoides grimmi*	Sars, 1896	Caspian	Valid	
Pontogammaridae	*Obesogammarus acuminatus*	Stock et al., 1998	Caspian	Valid	
Pontogammaridae	*Obesogammarus boeoticus*	(Schellenberg, 1944)	Balkan	Valid	Poorly described, generic status needs revision
Pontogammaridae	*Obesogammarus crassus*	(Sars, 1894b)	Caspian, Ponto-Azov	Valid	Synonyms: *Obesogammarus crassus* f. *medi-odanubialis* (Karaman, 1953)
Pontogammaridae	*Obesogammarus obesus*	(Sars, 1894b)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Obesogammarus olvianus*	(Sowinsky, 1904)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Obesogammarus platycheir*	(Sars, 1896)	Caspian	Valid	
Pontogammaridae	*Obesogammarus subnudus*	(Sars, 1896)	Caspian, Ponto-Azov	Valid	Provisionally placed in *Obesogammarus*. Generic status needs revision
Pontogammaridae	*Pandorites podoceroides*	Sars, 1895	Caspian	Valid	
Pontogammaridae	*Paraniphargoides derzhavini*	(Pjatakova, 1962b)	Caspian	Valid	
Pontogammaridae	*Paraniphargoides motasi*	(Cărăuşu, 1943)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Pontogammarus abbreviatus*	(Sars, 1894b)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Pontogammarus aestuarius*	(Derzhavin, 1924)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Pontogammarus borceae*	Cărăuşu, 1943	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Pontogammarus palmatus*	(Martynov, 1925b)	Caspian	Doubtful	Poor description without illustrations
Pontogammaridae	*Pontogammarus robustoides*	(Sars, 1894b)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Pontogammarus setosus*	(Schäferna, 1914)	Caucasus	Valid	
Pontogammaridae	*Pontogammarus* (=*Euxinia*) *maeoticus*	(Sowinsky, 1894)	Caspian, Ponto-Azov	Valid	Removed to *Pontogammarus* since *Euxinia* Tucolesco, 1933 is preoccupied by the platyhelminth genus *Euxinia* Graff, 1911. According to ICZN articles 23.1 and 52.4 Synonyms: *Euxinia fagei* Tucolesco 1933
Pontogammaridae	*Pontogammarus* (=*Euxinia*) *sarsi*	(Sowinsky, 1898)	Caspian, Ponto-Azov	Valid	Removed to *Pontogammarus* since *Euxinia* Tucolesco, 1933 is preoccupied by the platyhelminth genus *Euxinia* Graff, 1911. According to ICZN articles 23.1 and 52.4
Pontogammaridae	*Pontogammarus* (=*Euxinia*) *weidemanni*	(Sars, 1896)	Caspian, Ponto-Azov	Valid	Removed to *Pontogammarus* since *Euxinia* Tucolesco, 1933 is preoccupied by the platyhelminth genus *Euxinia* Graff, 1911. According to ICZN articles 23.1 and 52.4
Pontogammaridae	*Stenogammarus compressus*	(Sars, 1894b)	Caspian, Ponto-Azov	Valid	

Table 1 (continued)

Family	Species	Authority	Distribution basin	Status	Taxonomic remarks
Pontogammaridae	*Stenogammarus compressosimilis*	Cărăuşu 1955	Caspian, Ponto-Azov	Valid	Original spelling: *S. compresso-similis* Emended according to ICZN article 32.5.2.3 Synonyms: *Stenogammarus kereuschi* Derzhavin & Pjatakova, 1962 according to ICZN article 23.3.7
Pontogammaridae	*Stenogammarus deminutus*	(Stebbing, 1906)	Caspian, Ponto-Azov	Valid	Nom. nov. for *Gammarus minutus* Sars, 1894b
ontogammaridae	*Stenogammarus macrurus*	(Sars, 1894b)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Stenogammarus micrurus*	Derzhavin & Pjatakova, 1996	Caspian	Valid	
Pontogammaridae	*Stenogammarus similis*	(Sars, 1894b)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Turcogammarus aralensis*	(Uljanin, 1875)	Aral, Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Turcogammarus spandli*	(Karaman, 1931)	Balkan	Valid	
Pontogammaridae	*Turcogammarus turcarum*	(Stock, 1974)	Caucasus	Doubtful	Probably junior synonym of *Pontogammarus setosus* (Schäferna, 1914). Further research needed
Pontogammaridae	*Uroniphargoides spiniccaudatus*	(Cărăuşu, 1943)	Caspian, Ponto-Azov	Valid	
Pontogammaridae	*Wolgagammarus dzjubani*	(Mordukhai-Boltovskoi & Lyakhov, 1972)	Caspian	Valid	
Fossil taxa					
Pontogammaridae	*Andrussovia bogacevi*	Derzhavin, 1927†	Caspian	Valid	
Pontogammaridae	*Andrussovia sokolovi*	Derzhavin, 1927†	Caspian	Valid	
Pontogammaridae	*Andrussovia vassoievitschi*	Derzhavin, 1941†	Caspian	Valid	
Pontogammaridae	*Praegmelina andrussovi*	Derzhavin, 1927†	Caspian	Valid	
Pontogammaridae	*Praegmelina archangelskii*	Derzhavin, 1927†	Caspian	Valid	
Hellenidae	*Hellenis saltatorius*	Petunnikoff, 1914†	Caspian	Valid	Uncertain affiliation with extant Ponto-Caspian taxa

† fossil taxa

Fig. 3 (a) Species richness within genera and families. Only valid and extant species were considered. (b) Trends in species descriptions through time. The thick grey 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
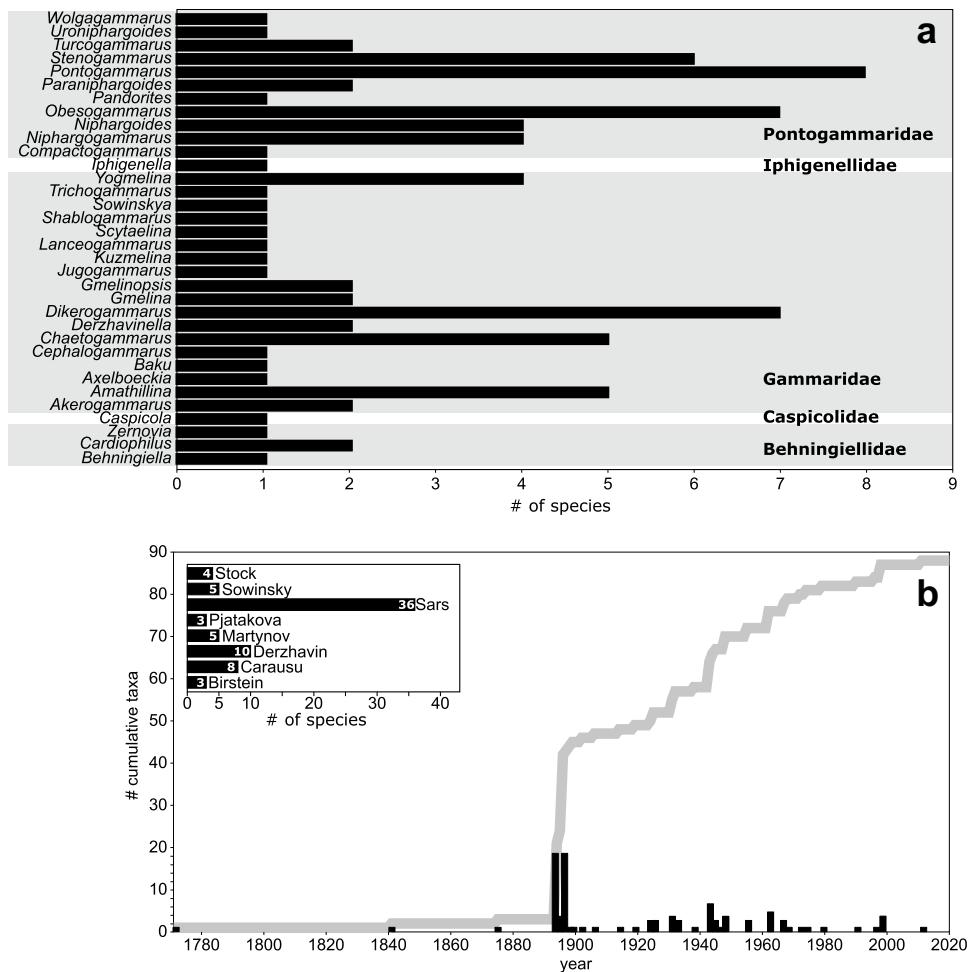
included. We acknowledge that these illustration obtained ratios do not provide the most exhaustive nor precise morphological detail. However, given that these data have a broad taxonomic coverage, we consider this analysis as a crucial preliminary step in quantifying and understanding the morphological 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 ratios + 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. 4. Body size varies by almost an order of magnitude (3.5 to 27 mm) (Figs. 4 and 8). The PCA plot indicates significant morphological disparity (Fig. 5). 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. 5a; Figs. S2, S3 and S4). 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. 5a; Figs. S2, S3 and S4). A biplot is presented in Supplementary information Fig. S2. Values for PCA loadings and PCA scores are shown in Tables S3 and S4, respectively.

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. 4).

Most genera seem to be relatively well defined in morphospace. However, *Amathillina* and *Obesogammarus* overlap broadly with other genera (Fig. 5a). The monotypic genera (shown with black and white symbols in Fig. 5a) are generally distinct from the more speciose ones, often lying towards the extreme ends of the morphological gradients.
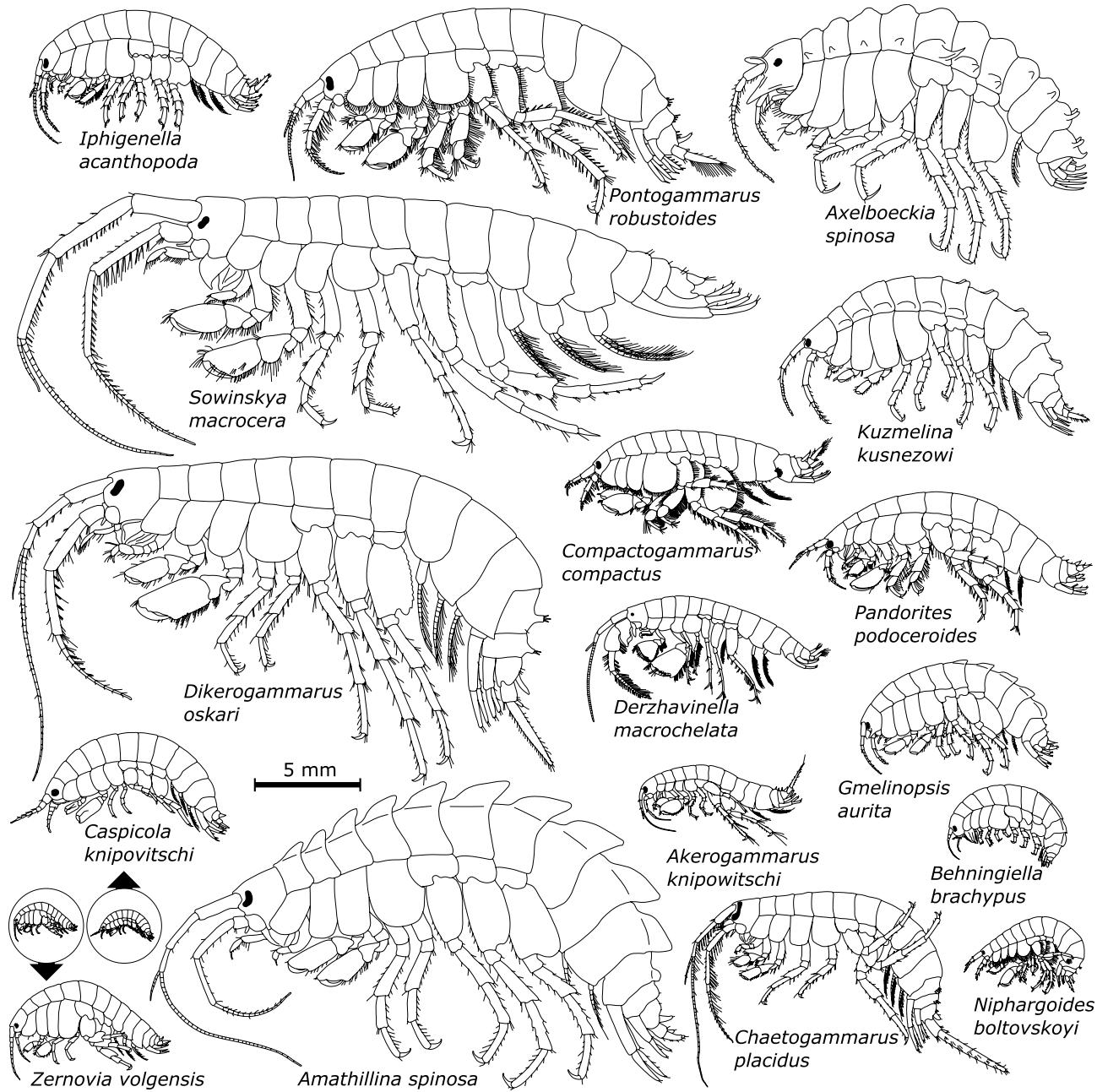
Fig. 4 Habitus and morphological diversity of the endemic Ponto-Caspian gammaroid radiation. *Caspicola knipovitschi* and *Zernovia volgensis* are shown to scale in circles and enlarged outside the circles. All images are redrawn after the original

Ecology

To provide a synopsis of ecology, we reviewed all the original species descriptions and the relevant literature (Birstein & Romanova, 1968; Pjatakova & 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. 6). With respect

Fig. 5 (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

Proposed ecomorphs
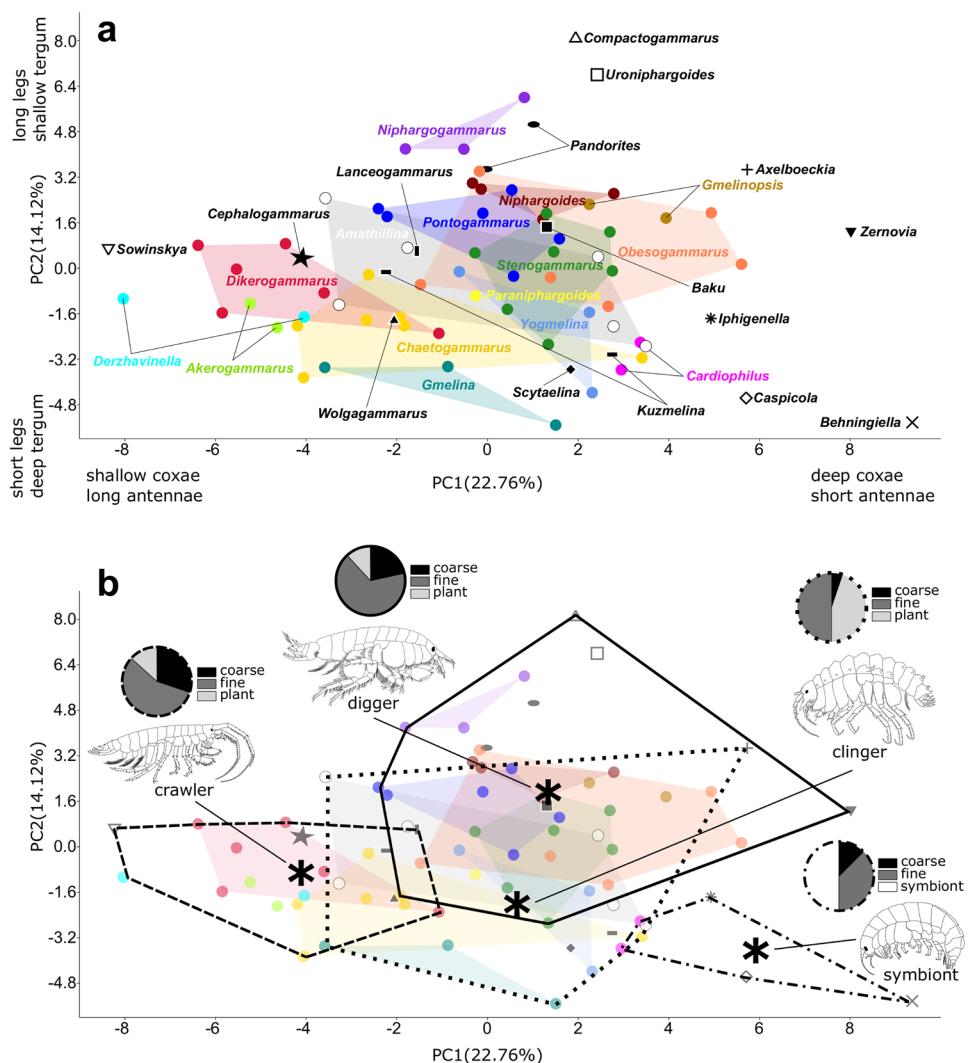
to salinity, it appears that most species are euryhaline, tolerating both fresh as well as brackish waters. However, salinity preference is not known for many species. With respect to substrate, the great majority of species occur on sandy and muddy substrates, followed by stones and plants. Four species seem to be associated with other organisms such as bivalve molluscs and crayfish (Table 2; Fig. 6). All of the ecological data is summarized in Table 2.

The depth gradient is broad, ranging from the wet sand of the supra-littoral to more than 500 m depth (Table 2; Fig. 7). 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) and then rapidly decreases to below 10 species in the 250–550-m interval (Fig. 7). The only species known to occur at depths greater than 500 m is *Chaetogammarus pauxillus*.

By integrating morphology and substrate type, we aimed to classify the species into putative ecomorphs. Specifically, we looked for common morphological characteristics among taxa, while taking into account their similarity in PCA morphospace. We also took into account previous informal groupings of genera (Barnard & Barnard, 1983). Once these groups were identified, their substrate preference was established by estimating the proportion of species occurring on a particular substrate. The substrate classification was simplified and divided into four groups: coarse (corresponding to stones and gravel), fine (corresponding to sand, mud and clay), plant and symbiotic. We acknowledge that this is a somewhat arbitrary approach. However, more sophisticated analyses could not be performed given the scarce data at hand. Quantitative data regarding ecology (substrate or trophic niche)

Table 2 Ecological diversity of the endemic Ponto-Caspian gammaroid radiation

Species	Min. depth	Max. depth	Sto[1]	San[2]	Mud	Cla[3]	Pla[4]	Symbiont	Salinity	Sea	Lag[5]	Res[6]	Riv[7]	Spr[8]	Ecomorph
Behningiella brachypus	10	30	x	x					?	x					Symbiont
Cardiophilus baeri	7	92			?	?		Cardium	?	x					Symbiont
Cardiophilus marisnigrae	16	80		x		x		Mytilus	?	x					Symbiont
Zernovia volgensis	2	100							?	x			x		Digger
Caspicola knipovitschi	1.5	29		x				Possibly molluscs	Euryh	x			x		Symbiont
Akerogammarus contiguus	0.2	50	x	x	x				?	x					Crawler
Akerogammarus knipowitschi	30	105			x				?	x					Crawler
Amathillina affinis	3.5	75					x		Euryh	x					Clinger
Amathillina cristata	0.5	75					x		Euryh	x	x		x		Clinger
Amathillina maximowiczi	10	220					?		?	x	x				Clinger
Amathillina pusilla	7	204					x		?	x					Clinger
Amathillina spinosa	6.4	274		x	x		?		Euryh	x					Clinger
Axelboeckia spinosa	5	150			?		x		Euryh	x			x		Clinger
Baku paradoxus	25	100			x				?	x					Digger
Cephalogammarus macrocephalus	35	75			x				?	x					Crawler
Chaetogammarus hyrcanus		98			x				?	x					Crawler
Chaetogammarus ischnus	0	300	x	x	x		x		Euryh	x	x	x	x		Crawler
Chaetogammarus pauxillus	7	538		x					Euryh	x	x				Crawler
Chaetogammarus placidus	5	200			x				Euryh	x		x	x		Crawler
Chaetogammarus warpachowskyi	0.5	10	x	x	x		x		Euryh	x	x	x	x		Clinger
Derzhavinella cava	45	100							?	x		x			Crawler
Derzhavinella macrochelata	15	75			x				?	x					Crawler
Dikerogammarus aralychensis	0.2	3		x	x				Stenoh		x	x	x		Digger
Dikerogammarus bispinosus	0	7	x	x					Euryh	x	x	x	x		Crawler
Dikerogammarus caspius	1.2	60	x						Euryh	x	x	x	x		Crawler
Dikerogammarus fluviatilis	0	15	x	x	x		x		Euryh				x		Crawler
Dikerogammarus gruberi									?			x			?
Dikerogammarus haemobaphes	0	118	x	x	x				Euryh	x	x	x	x		Crawler
Dikerogammarus istanbulensis	0.2	1			x				?			x			Crawler
Dikerogammarus oskari	35	197			x				?	x					Crawler
Dikerogammarus villosus	0	2	x				x		Euryh	x	x	x	x		Crawler
Gmelina aestuarica	0	2		x	x	x			Euryh		x		x		Clinger
Gmelina costata	0	38	x	x			x		Euryh	x			x		Clinger
Gmelinopsis aurita	25	197							?	x					Digger

Table 2 (continued)

Species			Salinity		Notes	Mode
Gmelinopsis tuberculata	10	100	Euryh			Digger
Kuzmelina kusnezowi	1	4	Euryh			Clinger
Jugogammarus kusceri	0	1	Stenoh			Clinger
Lanceogammarus andrussowi	0.5	260	Euryh			Crawler
Scytaelina simplex		75	?			Clinger
Shablogammarus shablensis	0	1.5	Euryh			Crawler
Sowinskya macrocera		73	?			Crawler
Trichogammarus trichiatus	0	2	Euryh			Crawler
Yogmelina brachyura	0.3	98	?			Clinger
Yogmelina laeviuscula	29	200	?			Clinger
Yogmelina limana		1	Euryh			Clinger
Yogmelina pusilla	1	8	Euryh			Clinger
Iphigenella acanthopoda	1	60	Euryh		Possibly Astacidae	Symbiont
Compactogammarus compactus	6	50	Euryh			Digger
Niphargogammarus aequimanus	4	100	Stenoh			Digger
Niphargogammarus borodini	3	26	?			Digger
Niphargogammarus intermedius	1	16	Euryh			Digger
Niphargogammarus quadrimanus	4	260	Stenoh			Digger
Niphargoides boltovskoyi	96	311	?			Digger
Niphargoides caspius	20	200	Stenoh			Digger
Niphargoides corpulentus	1	165	Euryh			Digger
Niphargoides grimmi	10	400	Stenoh			Digger
Obesogammarus acuminatus	0.2	1	Euryh			Digger
Obesogammarus boeoticus	0.2	1	Stenoh			Digger
Obesogammarus crassus	0.2	197	Euryh			Digger
Obesogammarus obesus	0.5	15	Euryh			Digger
Obesogammarus olvianus	0.5	7	Euryh			Digger
Obesogammarus platycheir	1	10	Euryh			Digger
Obesogammarus subnudus	3	75	?			Digger
Pandorites podoceroides	4	480	Euryh			Digger
Paraniphargoides derzhavini	10	90	?			Digger
Paraniphargoides motasi	3	150	?			Digger
Pontogammarus abbreviatus	0.5	25	Euryh			Digger
Pontogammarus aestuarius	1.5	12	Euryh			Digger
Pontogammarus borceae	0	0.1	Euryh			Digger
Pontogammarus maeoticus	0	10	Euryh			Digger
Pontogammarus robustoides	0	198	Euryh			Digger

Table 2 (continued)

Species			Stony[1]	Sandy[2]	Clay[3]	Plant[4]	Lagoon[5]	Halinity	Reservoir/lake[6]	River[7]	Spring[8]	Feeding
Pontogammarus sarsi	0.5	15		x	x	x	x	Euryh	x	x	x	Digger
Pontogammarus setosus	0	2	x		x	x		Stenoh		x	x	Digger
Pontogammarus weidemanni	0	5		x			x	Euryh			x	Digger
Stenogammarus compressus	1	100		x	x		x	Euryh	x	x		Digger
Stenogammarus compressosimilis	3.5	9	x	x	x	x		Euryh	x	x		Digger
Stenogammarus deminutus	1	120		x	x	x		Euryh	x	x	x	Digger
Stenogammarus macrurus	1	100	x	x	x	x		Euryh	x	x	x	Digger
Stenogammarus micrurus	84	84		x	x			?				Digger
Stenogammarus similis	1	100	x	x	x	x	x	Stenoh	x			Digger
Turcogammarus aralensis	0	10	x	x				Euryh	x	x		Digger
Turcogammarus spandli	0	0.5	x					Stenoh	x	x	x	Crawler
Turcogammarus turcarum	0	1	x	x				Stenoh		x	x	Crawler
Uroniphargoides spinicaudatus	2	10	x	x	x		x	Stenoh	x	x		Digger
Wolgagammarus dzjubani	1	8	x	x	x			Stenoh	x	x	x	Digger

[1]Stony
[2]Sandy
[3]Clay
[4]Plant
[5]Lagoon
[6]Reservoir/lake
[7]River
[8]Spring

Fig. 6 Number of species occurring on various substrates, habitats and salinities
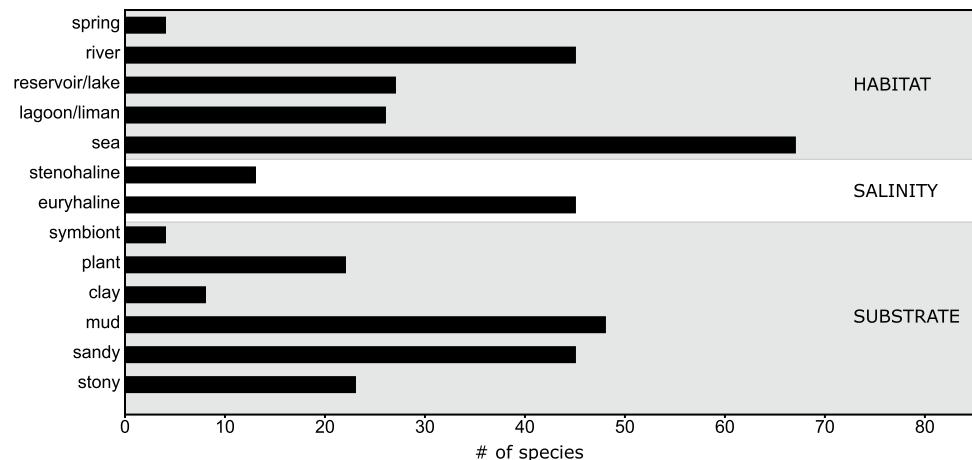
are only limited to a few invasive species that have spread beyond the Ponto-Caspian realm. Likewise, morphology is incompletely known in many species (especially mouthparts). We emphasize that our goal here was to provide a first exploratory step into understanding the connection between morphology and ecology.

We tentatively defined four ecomorphs: clingers, crawlers, diggers and symbionts. Loosely, these ecomorphs correspond with the currently recognized families and informal groupings of Barnard and Barnard (1983): crawlers with Gammaridae or "Echinogammarids" + "Dikerogammarids" (sensu Barnard & Barnard, 1983), clingers with Gammaridae or "Gmelinids" (sensu Barnard & Barnard, 1983), diggers with Pontogammaridae or "Pontogammarids" + "Compactogammarids"

(sensu Barnard & Barnard, 1983) and symbionts with Behningiellidae, Caspicolidae and Iphigenellidae or "Cardiophilids" (sensu Barnard & Barnard, 1983). Below we describe the morphological and ecological peculiarities of each ecomorph.

(1) Clinger. Stout body often keeled and/or ornamented with spines and tubercles, antennae are slender, short to medium length, coxal plates medium to deep, gnathopods weak and pereopods short to medium length with pairs 3–4 strongly opposable to pairs 5–7 (Fig. 8). Clingers are intermediate in morphospace between crawlers and diggers, although there is significant overlap with the latter group (Fig. 5b). Most species
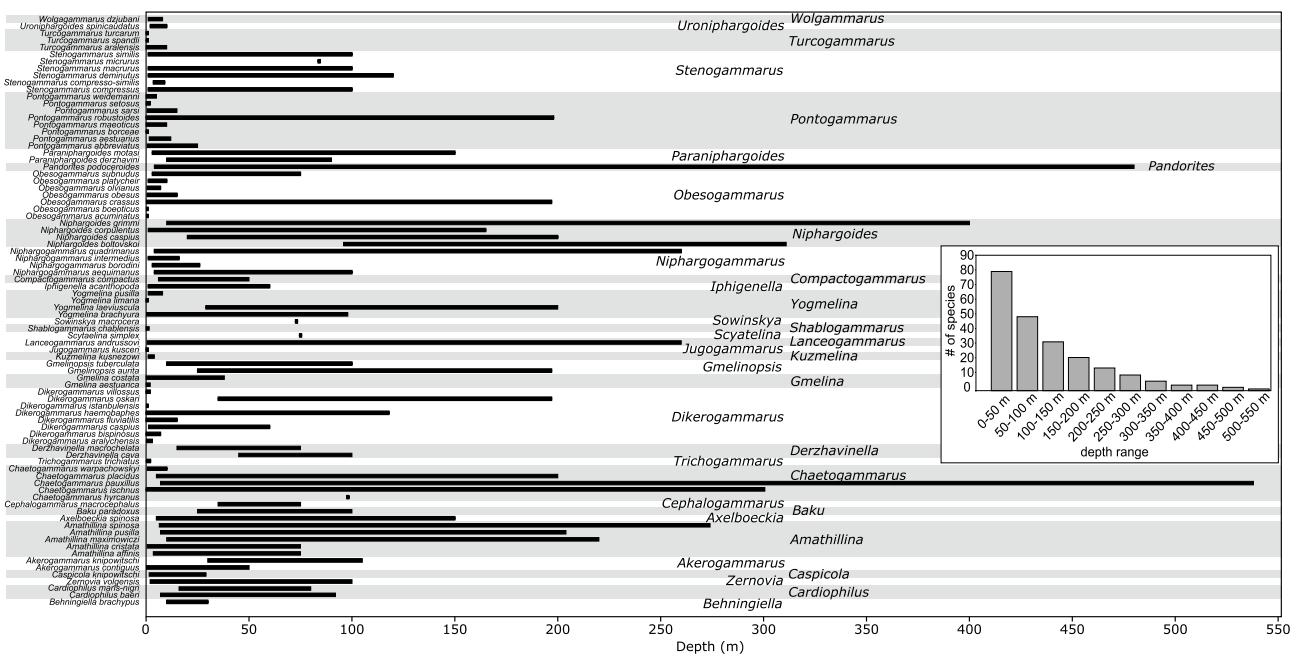

Fig. 7 Depth ranges structured by taxonomic composition. The inset graph depicts the number of species occurring in 50 m depth intervals
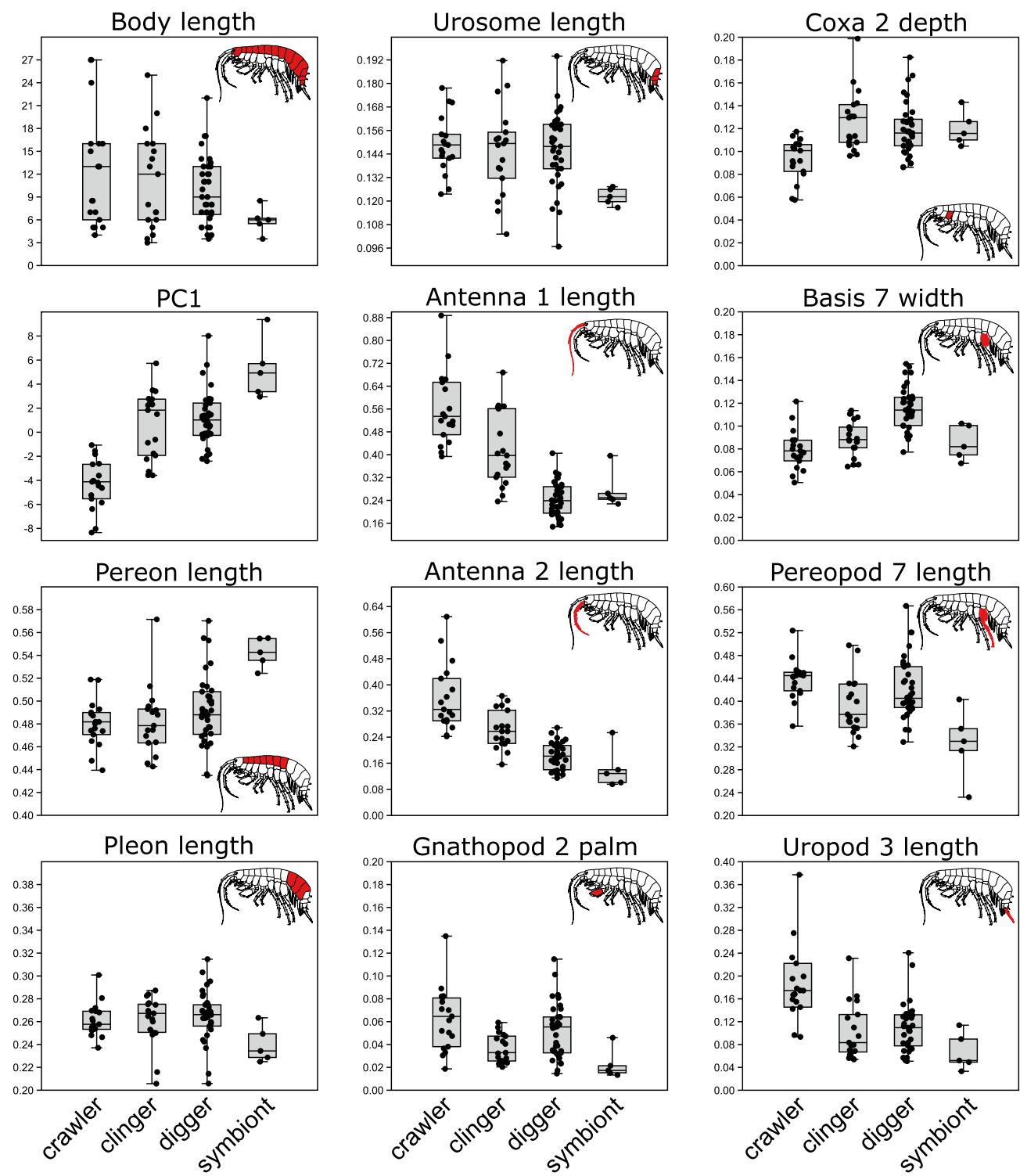
Fig. 8 Boxplots comparing selected traits among the four proposed ecomorphs. PC1 refers to the first principal component resulting from the PCA analysis. It mainly describes the gradient from slender bodies with long antennae (negative values) to stout bodies with short antennae (positive values). All traits except body length and PC1 values are presented relative to total body length

are associated with plants and fine substrate (Fig. 5b). Around 19% of all species belong to this ecomorph. Taxonomic composition is given in Table 2. Representative genera: *Axelboeckia* and *Gmelina*.

(2) Crawler. Body is slender and generally smooth, antennae are long and slender, coxal plates shallow, pereopods slender, short to medium, gnathopods generally strong and uropods long (Fig. 8). It is generally well-defined in morphospace having little overlap with clingers and diggers (Fig. 5b). Species are mainly associated with fine and coarse substrates (Fig. 5b). Around 26% of species belong to this ecomorph. Taxonomic composition is given in Table 2. Representative genera: *Chaetogammarus* and *Dikerogammarus*.

(3) Digger. Stout and fusiform body and almost exclusively smooth, antennae very short and thick, with 1st article of antenna 1 often swollen, coxal plates deep, gnathopods generally strong, pereopods medium to long, with broadened articles often fringed with long and dense setae (Fig. 8). Diggers are very distinct in morphospace from crawlers and symbionts, but overlap noticeably with clingers (Fig. 5b). Species of this ecomorph predominantly occur on fine substrates and are characterized by a fossorial behaviour (Fig. 5b). 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, and usually characterized by diminished mouthparts (palps of maxilla 2 and maxilliped), pleon, urosome, antennae and pereopods (Fig. 8). 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. 5b). Its species are known to live on or inside bivalve molluscs (*Cardiophilus* and *Caspicola*), commensals with crayfish (*Iphigenella*) or even occurring in the marsupium (brood chamber) of other amphipods (*Cardiophilus*) (Derzhavin, 1944; Mirzajani & Vonk, 2006; Osadchikh, 1977; Sars, 1896). This ecomorph is the rarest and accounts for 6% of all species. Taxonomic composition is given in Table 2. Representative genera: *Cardiophilus* and *Iphigenella*.

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 gammaroid amphipods — an adaptive radiation?

The main characteristics that define an adaptive radiation are as follows: 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 & Tarasov, 1996). A significant number of species are also found in sympatry in the Ponto-Azov region (Cărăuşu 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 (Fig. 2) (Copilaş-Ciocianu et al., 2020a; Hou & Sket, 2016; Hou et al., 2014; Sket & 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 in the context of adaptive radiation. 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 millimetres), stout-bodied symbiotic species with attenuated appendages, to large and slender (several centimetres), stocky and setose or heavily armoured 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 criteria that define an adaptive radiation. 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 (Copilaș-Ciocianu et al., 2021; Kralj-Fišer et al., 2020; Premate et al., 2021). Furthermore, it is important to test whether these ecomorphs have a common ancestor or evolved several times independently (Borko et al., 2021; 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 (Naumenko et al., 2017). A well-sampled time-calibrated molecular phylogeny could also prove invaluable for understanding the historical circumstances that promote the evolution of species prone to becoming invasive.

Morphological evolution

Recent molecular phylogenies revealed that the morphologically diverse Ponto-Caspian gammaroid radiation (comprising several families) is nested within the *Echinogammarus* clade (Hou & Sket, 2016; Sket & 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 & Barnard, 1983). A similar pattern is also encountered in the two highly diverse Baikal amphipod radiations which are classified into several families (Hou & Sket, 2016; Lowry & 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 (Copilaș-Ciocianu & 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 *Hyalella* 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 & 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 lifestyle and a conserved, non-specialized morphology (Wellborn & 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 & 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.

We propose that the ecological and morphological diversity of Ponto-Caspian gammaroids 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. 9 and 10). 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 lifestyle. We highlight a striking resemblance between the Ponto-Caspian genus *Behningiella* and the oceanic algae-boring genus *Bircenna* Chilton, 1884 (Fig. 9a). 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 *Pachyschesis* (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, fusiform, 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 & Myers, 2017). However, molecular phylogenies indicate that the fossorial body type evolved multiple times independently (Copilaș-Ciocianu et al., 2020a; Hancock et al., 2021). A noticeable resemblance can be observed between the Ponto-Caspian genus *Compactogammarus* and the hyaloidean *Proboscinotus* Barnard, 1967 (Fig. 9b). Additionally, in Lake Baikal, this ecomorph is possibly represented by the Micruropodidae 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

Fig. 9 Examples of putative ecomorphological convergence of Ponto-Caspian and distantly related oceanic taxa. Ponto-Caspian species are shown with a green star. **(a)** Symbiotic ecomorph adapted to piercing various organic substrates (redrawn from Derzhavin (1948) and Lorz 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 lifestyle, 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. (2020a)
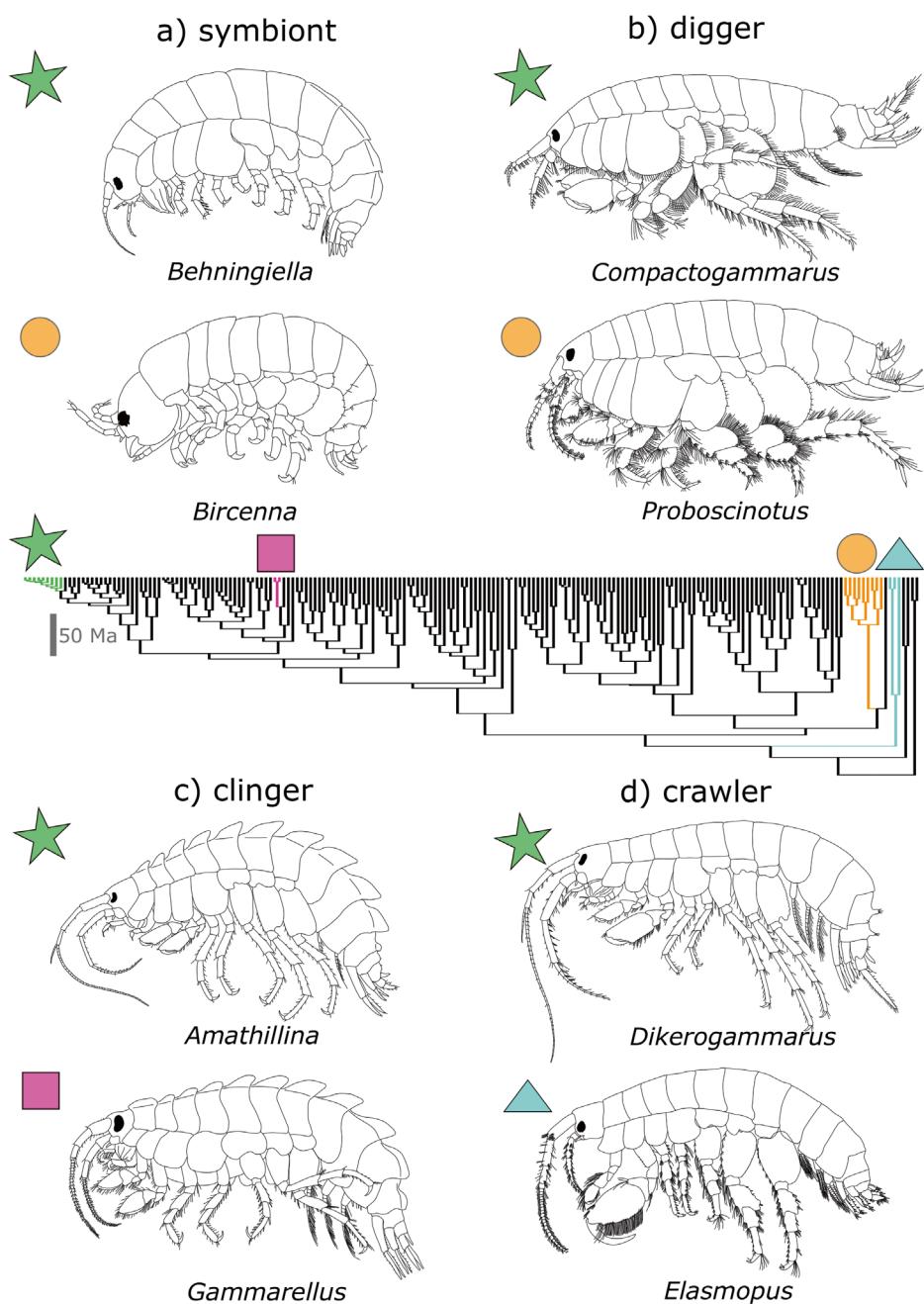
(plant) substrate. These species often have elongated and curved dactyls for improved grasping of the substrate. Given the exposed nature of their lifestyle, the armature might serve as protection against predators (Bollache et al., 2006; Copilaş-Ciocianu et al., 2020c) or, in combination with variegated coloration (as is often the case with armoured taxa), may act as camouflage by disrupting the body contour (d'Udekem d'Acoz & Verheye, 2017). We point out the high similarity among the Ponto-Caspian genus *Amathillina* and the oceanic algae-clinging *Gammarellus* Herbst, 1793

(Fig. 9c). Although the Ponto-Caspian clingers are diverse in ornamentation and armature, some striking resemblance can be observed with Baikal Lake taxa as well, for example, *Amathillina* and Baikalian *Eucarinogammarus*; *Axelboeckia* and Baikalian *Acanthogammarus*; and *Kuzmelina* and Baikalian *Propachygammarus* (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,
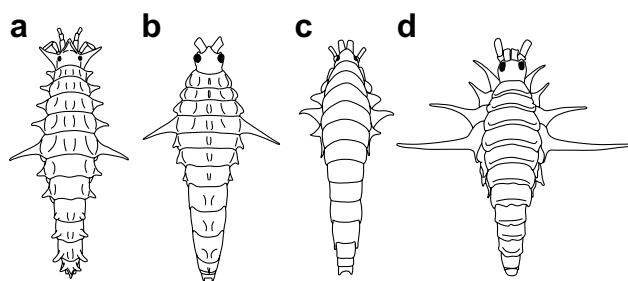
Fig. 10 Examples of evolutionary convergent patterns in body armature of species inhabiting various ancient lakes. (**a**) *Axelboeckia spinosa* (Caspian Sea, redrawn after Sars (1894b)), (**b**) *Acanthogammarus lappaceus* (Lake Baikal, redrawn after Daneliya et al. (2011)), (**c**) *Issykogammarus hamatus* (Lake Issyk-Kul, redrawn after Chevreux (1908)) and (**d**) *Hyalella armata* (Lake Titicaca, redrawn after González and Coleman (2002))

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 (Copilaș-Ciocianu et al., 2020; Lowry & 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. 9d). 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 (Copilaș-Ciocianu et al., 2020a; Lowry & 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. 10). In some cases the spine is an outgrowth of the tergum, while in others an outgrowth of the coxal plate. These analogous convergent structures indicate that they are the product of strong selective pressure. Most likely these spines function as a mechanism for deterring ingestion by predatory fish (Bollache et al., 2006; Copilaș-Ciocianu et al., 2020c), although the exact mechanical interactions are unknown.

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 or Atlantic origin. Specifically, its sister clade is represented by the genus *Dinarogammarus*, which is endemic to freshwaters of the Western

Balkans (Sket & Hou, 2018). Regarding the temporal time frame, several recent studies proposed a Middle Miocene origin (ca.12–14 Ma) (Copilaș-Ciocianu et al., 2020; Hou & 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 (Palcu et al., 2015; Popov et al., 2004; Rögl, 1999). This time frame is also supported by Late Miocene (ca. 9–10 Ma) Caucasian amphipod fossil taxa (two genera and five species) that have clear affinities with extant Ponto-Caspian genera *Axelboeckia*, *Gmelina*, *Kuzmelina* and *Yogmelina* (Derzhavin, 1927, 1941). Furthermore, a similar time frame has been inferred for other organismal groups such as the endemic Bentophillinae fish and mysid crustaceans (Audzijonyte et al., 2008; Neilson & Stepien, 2009). 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 a biogeographical calibration of the molecular clock rather than fossils, thus possibly resulting in biased inferences (Ho 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 gammaroids. Furthermore, such a phylogeny could complement geological studies regarding the palaeogeographic history of the Paratethyan region, as seen with other freshwater gammarids (Copilaș-Ciocianu & Petrusek, 2017; Copilaș-Ciocianu et al., 2019b; 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: Behningielli-dae, Caspicolidae, Gammaridae, Iphigenellidae and Pontogammaridae. However, molecular research has revealed that Pontogammaridae is nested within Gammaridae and also harbours the gammarid genera *Dikerogammarus* and *Shablogammarus* (Copilaș-Ciocianu et al., 2020a; Hou et al., 2014; Sket & Hou, 2018). Members of this family correspond to the digger ecomorph, which probably evolved more than once. Moreover, the Ponto-Caspian "Gammaridae" form a paraphyletic grade at the base of Pontogammaridae (Fig. 3) (Sket & Hou, 2018). Morphologically,

Pontogammaridae is also not readily distinguishable from Gammaridae, being mainly defined by character states that are not representative. For example, Lowry and Myers (2013) characterize Pontogammaridae as having the antenna 2 first peduncular article not enlarged (not bulbous), whereas it is enlarged (bulbous) in Gammaridae. However, this state is not clearly defined. Most pontogammarid genera obviously have a large and bulbous first peduncular article (e.g. Sars, 1894a), not readily distinguishable from that of gammarid taxa. Another pontogammarid characteristic trait defined by Lowry and Myers (2013) is that the 2nd urosomite does not have dorsal setae, whereas gammarids have multiple setae. This is again not true since many if not most pontogammarid taxa do indeed have setal ornamentation on the second urosomal segment (e.g. Cărăuşu et al., 1955; Sars, 1894a, 1896). Furthermore, the genus *Dikerogammarus* has typical pontogammarid features such lack of calceoli and no medial palmar spines on gnathopod propodi, but it is classified as a gammarid. A taxonomically more inclusive morphological and molecular study will provide more clarity, but most likely will not recover the current version of 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 Iphigenellidae are poorly known and have not yet been sequenced. Behningiellidae and Iphigenellidae have been classified into Gammaroidea based on a morphological cladistic analysis (Lowry & 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 & 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 uniarticulate. 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 infraorder (Lowry & Myers, 2013). Behningiellidae, Caspicolidae and Iphigenellidae 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 gammaroids, possibly related to the various genera of the gmelinid facies (*Gmelina*, *Kuzmelina* and *Yogmelina*) (Barnard & 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 a thorough, modern revision using morphology, multilocus DNA sequences and ecology, which has proven very useful for gammarid amphipods (Cannizzaro et al., 2020; Copilaș-Ciocianu et al., 2019b; Hupało et al., 2018). Many species are only partially illustrated and intraspecific variability has been studied in only a handful of taxa (Cărăuşu, 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 & 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 posteroventral 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 (Copilaș-Ciocianu et al., 2019a, 2020a). Two more Miocene fossil taxa have been reported from the Caucasus that have a 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 gammaroid 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 results are only preliminary and a lot of in depth eco-evolutionary study is further needed. Moreover, most species need a modern integrative taxonomic revision that combines multilocus DNA data with morphology and ecology. 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.

Appendix

Key to all 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 well 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 7 .... **Pontoporeiidae**
- Pereopod 6 as long as or slightly longer than pereopods 5 and 7 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 (endemic Ponto-Caspian gammaroid radiation)

1. Gnathopods chelate ....…… *Caspicola* (monotypic: *Caspicola knipovitschi* (Derzhavin, 1944)
- 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* (Sars, 1894a, 1894b))
- 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 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
9. Pereopod 7 basis with a large downward pointing postero-distal lobe .... ***Jugogammarus*** (monotypic: *Jugogammarus kusceri* (Karaman, 1931))
- Pereopod 7 basis with minute/without a downward pointing postero-distal lobe .... ***Yogmelina***
10. Gnathopod 1 broader and larger than gnathopod 2 11
- Gnathopod 1 equal or smaller than gnathopod 2 13
11. Uropod 3 reduced, exopod shorter than twice the peduncle length ....***Baku*** (monotypic: *Baku paradoxus* (Derzhavin in Derzhavin & Pjatakova, 1967))
- Uropod 3 normal, exopod at least twice the peduncle length 12
12. Dactyli of pereopods 3–7 prehensile ...... ***Iphigenella*** (monotypic: *Iphigenella acanthopoda* (Sars, 1896))
- Dactyli of pereopods 3–7 not prehensile .... ***Lanceogammarus*** (monotypic: *Lanceogammarus andrussowi* (Sars, 1896))
13. Pereopod 7 basis not lobed 14
- Pereopod 7 basis lobed 18
14. Antenna 1 accessory flagellum bi-articulated ....***Cardiophilus***
- Antenna 1 accessory flagellum tri- or more articulated 15
15. Antenna 2 peduncle greatly expanded, article 3 with a downward projection ....***Derzhavinella***

- Antenna 2 peduncle normal, article 3 without a downward projection 16

16. Antenna 1 peduncle article 3 longer or equal with article 1 .... ***Sowinskya*** (monotypic: *Sowinskya macrocera* (Derzhavin, 1948))

- Antenna 1 peduncle article 3 shorter than article 1 ... 17

17. Uropod 3 setae curled, longer than spines .... ***Trichogammarus*** (monotypic: *Trichogammarus trichiatus* (Martynov, 1932))

- Uropod 3 setae straight, shorter than spines .... ***Chaetogammarus***

18. Pereopod 6 basis lobed 19
- Pereopod 6 basis not lobed 20

19. Pereopod 5–7 meral articles with a postero-distal lobe .... ***Zernovia*** (monotypic: *Zernovia volgensis* (Derzhavin, 1948))

- Pereopod 5–7 meral articles without a postero-distal lobe .... ***Shablogammarus*** (monotypic: *Shablogammarus shablensis* (Cărăușu, 1943))

20. Antenna 1 flagellum shorter than peduncle 21
- Antenna 1 flagellum equal/longer than peduncle 25

21. Epimeron 3 with postero-ventral setal fan 22
- Epimeron 3 without postero-ventral setal fan 24

22. Uropod 3 endopod longer than half of exopod .... ***Uroniphargoides*** (monotypic: *Uroniphargoides spinicaudatus* (Cărăușu, 1943))

- Uropod 3 endopod shorter than half of exopod 23

23. Ganthopod 2 propodus palm longer than posterior margin .... ***Compactogammarus*** (monotypic: *Compactogammarus compactus* (Sars, 1895))

- Ganthopod 2 propodus palm shorter than posterior margin .... ***Niphargoides***

24. Uropod 3 exopod 2nd article well developed, bearing lateral setae .... ***Niphargogammarus***

- Uropod 3 exopod 2nd article minute/absent, bearing no lateral setae .... ***Paraniphargoides***

25. Eyes round to ovoid, gnathopod 2 propodus large and triangular, armed with a palmar spine as long as 1/3 of dactylus .... ***Pandorites*** (monotypic: *Pandorites podoceroides* (Sars, 1896))

- Eyes reniform, gnathopod 2 propodus armed with a palmar spine(s) shorter than 1/3 of dactylus 26

26. Antenna 1 peduncular article 1 slender, width not exceeding 1/3 of length, pereopods 3–4 with sparse setae shorter than the width of underlying segment 27

- Antenna 1 peduncular article 1 robust, width exceeding 1/3 of length, pereopods 3–4 with dense setae as long as/longer than the width of underlying segment (except *O. subnudus*) 30

27. Body with a central dorsal a keel .... ***Amathillina***
- Body without a keel 28

28. Head swollen and enlarged .... ***Cephalogammarus*** (monotypic: *Cephalogammarus macrocephalus* (Sars, 1896))

- Head normal 29

29. Urosomites 1–2 with columnar tubercles .... ***Dikerogammarus***

- Urosomites 1–2 without columnar tubercles .... ***Akerogammarus***

30. Uropod 3 exopod 2nd article at least 1/5 the length of 1st article 31

- Uropod 3 exopod 2nd article much shorter than 1/5 the length of 1st article 32

31. Uropod 3 exopod outer margin armed with few simple setae .... ***Stenogammarus***

- Uropod 3 exopod outer margin armed with many plumose setae .... ***Wolgagammarus*** (monotypic: *Wolgagammarus dzjubani* (Mordukhai-Boltovskoi & Ljakhov, 1972))

32. Setae on posterior margin of carpal articles of pereopods 3–4 arranged in a continuous fan .... ***Pontogammarus***

- Setae on posterior margin of carpal articles of pereopods 3–4 arranged in clusters 33

33. Urosomites 1–2 with noticeable dorsal knobs .... ***Turcogammarus***

- Urosomites 1–2 flat or humped .... ***Obesogammarus***

Key to species

Doubtful species are indicated with an asterisk (*).

Key to species of *Akerogammarus*

1. Propodi of gnathopods 1 and 2 similar in size, telson with short apical setae .... *A. contiguus*

- Propodus of gnathopod 2 larger than gnathopod 1, telson with long apical setae .... *A. knipowitschi*

Key to species of *Amathillina*

1. Body keel starts from the first to third pereonite 2
- Body keel starts from the sixth pereonite or later 3

2. Pereonites 1–2 with well-developed dorsal spines, urosomite 1 humped .... *A. spinosa*

- Pereonites 1–2 with barely visible crest, urosomite 1 not humped .... *A. cristata*

3. Body keel present only on pleosome ... *A. maximowiczi*
- Body keel present on pereonites 6–7 and pleosome ... 4

4. Antenna 1 accessory flagellum bi-articulated, last pleonal projection rounded .... *A. pussila*

- Antenna 1 accessory flagellum tri-articulated, last pleonal projection triangular .... *A. affinis*

Key to species of *Cardiophilus*

1. Uropod 3 exopod less than twice the length of peduncle, 2nd article present .... *C. baeri*

- Uropod 3 exopod twice the length of peduncle, 2nd article absent .... *C. marisnigrae*

Key to species of *Chaetogammarus*

1. Antenna 1 accessory flagellum bi-articulated ... *C. warpachowskyi*

- Antenna 1 accessory flagellum at least three articles ... 2

2. Pleosome covered with small spines .... *C. hyrcanus*

- Pleosome bare 3

3. Eyes very elongated and constricted in the middle ... *C. placidus*

- Eyes regular (reniform) 4

4. Antenna 1 and 2 set with dense setae longer than the underlying segment .... *C. ischnus*

- Antenna 1 and 2 set with sparse setae shorter/equal with the underlying segment .... *C. pauxillus*

Key to species of *Chelicorophium*

1. Antenna 2 peduncular article 4 distal tooth simple ... *C. monodon*

- Antenna 2 peduncular article 4 distal tooth with an additional simple or bidentate tooth 2

2. Antenna 2 peduncular article 4 distal tooth with an additional simple tooth 3

- Antenna 2 peduncular article 4 distal tooth with an additional bidentate tooth 6

3. Pereopods 3–4 meral articles stout, length is less than twice the width .... *C. mucronatum*

- Pereopods 3–4 meral articles slender, length is twice the width 4

4. Antenna 2 peduncular article 5 with a proximal and distal tooth .... *C. chelicorne*

- Antenna 2 peduncular article 5 with either a proximal or distal tooth 5

5. Antenna 2 peduncular article 5 with a small proximal tooth, distal tooth missing .... *C. nobile*

- Antenna 2 peduncular article 5 with a strong distal tooth, proximal tooth missing .... *C. spinulosum.*

6. Antenna 2 peduncular article 5 with a proximal and distal tooth 7

- Antenna 2 peduncular article 5 with a proximal tooth only 8

7. Antenna 2 peduncular article 5 proximal tooth situated in the distal half of the article, inner side of uropod 1 peduncle without spines .... *C. maeoticum*

- Antenna 2 peduncular article 5 proximal tooth situated in the proximal half of the article, inner side of uropod 1 peduncle with spines .... *C. robustum*

8. Antenna 1 flagellum as long as peduncle .... *C. sowinskyi*

- Antenna 1 flagellum half as long as peduncle .... *C. curvispinum*

Key to species of *Derzhavinella*

1. Anterior margin of pereopod 7 with long setae ... *D. macrochelata*

- Anterior margin of pereopod 7 with short setae ... *D. cava.*

Key to species of *Dikerogammarus*

1. Pleosome segments keeled .... *D. caspius*

- Pleosome segments flat 2

2. Urosomal tubercles low .... *D. fluviatilis**

- Urosomal tubercles columnar, well developed 3

3. Antenna 1 accessory flagellum bi-articulated ... *D. gruberi*

- Antenna 1 accessory flagellum 4 or more articles 4

4. Propodi of gnathopods 1 and 2 with mid-palmar spine .... *D. aralychensis**

- Propodi of gnathopods 1 and 2 without mid-palmar spine 5

5. Medial surface of pereopod 7 basis with setae 6

- Medial surface of pereopod 7 basis without setae 7

6. Antenna 2 peduncular segments with numerous clusters of setae longer than the underlying segment ... *D. bispinosus*

- Antenna 2 peduncular segments with few clusters of setae shorter than the underlying segment ... *D. istanbulensis*

7. Propodi of gnathopods 1 and 2 with setae as long as propodus width .... *D. villosus*

- Propodi of gnathopods 1 and 2 with setae much shorter than propodus width 8

8. Uropod 3 exopod with spines on inner and outer margins .... *D. haemobaphes*

- Uropod 3 exopod without spines .... *D. oskari.*

Key to species of *Gmelina*

1. Pleonal humps high and triangular .... *G. costata*

- Pleonal humps low and rounded .... *G. aestuarica.*

Key to species of *Gmelinopsis*

1. Head lateral projections blunt, tubercle-like ... *G. tuberculata*

- Head lateral projections pointed, spear-like ... *G. aurita.*

Key to species of *Niphargogammarus*

1. Antenna 1 main flagellum as long as the first peduncular article 2

- Antenna 1 main flagellum shorter than the first peduncular article 3

2. Body size ca. 10 mm, gnathopod 2 propodus larger than gnathopod 1, telson lobes diverging and armed with 1 apical spine .... *N. quadrimanus*

- Body size ca. 5 mm, propodi of both gnathopods similar in size, telson lobes not diverging and armed apically with 2 spines .... *N. aequimanus*

3. Body size ca. 13 mm, urosomite 1 bare, uropod 3 exopod external margin armed with many setae ... *N. borodini*

- Body size ca. 7 mm, urosomite 1 armed with small setae, uropod 3 exopod external margin armed with few distal setae .... *N. intermedius*

Key to species of *Niphargoides*

1. Posterior margin of pereopod 6 basis armed with a few short setae proximally .... *N. grimmi*

- Posterior margin of pereopod 6 basis armed with long setae along its entire length 2

2. Ventral margin of coxal plate 4 armed with setae shorter than 1/2 of its length .... *N. corpulentus*

- Ventral margin of coxal plate 4 armed with setae longer than 1/2 of its length 3

3. Uropod 3 exopod bares a well-developed setal fan .... *N. caspius*

- Uropod 3 exopod lacks setal fan, armed with strong spines .... *N. boltovskoyi*

Key to species of *Obesogammarus*

1. Posterior margin of pereopods 3–4 with few sparse setae shorter than the underlying segment ...... *O. subnudus*

- Posterior margin of pereopods 3–4 with numerous setae as long as/longer than the underlying segment 2

2. Uropod 3 exopod less than twice peduncle length ... 3

- Uropod 3 exopod at least twice as long as peduncle ... 4

3. Posterior margin of basis of pereopods 5–7 with short setae .... *O. olvianus*

- Posterior margin of basis of pereopods 5–7 with long setae .... *O. obesus*

4. Coxae 1–2 tapering towards distal end, propodus of gnathopod 2 triangular .... *O. platycheir*

- Coxae 1–2 not tapering, propodus of gnathopod 2 roughly rectangular 5

5. Medial surface of pereopod 7 basis without setae .... *O. crassus*

- Medial surface of pereopod 7 basis armed with clusters of setae 6

6. Posterior margin of pereopod 7 basis sparsely armed with setae .... *O. boeoticus*

Posterior margin of pereopod 7 basis densely armed with setae .... *O. acuminatus*

Key to species of *Onisimus*

1. Antenna 1 peduncle article 1 longer than head, accessory flagellum 6-segmented, postero-ventral corner of 3rd epimere almost straight .... *O. platyceras*

2. Antenna 1 peduncle article 1 shorter than head, accessory flagellum 4-segmented, postero-ventral corner of 3rd epimere sharp .... *O. caspius*

Key to species of *Paraniphargoides*

1. Uropod 3 exopod without 2nd article, plumose setae absent .... *P. derzhavini*

- Uropod 3 exopod with minute 2nd article, plumose setae present .... *P. motasi*

Key to species of *Pontogammarus*

1. Uropod 3 endopod reaches half the length of the exopod 1st article 2

- Uropod 3 endopod shorter than half the length of the exopod 1st article 4

2. Dactylus nail of pereopods 5–7 hook-like ...... *P. sarsi*

- Dactylus nail of pereopods 5–7 straight 3

3. Mandibular palp very large, plumose D-setae present, last article of antenna 2 bares continuous setal fan ... *P. maeoticus*

- Mandibular palp normal, D-setae absent, last article of antenna 2 bares several setal clusters .... *P. weidemanni*

4. Urosome with dorsal elevations 5

- Urosome flat 7

5. Dorsal elevations tall, pillar-like .... *P. setosus*

- Dorsal elevations low, hump-like 6

6. Urosomite 1 armed with a crown of spines .... *P. robustoides*

- Urosomite 1 armed with setae only .... *P. aestuarius*

7. Uropod 3 exopod 2nd article as long as broad, uropod 2 exopod devoid of spines .... *P. borceae*

- Uropod 3 exopod 2nd article longer than broad, uropod 2 exopod with 1 spine .... *P. abbreviatus*

Key to species of *Stenogammarus*

1. Uropod 3 reduced, 1st exopod article 1 as long as peduncle .... *S. micrurus*

- Uropod 3 not reduced, 1st exopod article longer than peduncle 2

2. Uropod 3 exopod inner margin bare/with 1 long seta 3

- Uropod 3 exopod inner margin with multiple long setae .... 4.

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 ... *S. compresso-similis*

- Pereopods 6–7 basis medial surface bare, basis 6 with short setae on posterior margin, basis 7 with short setae on anterior margin .... *S. deminutus*.

4. Uropod 3 exopod 2nd article shorter than half of 1st article .... *S. similis*

- Uropod 3 exopod 2nd article as long/longer than half of 1st article .... 5.

5. Uropod 3 endopod longer than 2nd exopod article and is 1/2 of 1st article .... *S. compressus*

- Uropod 3 endopod shorter than 2nd exopod article and is 1/3 1st article .... *S. macrurus*

Key to species of *Turcogammarus*

1. Pleosome segments keeled .... *T. spandli*

- Pleosome segments flat 2

2. Urosomal tubercles low .... *T. aralensis*

- Urosomal tubercles tall and columnar ..... *T. turcarum**

Key to species of *Yogmelina*

1. Uropod 3 reduced, 1st article of exopod as long as peduncle .... *Y. brachyura*

- Uropod 3 not reduced, 1st article of exopod longer than peduncle 2

2. Basis of pereopod 7 truncated, abruptly tapering towards the distal edge .... *Y. ovata**

- Basis of pereopod 7 not truncated, gradually tapering towards the distal edge 3

3. Lateral head lobes rounded, coxal plate 1 slightly bent forwards, fringed with short setae .... *Y. laeviuscula*

- Lateral head lobes acute, coxal plate 1 strongly bent forwards fringed with long setae 4

4. Urosomites without setae, epimeral plates 2–3 with short distal setae .... *Y. pusilla*

- Urosomites with setae, epimeral plates 2–3 with long distal setae .... *Y. limana.*

Declarations

Conflict of interest The authors declare no competing interests.

References

Adamowicz, S. J., Marinone, M. C., Menu-Marque, S., Martin, J. W., Allen, D. C., Pyle, M. N., et al. (2018). The Hyalella (Crustacea: Amphipoda) species cloud of the ancient Lake Titicaca originated from multiple colonizations. *Molecular Phylogenetics and Evolution, 125*, 232–242. https://doi.org/10.1016/j.ympev.2018.03.004

Adrian-Kalchhauser, I., Blomberg, A., Larsson, T., Musilova, Z., Peart, C. R., Pippel, M., et al. (2020). The round goby genome provides insights into mechanisms that may facilitate biological invasions. *BMC Biology, 18*(1), 1–33. https://doi.org/10.1186/s12915-019-0731-8

Arbačiauskas, K., Lesutiene, J., & Gasiunaite, Z. R. (2013). Feeding strategies and elemental composition in Ponto-Caspian peracaridans from contrasting environments: Can stoichiometric plasticity promote invasion success? *Freshwater Biology, 58*(5), 1052–1068. https://doi.org/10.1111/fwb.12108

Audzijonyte, A., Baltrunaite, L., Väinölä, R., & Arbačiauskas, K. (2015). Migration and isolation during the turbulent Ponto-Caspian Pleistocene create high diversity in the crustacean *Paramysis lacustris. Molecular Ecology, 24*(17), 4537–4555. https://doi.org/10.1111/mec.13333

Audzijonyte, A., Daneliya, M. E., Mugue, N., & Väinölä, R. (2008). Phylogeny of Paramysis (Crustacea: Mysida) and the origin of Ponto-Caspian endemic diversity: Resolving power from nuclear protein-coding genes. *Molecular Phylogenetics and Evolution, 46*(2), 738–759. https://doi.org/10.1016/j.ympev.2007.11.009

Barnard, J. L. (1958). Index to the families, genera and species of the gammaridean Amphipoda (Crustacea). *Occasional Papers of the Allan Hancock Foundation, 19*, 1–145.

Barnard, J. L. (1967). New and old dogielinotid marine Amphipoda. *Crustaceana, 13*, 281–291.

Barnard, J. L., & Barnard, C. M. (1983). *Freshwater Amphipoda of the world. Mt.* Hayfield Associates.

Behning, A. L. (1914). Gammarus sowinskyi n.sp. aus der Umgebung von Kiev. *Zoologischer Anzeiger*, *44*(1), 42–44.

Birstein, J. A. (1932). *Malacostraca Armenii. Trudy Sevanskoi Gidrobiologicheskoi Stantsii, 4*(1–2), 139–166.

Birstein, J. A. (1938). *Derzhavinella macrochelata* n. gen. n. sp. Noviy rod i vid Amphipoda iz severnogo Kaspiya. *Zoologicheskii Zhurnal, 17*(1), 180–183.

Birstein, J. A. (1945). Revizija sistemy Kaspiiskih Gammaridae. *Doklady Akademii Nauk SSSR, 50*, 517–520.

Birstein, J. A., & Romanova, N. N. (1968). Amphipoda. In J. A. Birstein, L. G. Vinogradova, & N. N. Kondakova (Eds.), *Atlas bespozvonochnykh Kaspiiskogo morya* (pp. 241–289). Pishevaya Promyshlennost Publ.

Birstein, J. A., Vinogradov, L. G., Kondakov, N. N., & Kun, M.., Astakhova, T. V., & Romanova, N. N. (1968). *Atlas bespozvonochnykh Kaspiiskogo morya (Atlas of invertebrates of the Caspian Sea)*. Pishevaya Promyshlennost Publ.

Bollache, L. Ï., Kaldonski, N., Troussard, J. P., Lagrue, C., & Rigaud, T. (2006). Spines and behaviour as defences against fish predators in an invasive freshwater amphipod. *Animal Behaviour, 72*(3), 627–633. https://doi.org/10.1016/j.anbehav.2005.11.020

Borko, Š, Trontelj, P., Seehausen, O., Moškrič, A., & Fišer, C. (2021). A subterranean adaptive radiation of amphipods in Europe. *Nature Communications, 12*(1), 1–12. https://doi.org/10.1038/s41467-021-24023-w

Bousfield, E. L. (1970). Adaptive Radiation in Sand-burrowing Amphipod Crustaceans. *Chesapeake Science, 11*(3), 143–154.

Bousfield, E. L. (1977). A new look at the systematics of Gammaroidean amphipods of the world. *Crustaceana, 4*(4), 282–316. https://doi.org/10.2307/25027471

Cannizzaro, A. G., Balding, D., Lazo-Wasem, E. A., & Sawicki, T. R. (2020). A new species rises from beneath Florida: Molecular phylogenetic analyses reveal cryptic diversity among the metapopulation of *Crangonyx hobbsi* Shoemaker, 1941 (Amphipoda: Crangonyctidae). *Organisms Diversity and Evolution, 20*(3), 387–404. https://doi.org/10.1007/s13127-020-00433-4

Cărăuşu, S. (1936). Etude sue le *Pontogammarus maeoticus* (Sow.) Mart. *Annales Scientifique de l'Universite de Jassy*, *13*(1–4), 133–156.

Cărăuşu, S. (1943). *Amphipodes de Roumanie I. Gammarides de type Caspian*. Institutul de Cercetari Piscicole al Romaniei.

Cărăuşu, S., Dobreanu, E., & Manolache, C. (1955). *Fauna Republicii Populare Romîne. Crustacea. Amphipoda Forme Salmastre şi de Apă Dulce*. Bucharest: Editura Academiei RPR.

Chertoprud, E. S., Sokolova, A. M., & Garlitska, L. A. (2018). Harpacticoida (Copepoda) of the Caspian Sea: Faunistics, ecology and biogeography. *Journal of Experimental Marine Biology and Ecology, 502*, 63–70. https://doi.org/10.1016/j.jembe.2017.03.011

Chevreux, E. (1908). Études sur la faune du Turkestan basées sur les matériaux recueillis par D.D. Pedaschenko (1904–1906). In *II. Crustacés Amphipodes* (pp. 91–110).

Copilaş-Ciocianu, D., Berchi, G. M., & Mumladze, L. (2020b). First survey of shallow-water Amphipoda along the Georgian Black Sea coast reveals new faunistic records and the unexpected Atlantic invader *Melita nitida. Mediterranean Marine Science, 21*(2), 460–463. https://doi.org/10.12681/mms.22844

Copilaş-Ciocianu, D., Borko, Š., & Fišer, C. (2020a). The late blooming amphipods: Global change promoted post-Jurassic ecological radiation despite Palaeozoic origin. *Molecular Phylogenetics and Evolution*, *143*(October 2019), 106664. https://doi.org/10.1016/j.ympev.2019.106664

Copilaș-Ciocianu, D., Boros, B. V., & Šidagytė-Copilas, E. (2021). Morphology mirrors trophic niche in a freshwater amphipod community. *Freshwater Biology, 66*(10), 1968–1979. https://doi.org/10.1111/fwb.13804

Copilaș-Ciocianu, D., Borza, P., & Petrusek, A. (2020c). Extensive variation in the morphological anti-predator defense mechanism of Gammarus roeselii Gervais, 1835 (Crustacea:Amphipoda). *Freshwater Science, 39*(1), 47–55. https://doi.org/10.1086/707259

Copilaș-Ciocianu, D., & Petrusek, A. (2015). The southwestern Carpathians as an ancient centre of diversity of freshwater gammarid amphipods: Insights from the *Gammarus fossarum* species complex. *Molecular Ecology, 24*(15), 3980–3992. https://doi.org/10.1111/mec.13286

Copilaș-Ciocianu, D., & Petrusek, A. (2017). Phylogeography of a freshwater crustacean species complex reflects a long-gone archipelago. *Journal of Biogeography, 44*, 421–432. https://doi.org/10.1111/jbi.12853

Copilaș-Ciocianu, D., Sidorov, D. A., & Gontcharov, A. A. (2019a). Adrift across tectonic plates: Molecular phylogenetics supports the ancient Laurasian origin of old limnic crangonyctid amphipods. *Organisms Diversity & Evolution, 19*, 191–207. https://doi.org/10.1007/s13127-019-00401-7

Copilaș-Ciocianu, D., Zimța, A.-A., & Petrusek, A. (2019b). Integrative taxonomy reveals a new *Gammarus* species (Crustacea, Amphipoda) surviving in a previously unknown southeast European glacial refugium. *Journal of Zoological Systematics and Evolutionary Research*, *57*(2). https://doi.org/10.1111/jzs.12248

Cristescu, M. E. A., & Hebert, P. D. N. (2005). The "Crustacean Seas" — An evolutionary perspective on the Ponto-Caspian peracarids. *Canadian Journal of Fisheries and Aquatic Sciences, 62*(3), 505–517. https://doi.org/10.1139/f04-210

Cristescu, M. E. A., Witt, J. D. S., Grigorovich, I. A., Hebert, P. D. N., & MacIsaac, H. J. (2004). Dispersal of the Ponto-Caspian amphipod *Echinogammarus ischnus*: Invasion waves from the Pleistocene to the present. *Heredity, 92*(3), 197–203. https://doi.org/10.1038/sj.hdy.6800395

Cristescu, M. E., Adamowicz, S. J., Vaillant, J. J., & Haffner, D. G. (2010). Ancient lakes revisited: From the ecology to the genetics of speciation. *Molecular Ecology, 19*(22), 4837–4851. https://doi.org/10.1111/j.1365-294X.2010.04832.x

Cuthbert, R. N., Kotronaki, S. G., Dick, J. T. A., & Briski, E. (2020). Salinity tolerance and geographical origin predict global alien amphipod invasions. *Biology Letters, 16*(9), 2–7. https://doi.org/10.1098/rsbl.2020.0354

d'Udekem d'Acoz, C., & Verheye, M. L. (2017). Epimeria of the Southern Ocean with notes on their relatives (Crustacea, Amphipoda, Eusiroidea). *European Journal of Taxonomy, 359*, 1–553. https://doi.org/10.5852/ejt.2017.359

Daneliya, M. E., Kamaltynov, R. M., & Väinölä, R. (2011). Phylogeography and systematics of *Acanthogammarus* s. str., giant amphipod crustaceans from Lake Baikal. *Zoologica Scripta, 40*(6), 623–637. https://doi.org/10.1111/j.1463-6409.2011.00490.x

Derzhavin, A. N. (1924). Presnovodnye Peracarida chernomorskogo poverezhya Kavkaza. *Russkii Gidrobiologicheskii Zhurnal, 3*(6–7), 113–130.

Derzhavin, A. N. (1927). Notes on the Upper Sarmatian amphipods of the Ponto-Caspian region. *Bulletin De La Societe Des Naturalistes De Moscou, 2*, 183–196.

Derzhavin, A. N. (1941). Iskolaemyye bokoplavii Eldara. *Izvestyia Azerbaidzhanskogo Filiala Akademii Nauk SSSR, 2*, 65–69.

Derzhavin, A. N. (1944). A new family Caspiellidae from the Caspian Sea. *Bulletin of the Azerbaijan Filiation of the Academy of Sciences of the USSR, 8*, 20–24.

Derzhavin, A. N. (1948). Novye formy gammarid iz Kaspiiskogo Morya. *Pamiaty akademika Sergeia Aleksandrovicha Zernova* (pp. 280–286). USSR Academy of Sciences Publishing House.

Derzhavin, A. N., & Pjatakova, G. M. (1962). Novye vidy gammmarid Kaspiiskich Amfipod. *Doklady Akademii Nauk Azerbaidzhanskoi SSR, 18*(9), 53–57.

Derzhavin, A. N., & Pjatakova, G. M. (1967). Novye vidy gammmarid Kaspiiskogo Morya. In M. A. Musaev, A. G. Kasymov, & Y. A. Abdurachmanov (Eds.), *Biologicheskaia produktivnost' Kyrinsko-Kaspiiskogo rybolovnogo raiona* (pp. 79–84). AN Azerb. SSR Publ.

Derzhavin, A. N., & Pjatakova, G. M. (1968). A new species of amphipod of the genus *Niphargoides* from the Caspian Sea. *Crustaceana, 15*(1), 98–100.

Derzhavin, A. N., & Pjatakova, G. M. (1996). A new species of the genus *Stenogammarus* Martynov, 1924 (Crustacea Amphipoda Gammaridae) from the Caspian Sea. *Arthropoda Selecta, 5*(3/4), 23–25.

Dumont, H. (1995). Ecocide in the Caspian sea. *Nature, 377*(6551), 673–674. https://doi.org/10.1038/377673a0

Eichwald, E. (1841). Fauna Caspio-Caucasia nonnullis observationibus novis illustravit. Petropol: Litteris Typographiae Dairii Gall. Politic. Petropol.

Fišer, C., Trontelj, P., Luštrik, R., & Sket, B. (2009). Toward a unified taxonomy of *Niphargus* (Crustacea: Amphipoda): A review of morphological variability. *Zootaxa, 2061*, 1–22.

Garcia-Madrigal, M. S. (2010). Littoral Maeridae and Melitidae (Amphipoda: Gammaridea) from the Gulf of Tehuantepec, Mexico. *Zootaxa, 2623*, 1–51.

Gogaladze, A., Raes, N., Biesmeijer, J. C., Ionescu, C., Pavel, A. B., Son, M. O., et al. (2020). Social network analysis and the implications for Pontocaspian biodiversity conservation in Romania and Ukraine: A comparative study. *PLoS One*, *15*(10 October), 1–20. https://doi.org/10.1371/journal.pone.0221833

González, E. R., & Coleman, C. O. (2002). *Hyalella armata* (Crustacea, Amphipoda, Hyalellidae) and the description of a related new species from Lake Titicaca. *Organisms Diversity and Evolution, 2*(3), 271–273. https://doi.org/10.1078/1439-6092-00047

Grabowski, M., Bacela, K., & Konopacka, A. (2007). How to be an invasive gammarid (Amphipoda: Gammaroidea) - Comparison of life history traits. *Hydrobiologia, 590*(1), 75–84. https://doi.org/10.1007/s10750-007-0759-6

Hancock, Z. B., Ogawa, H., Light, J. E., & Wicksten, M. K. (2021). Origin and evolution of the Haustoriidae (Amphipoda): A eulogy for the Haustoriidira. *Zoological Journal of the Linnean Society*. https://doi.org/10.1093/zoolinnean/zlab023

Ho, S. Y. W., Tong, K. J., Foster, C. S. P., Ritchie, A. M., Lo, N., & Crisp, M. D. (2015). Biogeographic calibrations for the molecular clock. *Biology Letters*, *11*(9). https://doi.org/10.1098/rsbl.2015.0194

Horton, T., Lowry, J., De Broyer, C., Bellan-Santini, D. Coleman, C. O., Corbari, L., Costello, M. J. Daneliya, M., et al. (2020). World Amphipoda Database. *Accessed at* http://www.marinespecies.org/amphipoda *on 2020–11–10.* https://doi.org/10.14284/368. http://www.marinespecies.org/amphipoda. *Accessed 29 March 2019.*

Hou, Z., & Sket, B. (2016). A review of Gammaridae (Crustacea: Amphipoda): The family extent, its evolutionary history, and taxonomic redefinition of genera. *Zoological Journal of the Linnean Society, 176*(2), 323–348. https://doi.org/10.1111/zoj.12318

Hou, Z., Sket, B., Fišer, C., & Li, S. (2011). Eocene habitat shift from saline to freshwater promoted Tethyan amphipod diversification. *Proceedings of the National Academy of Sciences of the United States of America, 108*(35), 14533–14538. https://doi.org/10.1073/pnas.1104636108

Hou, Z., Sket, B., & Li, S. (2014). Phylogenetic analyses of Gammaridae crustacean reveal different diversification patterns among sister lineages in the Tethyan region. *Cladistics, 30*(4), 352–365. https://doi.org/10.1111/cla.12055

Hupało, K., Mamos, T., Wrzesińska, W., & Grabowski, M. (2018). First endemic freshwater *Gammarus* from Crete and its evolutionary history-an integrative taxonomy approach. *PeerJ, 2018*(3). https://doi.org/10.7717/peerj.4457

Jarzembowski, E. A., Chény, C., Fang, Y., & Wang, B. (2020). First Mesozoic amphipod crustacean from the Lower Cretaceous of SE England. *Cretaceous Research, 112*, 104429. https://doi.org/10.1016/j.cretres.2020.104429

Jażdżewska, A. M., Rewicz, T., Mamos, T., Wattier, R., Bącela-Spychalska, K., & Grabowski, M. (2020). Cryptic diversity and mtDNA phylogeography of the invasive demon shrimp, *Dikerogammarus haemobaphes* (Eichwald, 1841), in Europe. *NeoBiota, 57*, 53–86. https://doi.org/10.3897/neobiota.57.46699

Jurado-Rivera, J. A., Zapelloni, F., Pons, J., Juan, C., & Jaume, D. (2020). Morphological and molecular species boundaries in the Hyalella species flock of Lake Titicaca (Crustacea: Amphipoda). *Contributions to Zoology, 89*(4), 353–372. https://doi.org/10.1163/18759866-bja10004

Kamaltynov, R. M. (2001). Amfipody (Amphipoda: Gammaroidea). In O. A. Timoshkin (Ed.), *Annotirovannyi spisok fauny ozera Baikal i ego vodosbornogo basseina. Tom I: Ozero Baikal. Kniga 1* (pp. 572–831). Novosibirsk: Nauka.

Karaman, G. S., & Pinkster, S. (1977). Freshwater *Gammarus* species from Europe, North Africa and adjacent regions of Asia (Crustacea-Amphipoda). Part I. *Gammarus pulex*-group and related species. *Bijdragen Tot De Dierkunde, 47*, 1–97.

Karaman, G. S., & Barnard, J. L. (1979). Classificatory Revisions In Gammaridean Amphipoda Crustacea 1. *Proceedings of The Biological Society of Washington, 92*(1), 106–165. http://biostor.org/reference/81275

Karaman, S. (1931). Beitrag zur Kenntnis der Amphipoden Jugoslaviens, sowie einiger Arten aus Griechenland. *Prirodoslovne Razprave, 1*, 31–66.

Karaman, S. (1953). Pontokaspische Amphipoden der Jugoslavischen fauna. *Acta Musei Macedonici Scientiarum Naturalium, 12*, 21–60.

Katouzian, A.-R., Sari, A., Macher, J. N., Weiss, M., Saboori, A., Leese, F., & Weigand, A. M. (2016). Drastic underestimation of amphipod biodiversity in the endangered Irano-Anatolian and Caucasus biodiversity hotspots. *Scientific Reports, 6*(1), 22507. https://doi.org/10.1038/srep22507

Khusainova, N. Z. (1959). Genesis of the bottom fauna of the Aral Sea. In *Sbornik rabot po ikhtiologii i gidrobiologii* (pp. 3–33). Alma-Ata: Izvestiia Akademii nauk Kazakhskoii SSR.

Kralj-Fišer, S., Premate, E., Copilaş-Ciocianu, D., Volk, T., Fišer, Z., Balázs, G., et al. (2020). The interplay between habitat use, morphology and locomotion in subterranean crustaceans of the genus Niphargus. *Zoology, 139*, 125742. https://doi.org/10.1016/j.zool.2020.125742

Krapp-Schickel, T., & Sket, B. (2015). *Melita mirzajanii* n. sp. (Crustacea: Amphipoda: Melitidae), a puzzling new member of the Caspian fauna. *Zootaxa, 3948*(2), 248–262. https://doi.org/10.11646/zootaxa.3948.2.6

Krijgsman, W., Tesakov, A., Yanina, T., Lazarev, S., Danukalova, G., Van Baak, C. G. C., et al. (2019). Quaternary time scales for the Pontocaspian domain: Interbasinal connectivity and faunal evolution. *Earth-Science Reviews, 188*(October 2018), 1–40. https://doi.org/10.1016/j.earscirev.2018.10.013

Lattuada, M., Albrecht, C., & Wilke, T. (2019). Differential impact of anthropogenic pressures on Caspian Sea ecoregions. *Marine Pollution Bulletin, 142*, 274–281. https://doi.org/10.1016/j.marpolbul.2019.03.046

Lorz, A. N., Kilgallen, N. M., & Thiel, M. (2010). Algal-dwelling Eophliantidae (Amphipoda): Description of a new species and key to the world species, with notes on their biogeography. *Journal of the Marine Biological Association of the United Kingdom, 90*(5), 1055–1063.

Lowry, J. K., & Myers, A. A. (2013). A phylogeny and classification of the Senticaudata subord. nov. (Crustacea: Amphipoda). *Zootaxa, 3610*(1), 1–80. https://doi.org/10.11646/zootaxa.3610.1.1

Lowry, J. K., & Myers, A. A. (2017). A phylogeny and classification of the Amphipoda with the establishment of the new order Ingolfiellida (Crustacea: Peracarida). *Zootaxa, 4265*(1), 1–89. https://doi.org/10.11646/zootaxa.4265.1.1

Macdonald, K. S., Yampolsky, L., & Duffy, J. E. (2005). Molecular and morphological evolution of the amphipod radiation of Lake Baikal. *Molecular Phylogenetics and Evolution, 35*(2), 323–343. https://doi.org/10.1016/j.ympev.2005.01.013

MacNeil, C., Dick, J., & Elwood, R. (1997). The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): Problems and perspectives concerning the functional feeding group 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

Mamos, T., Wattier, R., Burzynski, A., & Grabowski, M. (2016). The legacy of a vanished sea: A high level of diversification within a European freshwater amphipod species complex driven by 15 My of Paratethys regression. *Molecular Ecology, 25*(3), 795–810. https://doi.org/10.1111/mec.13499

Mamos, T., Wattier, R., Majda, A., Sket, B., & Grabowski, M. (2014). Morphological vs. molecular delineation of taxa across montane regions in Europe: The case study of *Gammarus balcanicus* Schaferna, (Crustacea: Amphipoda). *Journal of Zoological Systematics and Evolutionary Research, 52*(3), 237–248. https://doi.org/10.1111/jzs.12062

Martens, K. (1997). Speciation in ancient lakes. *Trends in Ecology and Evolution, 12*(5), 177–182. https://doi.org/10.1016/S0169-5347(97)01039-2

Martens, K., & Schön, I. (1999). Crustacean biodiversity in ancient lakes: A review. *Crustaceana, 72*(8), 899–910.

Martynov, A. V. (1919). O vysshich rakoovraznych okrestnostei Rostova na Donu. *Acta Soc. Tanaitica Explor. Nat. (rostoff Am Don), 1*(3), 39–53.

Martynov, A. V. (1924). Études sur les Crustacés de Mer du Bassin du bas Don et leur distribution éthologique. *Annuaire du Musee Zoologique de l'Acad. des Sciences de Russie, 25*, 1–115.

Martynov, A. V. (1925a). Gammaridae nizhnego Dnepra. *Trudy Vseukrainskoi Gosudarstvennoi Chernomorsko-Azovskoi Nauchno-Promyspovoi Opytnoi Stantsii, 1*, 135–153.

Martynov, A. V. (1925b). Malacostraca, sobrannye D. A. Tarnogradskim v severnoi Persii (Enzeli) i na Kavkaze v 1921–23. *Travaux de le Station Biologique du Caucase du Nord de Gorsky Institut Agronomique, 1*(1), 26–28.

Martynov, A. V. (1930). Fauna Amphipoda Teletskogo ozera I ee proiskhozhdenie. *Izv. Gosud. Gidrob. Inst., 29*, 95–128.

Martynov, A. V. (1932). Contribution to the knowledge of the freshwater fauna of the Black Sea coast of Caucasus. I. Amphipoda. *Travaux De L'institut Zoologique De I'academie Des Seiences De l'URSS, 1*, 73–98.

Mateus, A., & Mateus, E. (1990). Etude d'une collection d'amphipodes specialement du sud-ouest asiatique - du Museum d'Histoire Naturelle de Vienne (Autriche). *Annalen Des Naturhistorischen Museums in Wien, 91*, 273–331.

Mejaes, A. B., Poore, A. G. B., & Thiel, M. (2015). Crustaceans inhabiting domiciles excavated from macrophytes and stone. In *The natural history of the Crustacea, Volume 2. Lifestyles and*

Feeding Biology (pp. 118–144). New York: Oxford University Press.

Miloslavskaja, N. M. (1931). Dopolnenya k faune Amphipoda Gammaroidea Chernogo morya. *Trudy Karadagskoi Biologicheskoi Statsii, 4*, 49–51.

Mirzajani, A. R., & Vonk, R. (2006). Spatial and temporal aspects of the lagoon cockle and its commensal amphipod in the southwestern caspian sea. *Zoology in the Middle East, 37*(1), 63–72. https://doi.org/10.1080/09397140.2006.10638149

Mordukhai-Boltovskoi, F. D. (1964). Caspian fauna beyond the Caspian Sea. *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie, 49*(1), 139–176. https://doi.org/10.1002/iroh.19640490105

Mordukhai-Boltovskoi, F. D. (1979). Composition and distribution of Caspian fauna in the light of modern data. *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie, 64*(1), 1–38. https://doi.org/10.1002/iroh.19790640102

Mordukhai-Boltovskoi, F. D., & Lyakhov, S. M. (1972). Novii vid amfipod roda *Stenogammarus* (Gammaridae) v basseine Volgi. *Zoologicheskii Zhurnal, 51*(1), 21–27.

Nahavandi, N., Ketmaier, V., Plath, M., & Tiedemann, R. (2013). Diversification of Ponto-Caspian aquatic fauna: Morphology and molecules retrieve congruent evolutionary relationships in *Pontogammarus maeoticus* (Amphipoda: Pontogammaridae). *Molecular Phylogenetics and Evolution, 69*(3), 1063–1076. https://doi.org/10.1016/j.ympev.2013.05.021

Naseka, A. M., & Bogutskaya, N. G. (2009). Fishes of the Caspian Sea: Zoogeography and updated check-list. *Zoosystematica Rossica, 18*(2), 295–317. https://doi.org/10.31610/zsr/2009.18.2.295

Naumenko, S. A., Logacheva, M. D., Popova, N. V., Klepikova, A. V., Penin, A. A., Bazykin, G. A., et al. (2017). Transcriptome-based phylogeny of endemic Lake Baikal amphipod species flock: Fast speciation accompanied by frequent episodes of positive selection. *Molecular Ecology, 26*(2), 536–553. https://doi.org/10.1111/mec.13927

Neilson, M. E., & Stepien, C. A. (2009). Escape from the Ponto-Caspian: Evolution and biogeography of an endemic goby species flock (Benthophilinae: Gobiidae: Teleostei). *Molecular Phylogenetics and Evolution, 52*(1), 84–102. https://doi.org/10.1016/j.ympev.2008.12.023

Osadchikh, V. F. (1977). A finding of *Cardiophilus baeri* in the marsupium of corophiids (Amphipoda, Gammaridae). *Zoologicheskii Zhurnal, 56*, 156–158.

Özbek, M., & Özkan, N. (2011). *Dikerogammarus istanbulensis* sp. n., a new amphipod species (Amphipoda: Gammaridae) from Turkey with a key for the genus. *Zootaxa, 2813*, 55–64.

Pallas, P. S. (1771). Reise durch verschiedene Provinzen des Russischen Reichs. Theil 1. Physicalische Reise durch verschiedene Provinzen des Russischen Reichs im 1768- und 1769 sten Jahren. *St. Petersburg: Kayserliche Akademie der Wissenschaften, 1*, 1–522.

Palcu, D. V., Patina, I. S., Şandric, I., Lazarev, S., Vasiliev, I., Stoica, M., & Krijgsman, W. (2021). Late Miocene megalake regressions in Eurasia. *Scientific Reports, 11*(1), 1–12. https://doi.org/10.1038/s41598-021-91001-z

Palcu, D. V., Popov, S. V., Golovina, L. A., Kuiper, K. F., Liu, S., & Krijgsman, W. (2019). The shutdown of an anoxic giant: Magnetostratigraphic dating of the end of the Maikop Sea. *Gondwana Research, 67*, 82–100. https://doi.org/10.1016/j.gr.2018.09.011

Palcu, D. V., Tulbure, M., Bartol, M., Kouwenhoven, J. J., & Krijgsman, W. (2015). The Badenian-Sarmatian extinction event in the Carpathian foredeep basin of Romania: Paleogeographic changes in the Paratethys domain. *Global and Planetary Change, 133*, 346–358. https://doi.org/10.1016/j.gloplacha.2015.08.014

Petunnikoff, G. A. (1914). Rakoovrazniya nizhnemiotsenovikh sloev bliz seleniya Binagady. *Ezhegodnik Po Geologii i Mineralogii Rossii, 16*, 148–154.

Pinkster, S. (1993). A revision of the genus *Echinogammarus* Stebbing, 1899 with some notes on related genera (Crustacea, Amphipoda). *Memorie Del Museo Civico Di Storia Naturale, 10*, 1–185.

Piscart, C., Navel, S., Maazouzi, C., Montuelle, B., Cornut, J., Mermillod-Blondin, F., et al. (2011). Leaf litter recycling in benthic and hyporheic layers in agricultural streams with different types of land use. *Science of the Total Environment, 409*(20), 4373–4380. https://doi.org/10.1016/j.scitotenv.2011.06.060

Pjatakova, G. M. (1962a). Novye formy gammarid Kaspiiskogo Morya. *Doklady Akademii Nauk Azerbaidzhanskoi SSR, 18*(6), 47–51.

Pjatakova, G. M. (1962b). *Niphargoides derzhavini*—Novy vid amfipod Kaspiiskogo Morya. *Doklady Akademii Nauk Azerbaidzhanskoi SSR, 18*(11), 71–73.

Pjatakova, G. M., & Tarasov, A. G. (1996). Caspian Sea amphipods: Biodiversity, systematic position and ecological peculiarities of some species. *International Journal of Salt Lake Research, 5*(1), 63–79. https://doi.org/10.1007/BF01996036

Ponyi, E. (1958). Neuere systematische Untersuchungen an den ungarischen Dicerogammarus-Arten. *Archiv Für Hydrobioloie, 54*(4), 488–496.

Popov, S. V., Rögl, F., Rozanov, A. Y., Steininger, F. F., Shcherba, I. G., & Kovac, M. (2004). Lithological-paleogeographic maps of paratethys. *CFS Courier Forschungsinstitut Senckenberg, 250*, 1–46.

Prange, M., Wilke, T., & Wesselingh, F. P. (2020). The other side of sea level change. *Communications Earth & Environment, 1*, 69. https://doi.org/10.1038/s43247-020-00075-6

Premate, E., Borko, Š., Delić, T., Malard, F., Simon, L., & Fišer, C. (2021). Cave amphipods reveal co-variation between morphology and trophic niche in a low-productivity environment. *Freshwater Biology, 66*(10), 1876–1888. https://doi.org/10.1111/fwb.13797

Reid, D. F., & Orlova, M. I. (2002). Geological and evolutionary underpinnings for the success of Ponto-Caspian species invasions in the Baltic Sea and North American Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences, 59*(7), 1144–1158. https://doi.org/10.1139/f02-099

Rewicz, T., Wattier, R., Grabowski, M., Rigaud, T., & Bacela-Spychalska, K. (2015). Out of the Black sea: Phylogeography of the invasive killer shrimp *Dikerogammarus villosus* across Europe. *PLoS ONE, 10*(2), 1–20. https://doi.org/10.1371/journal.pone.0118121

Rögl, F. (1999). Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geologica Carpathica, 50*(4), 339–349. http://www.nhm-wien.ac.at/jart/prj3/nhm/data/uploads/mitarbeiter_dokumente/roegl/1999_Roegl_Palgeo_GeolCarp.pdf

Salzburger, W., Bocxlaer, B. V., & Cohen, A. S. (2014). Ecology and evolution of the African great lakes and their faunas. *Annual Review of Ecology, Evolution, and Systematics, 45*, 519–545. https://doi.org/10.1146/annurev-ecolsys-120213-091804

Sars, G. O. (1894a). Crustacea caspia. Contributions to the knowledge of the carcinological fauna of the Caspian Sea. Part III. Amphipoda. *Bulletin de I'Academie Imperiale des Sciences de St.-Ptetersbourg, 1*(2), 179–223.

Sars, G. O. (1894b). Crustacea caspia. Contributions to the knowledge of the carcinological fauna of the Caspian Sea. Part III. Amphipoda. *Bulletin de I'Academie Imperiale des Sciences de St.-Ptetersbourg, 1*(4), 343–378.

Sars, G. O. (1895). Crustacea caspia. Contributions to the knowledge of the carcinological fauna of the Caspian Sea. Part III. Amphipoda. *Bulletin de I'Academie Imperiale des Sciences de St.-Ptetersbourg, 3*(3), 275–314.

Sars, G. O. (1896). Crustacea caspia. Contributions to the knowledge of the carcinological fauna of the Caspian Sea. *Bulletin*

de I'Academie Imperiale des Sciences de St.-Ptetersbourg, 4(5), 421–489.

Sars, G. O. (1897). On some additional Crustacea from the Caspian Sea. *Annales du Musée Zoologique Academie Imperiale des Sciences, St.-Petersburg, 2,* 273–305.

Schäferna, K. (1914). Über eine neue Dikerogammarusart aus dem Kaukasus. *Bulletin International De L'académie Des Sciences De Boheme Prague: Académie Des Sciences, 19,* 169–173.

Schellenberg, A. (1944). Über das Vorkommen pontokaspischer Amphipoden im Süd- und Westbalkan. *Zoologischer Anzeiger, 144*(9–10), 192–195.

Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press.

Seehausen, O. (2015). Process and pattern in cichlid radiations – Inferences for understanding unusually high rates of evolutionary diversification. *New Phytologist, 207*(2), 304–312. https://doi.org/10.1111/nph.13450

Simões, M., Breitkreuz, L., Alvarado, M., Baca, S., Cooper, J. C., Heins, L., et al. (2016). The evolving theory of evolutionary radiations. *Trends in Ecology and Evolution, 31*(1), 27–34. https://doi.org/10.1016/j.tree.2015.10.007

Sket, B., & Fišer, C. (2009). A new case of intralacustrine radiation in amphipoda. A new genus and three new species of Anisogammaridae (Crustacea, Amphipoda) from the ancient lake Fuxian Hu in Yunnan, China. *Journal of Zoological Systematics and Evolutionary Research, 47*(2), 115–123. https://doi.org/10.1111/j.1439-0469.2008.00477.x

Sket, B., & Hou, Z. (2018). Family Gammaridae (Crustacea: Amphipoda), mainly its *Echinogammarus* clade in SW Europe. Further elucidation of its phylogeny and taxonomy. *Acta Biologica Slovenica, 61*(1), 93–102.

Sowinsky, V. K. (1894). Sur les crustacés de la Mer d'Azov. *Mémoires De La Société Des Naturalistes De Kieff, 13,* 289–406.

Sowinsky, V. K. (1898). Nauchnye rezultaty ekspeditsii "Atmanaya". *Bulletin de l´Académie Impériale des Sciences de St.-Pétersbourg, 8*(5), 359–398.

Sowinsky, V. K. (1904). Introduction a l'étude de la faune du bassin marin Ponto-Aralo-Kaspien sous le point de vue d'une province zoogéographique indépendante. *Mémoires De La Société Des Naturalistes De Kieff, 8*(1), 1–487.

Stebbing, T. R. R. (1899). Amphipoda from the Copenhagen Museum and other sources, part II. *The Transactions of the Linnean Society of London: Zoology, 8*(2), 395–432.

Stebbing, T. R. R. (1906). *Amphipoda. i. Gammaridea. Das Tiereich, 21,* 1–806.

Stock, J. H. (1974). The systematics of certain Ponto-Caspian Gammaridae (Crustacea, Amphipoda). *Mitteilungen Aus Dem Hamburgischen Zoologischen Museum Und Institut, 70*(April), 75–95.

Stock, J. H., Mirzajani, A. R., Vonk, R., Naderi, S., & Kiabi, B. H. (1998). Limnic and brackish water Amphipoda (Crustacea) from Iran. *Beaufortia, 48*(9), 173–234.

Takhteev, V. V. (2000). Trends in evolution of Baikal amphipods and evolutionary parallels with some marine malacostracan faunas. In *Ancient lakes: Biodiversity, ecology and evolution* (Vol. 31, pp. 197–220). Amsterdam: Academic Press. https://doi.org/10.1016/S0065-2504(00)31013-3

Takhteev, V. V. (2019). On the current state of taxonomy of the Baikal Lake amphipods (Crustacea: Amphipoda) and the typological ways of constructing their system. *Arthropoda Selecta, 28*(3), 374–402. https://doi.org/10.15298/arthsel.28.3.03

Trontelj, P., Blejec, A., & Fišer, C. (2012). Ecomorphological convergence of cave communities. *Evolution, 66*(12), 3852–3865. https://doi.org/10.1111/j.1558-5646.2012.01734.x

Uljanin, V. N. (1875). Rakoobrazniya (Crustacea). Crustacea du voyage de Fendtchenko au Turkestan. In A. P. Fedchenko (Ed.). *Puteshestvie v Turkestan* (Part 3, pp. 1–63). Moscow: Izvestiya Imperatorskago Obshchestva Lyubitelei Estestvoznaniya Antropologii i Etnografii.

Väinölä, R., Vainio, J. K., & Palo, J. U. (2001). Phylogeography of "glacial relict" *Gammaracanthus* (Crustacea, Amphipoda) from boreal lakes and the Caspian and White seas. *Canadian Journal of Fisheries and Aquatic Sciences, 58,* 2247–2257.

Väinölä, R., Witt, J. D. S., Grabowski, M., Bradbury, J. H., Jazdzewski, K., & Sket, B. (2008). Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. *Hydrobiologia, 595*(1), 241–255. https://doi.org/10.1007/s10750-007-9020-6

Vanderploeg, H. A., Nalepa, T. F., Jude, D. J., Mills, E. L., Holeck, K. T., Liebig, J. R., et al. (2002). Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences, 59*(7), 1209–1228. https://doi.org/10.1139/f02-087

Wellborn, G. A., & Broughton, R. E. (2008). Diversification on an ecologically constrained adaptive landscape. *Molecular Ecology, 17*(12), 2927–2936. https://doi.org/10.1111/j.1365-294X.2008.03805.x

Wellborn, G. A., & Langerhans, R. B. (2015). Ecological opportunity and the adaptive diversification of lineages. *Ecology and Evolution, 5*(1), 176–195. https://doi.org/10.1002/ece3.1347

Wesselingh, F. P., Neubauer, T. A., Anistratenko, V. V., Vinarski, M. V., Yanina, T., ter Poorten, J. J., et al. (2019). Mollusc species from the Pontocaspian region - An expert opinion list. *ZooKeys, 2019*(827), 31–124. https://doi.org/10.3897/zookeys.827.31365

Witt, J. D. S., Threloff, D. L., & Hebert, P. D. N. (2006). DNA barcoding reveals extraordinary cryptic diversity in an amphipod genus: Implications for desert spring conservation. *Molecular Ecology, 15*(10), 3073–3082. https://doi.org/10.1111/j.1365-294X.2006.02999.x

Wysocka, A., Grabowski, M., Sworobowicz, L., Burzyński, A., Kilikowska, A., Kostoski, G., & Sell, J. (2013). A tale of time and depth: Intralacustrine radiation in endemic *Gammarus* species flock from the ancient Lake Ohrid. *Zoological Journal of the Linnean Society, 167*(3), 345–359. https://doi.org/10.1111/j.1096-3642.2012.00878.x

Wysocka, A., Grabowski, M., Sworobowicz, L., Mamos, T., Burzyński, A., & Sell, J. (2014). Origin of the Lake Ohrid gammarid species flock: Ancient local phylogenetic lineage diversification. *Journal of Biogeography, 41*(9), 1758–1768. https://doi.org/10.1111/jbi.12335