Chapter 8
An Overview on the Aquatic Cave Fauna

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8.1 Introduction

The community of organisms that live in groundwater, which is the obligate subterranean water community, was defined as stygon by Husmann (1966, 1967) who gave the name stygobiology to the science that studies groundwater life. Earlier, in 1925, Thienemann proposed a terminology for groundwater animals that paralleled the ecological classification of terrestrial cave fauna (see also Chaps. 1 and 4): (1) stygoxenes—occasionally found in groundwater, (2) stygophiles—live both in groundwater and in epigean habitats; (3) stygobionts—live only in groundwater.

The first discovered and described cave inhabitants were aquatic animals. In 1436, in Yunnan (China) a local doctor mentioned a cave fish, the stygophile *Sinocyclocheilus grahami* described centuries later (1904) by C. Tate Regan (Ma and Zhao 2012). In 1540, also in China, a stygobiont fish was mentioned by the local governor of Guangxi province and described as *Sinocyclocheilus hyalinus* in 1944 by Chen and Yang (Ma and Zhao 2012). Two centuries later, in 1768, the baby dragon—*Proteus anguinus*—was described by Laurenti from a small karstic source in Carniola (parts of the present-day Slovenia). This dragon was for a long time thought to be the first described cave species in the world.

In 1986, Botosaneanu stated that more than 7000 groundwater species occur worldwide, a number that was soon recognized to be an underestimate (Gibert and Culver 2005), and there has been a steady upward trend each year in the number of species known. Even without the description of new taxa the discovery of cryptic species, due to improvements in molecular techniques, is steadily increasing the number of known and described species (Trontelj et al. 2009; Fišer et al. 2018). Groundwater species richness is higher in Europe (~2000 species) compared with the other continents, ~561 species in Asia, ~500 species in North America, ~335

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species in Africa (Gibert and Culver 2005), and ~500 in Australia (Stuart Halse, personal communication), although this can be the result of a more concentrated effort of identification of new groundwater species in the Old Continent until relatively recently. Europe was the center of biospeleological researches for almost a century and the first researches on groundwater fauna were concentrated mostly on cave aquatic habitats, especially cave rivers and pools, and on wells and springs outside the caves (see also Chap. 3). It was only later that the hyporheic zone was described (Orghidan 1959; Motaș 1963) and studied more intensively than caves (reviews in Danielopol and Rouch 1991; Rouch 1992; Boulton et al. 2003; Di Lorenzo et al. 2013). The deeper aquatic zones, such as the phreatic zone (see Chap. 3) known to harbor specific fauna (Marmonier et al. 1993; Stoch et al. 2009), have been less studied due to limitations such as difficulties of access, boundaries assignment, and spatial heterogeneity (Larned 2012).

8.2 Groundwater Unicellular Organisms (see Table 8.1)

8.2.1 Protista: Protists

Protists are a group of unicellular eukaryotic organisms ranked as a separate kingdom. More than 180 species have been described from caves, of which ~20% occur in guano, decomposing organic matter, and humid clay (Golemansky and Bonnet 1994). They are also abundant in show caves, in pools and also around lampenflora (Varga 1959, 1963). Most of the studied groundwater protists are from interstitial habitats and display some adaptations such as small, fine, and transparent shells of Foraminifera that inhabit deep groundwater of the Kara-Kum desert (Brodsky 1928, 1929; Nikoljuk 1948, 1968 cited by Golemansky and Bonnet 1994). Protists are mostly introduced in caves by waters that come from the surface. The species found in deserts groundwater are sometimes remnants of ancient seas that covered the respective areas (Delamare-Debouteville 1960). In an unpublished study of Sheila Seale (cited by Lavoie 2015), protists were found in all aquatic pools and streams sampled in Mammoth Cave (USA) but not in drip water. González-López et al. (2013) also found protists on stalagmites in different caves around the world but all were edaphic species. Protists have also been found in the microbial mats of Movile Cave (Romania) together with bacteria and fungi (see also Chap. 16). Epibiontic and endoparasitic species of protists were found on and in cave animals and some are specific for their stygobiont hosts, such as *Lagenophrys monolistrae*and *Spelaeophrya troglocaridis* (Golemansky and Bonnet 1994).

Table 8.1 The main groundwater organismal groups of this chapter (in italics) and their simplified systematic position

Kingdom	Phylum	Subphylum	Class	Subclass	Superorder	Order	Suborder
Protista		*Foraminifera*					
Animalia	*Porifera*						
	Cnidaria		*Hydrozoa*				
	Platyhelminthes					*Tricladida* *Temnocephalida*	
	Rotifera						
	Kinorhyncha						
	Nematoda						
	Nemertea						
	Gastrotricha						
	Tardigrada						
	Annelida		*Aphanoneura*				
			Clitellata	*Oligochaeta* *Hirudinea*			
			Polychaeta				
	Mollusca		*Gastropoda* *Bivalvia*				
	Arthropoda	*Crustacea*	Branchiopoda			*Cladocera*	
			Remipedia				
			Maxillopoda	Copepoda		*Calanoida*	
						Cyclopoida	
						Harpacticoida	
						Gelyelloida	
			Ostracoda				
			Malacostraca		Eucarida	*Decapoda*	
					Peracarida	*Isopoda*	

(continued)

Table 8.1 (continued)

Kingdom	Phylum	Subphylum	Class	Subclass	Superorder	Order	Suborder
						Amphipoda	
						Spelaeogriphacea	
						Theormosbaenacea	
						Mysidacea	
						Bochusacea (Mictacea)	
					Syncarida	*Anaspidacea* *Bathynellacea*	
		Chelicerata	Arachnida	Acari		Trombidiformes	Prostigmata-*Hydrachnidia*
		Hexapoda	Insecta			*Coleoptera*	
	Chordata	Vertebrata	*Pisces*				
			Amphibia			*Urodela*	

8.3 Groundwater Multicellular Animal Groups (see Table 8.1)

8.3.1 Porifera: Sponges

Sponges, multicellular organisms with a body full of pores and channels, are poorly represented in caves or other subterranean environments, and the few that inhabit groundwaters are considered to be stygoxenes. The only true stygobiont sponge found to date occurs in Croatia, *Eunapius subterraneus*, with the following adaptive characteristics: gemmule reduction and reduced thickness of both skeleton and body consistence (Sket and Velikonja 1984, 1986; Fig. 8.1a).

There are sponges that inhabit marine caves, because of their constant conditions, without particular adaptations to life in caves (Vacelet 1990; Manconi et al. 2013).

8.3.2 Hydrozoa: Hydrozoans

The only known cave hydrozoan is *Velkovrhia enigmatica* described by Matjašič and Sket in 1971 from caves of the Dinaric karst. Other hydrozoans found in caves of Mexico, the USA, the Czech Republic, Austria, Australia, and Dinarides belong to the genus *Hydra* and are not adapted to subterranean life (Zagmajster et al. 2011).

8.3.3 Platyhelminthes: Flat Worms

The order Tricladida order contains stygobiont planarians that are depigmented, lack eyes or have reduced eyes and have slower biological processes (ontogenesis, respiration, and metabolism) than their epigean relatives (Fig. 8.1b). One of the peculiar characteristics of cave planarians is that they have a higher number of chromosomes (Gourbault 1968, 1970). Their origin can be either freshwater or marine waters, and half of the described freshwater species are hypogean. Among stygobionts the genus *Dendrocoelum* contains ~57 species inhabiting groundwaters in the Palearctic, including the special ecosystem of the Movile Cave (Stocchino et al. 2017; see also Chap. 16). Stygobiont planarians have also been described from the Americas and Australia. For example, *Hausera hauseri* is a typical stygobiont, unpigmented and eyeless, presumably an oceanic relict found in Brazil (Leal-Zanchet et al. 2014), while the genus *Girardia* has diversified in caves of Brazil and Mexico (Souza et al. 2016).

Most planarians, however, are considered stygophiles because the lack of eyes and depigmentation are the group characteristics and no other adaptations to groundwater were observed. There are studies indicating that the presence of planarians in groundwater could be a good indicator of organic pollution (Holsinger 1966; Eberhard 1990).

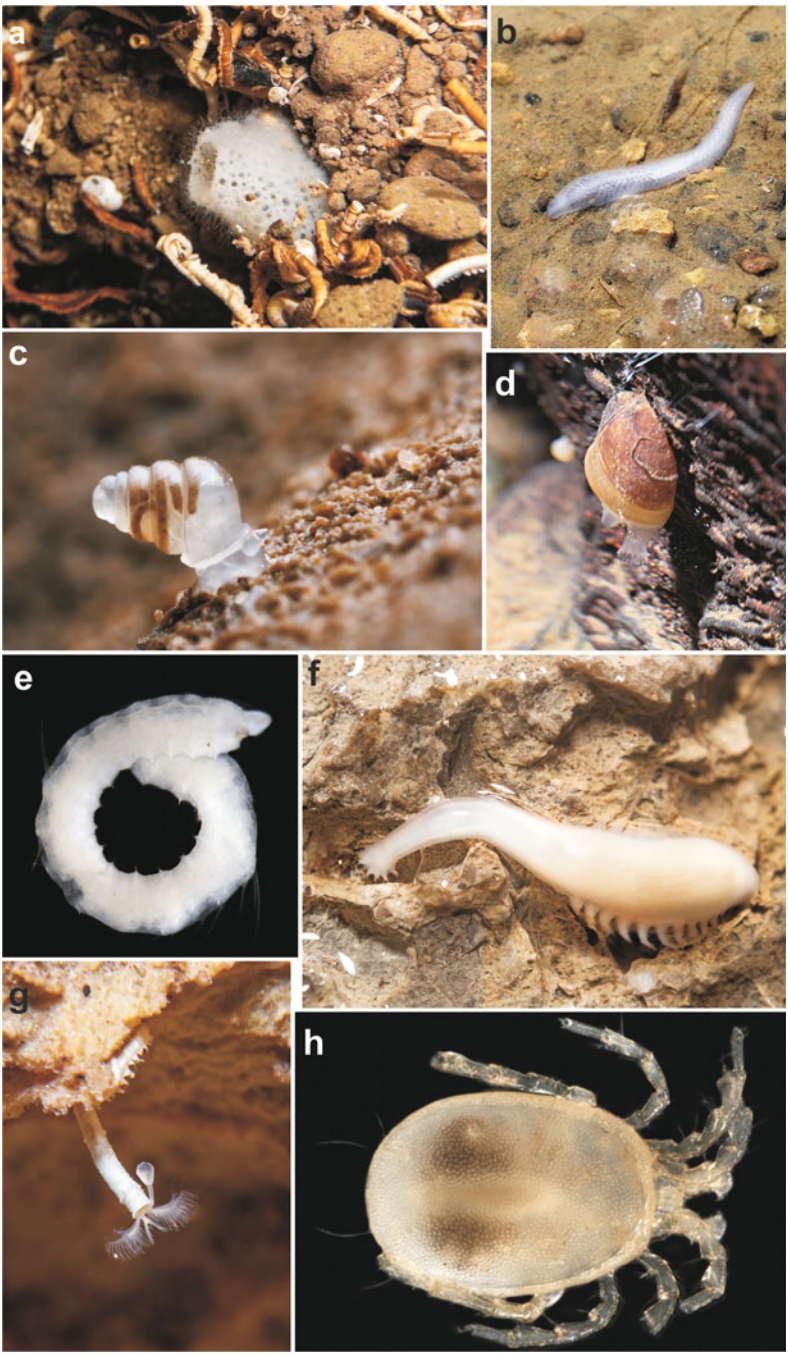

Fig. 8.1 Stygobiont invertebrates from caves and calcrete aquifers; (**a**) *Eunapius subterraneus* (Porifera), (**b**) *Dendrocoelum* sp. (Tricladida), (**c**) *Zospeum tholussum* (Gastropoda), (**d**) *Congeria* sp. (Bivalvia), (**e**) *Pristina pastoral* (Oligochaeta), (**f**) *Croatobranchus mestrovi* (Hirudinea), (**g**) *Marifugia cavatica* (Polychaeta), (**h**) *Arenurus* sp. (Hydrachnidia). Note that the relative size of the

The order Temnocephalida contains smaller parasitic species that live on cave crustaceans, with the exception of *Bubalocerus pretneri*, which is a predator. All subterranean described Temnocephalida lack eyes and most of the genera have been found in caves of the Dinaric range—*Stygodyticola*, *Scutariella*, *Subtelsonia*, and *Troglocaridicola*—, other than a single unidentified species from Papua New Guinea (Matjašič 1994).

8.3.4 *Rotifera: Rotifers*

Many rotifers have been observed in cave waters but none seem to be groundwater adapted, with the exception of some interstitial species, found outside caves (Pourriot 1994). Nevertheless, the presence and diversity of Rotifera in caves and other groundwater might be underestimated because most of the sampling has been done with larger mesh of planktonic nets unable to catch these extremely tiny organisms. A study on fauna in dripping water in caves in Brazil found rotifers to be more diverse than Copepoda as usually found in such habitats in Europe (Simões et al. 2013).

8.3.5 *Kinorhyncha: Mud Dragons*

Species of kinorhynch found in marine caves in the Mediterranean regions of Europe and Australia belong to *Echinoderes* (Sørensen et al. 2000), and those in Japan belong to *Ryuguderes* (Yamasaki 2016).

8.3.6 *Nematoda: Roundworms*

Nematodes colonized different environments and do not have pigments or eyes, which makes it difficult to distinguish stygobionts from epigean or stygophile species. There are a few species that were described from continental and marine caves that are considered to be cave adapted. They belong to genera such as *Desmocolex*, *Cylindrolaimus*, *Plectus*, *Halalaimus*, and *Thalassoalaimus* (Delamare-Debouteville 1960). In Movile Cave, five species live in the microbial mats: *Chronogaster troglodytes*—endemic to this cave—, *Panagrolaimus* sp., *Protorhabditis* sp., *Udonchus tenuicaudatus*, and probably a species of *Monhystrella* (Riess et al. 1999). Their

Fig. 8.1 (continued) animals is not respected. Photos by © Marko Lukić (**a**), © Jaroslav Stankovič (**b**), © Jana Bedek (**c**, **d**, **f**, **g**), © Jane McRae (**e**, **h**)

population is controlled by the abundant copepod *Eucyclops subterraneus scythicus*, revealing a trophic linkage between nematodes and copepods (Muschiol 2009).

8.3.7 Nemertea: Ribbon Worms

There is no evidence of subterranean adaptations in marine species, while some freshwater cave species are depigmented and lack eyes. Eyeless species of *Prostoma* have been described from cave waters in Europe (Botosaneanu 1998), as have species of *Potamonemertes* from gravel riverbeds in New Zealand (Moore and Gibson 1972).

8.3.8 Gastrotricha: Hairybacks

A single species can be considered as stygobiontic, *Marinellina flagelata*, a gastrotrich that lives in the hyporheic zone. This interstitial species has reduced size, reduced number of eggs, is depigmented, and lack eyes (Kisielewski 1998). Few gastrotrichs have also been recorded in continental cave waters, such as *Chaetonotus antrumus* from a cave in Montenegro (Kolicka et al. 2017). The only comprehensive study of the gastrotrich fauna in a cave habitat was carried out in an Italian sea cave by Todaro et al. (2006).

8.3.9 Tardigrada: Water Bears

Only interstitial stygobiont species are known from this group; there are no occurrences in continental caves. They are depigmented and lack eyes. Tardigrades in marine caves are more frequent although there is no information on their adaptation to the environment. However, Jørgensen et al. (2014) recently found dozens of species in marine caves, with nine from Australia; Fujimoto and Yamasaki (2017) described a new genus and species collected from sandy beaches of Ryukyu Archipelago, Japan.

8.3.10 Annelida: Segmented Worms

Representatives of the class Aphanoneura and subclass Oligochaeta (Clitellata class) occur frequently in continental and marine caves. Some terrestrial taxa also live in cave waters, such as *Fridericia* and *Allolobophora* (Dumnicka and Juberthie 1994). Cave Annelida do not show any adaptations to subterranean life, because they

already lack eyes and appendices (Fig. 8.1e), except for the smaller size and shorter hairs of some Naididae, or longer hairs of some Enchytraeidae (Dumnicka 1986; Dumnicka and Wojtan 1989). However, in a recent study Gonzalez et al. (2018) have shown that Aphroditiformia suborder show a significant elongation of sensory parapodial cirri (bundles of cilia), while lacking eyes and pigmentation (eyes could be also lost during colonization of deep-sea habitats).

In caves, the oligochetes prefer the sediments at the bottom of the water bodies, leaving only their posterior parts free, above the sediments, for respiration (Dumnicka and Juberthie 1994).

Some families, such as Potamodrilidae (Aphanoneura) and Dorydrilidae (Oligochaeta), live exclusively in groundwater habitats. Other representatives of Aelosomatidae (Aphanoneura) have been described from caves in Europe (*Rheomorpha neiswestnovae*, *Aeolosoma gineti*) and Cuba (*Aeolosoma cubana*), although their typical habitats are interstitial waters. Among oligochetes, Dorydrilidae has one groundwater genus (*Dorydrilus*), Haplotaxidae has three genera known only from caves, Lumbriculidae has seven genera with cave taxa, and Tubificidae has 14 genera of which five are known only from groundwater. Enchytraeidae, although known as soil inhabitants, has subterranean species that live exclusively in water, while stygobiont species of Naididae have been described only from the Antilles (Dumnicka and Juberthie 1994); groundwater appears to be an important habitat for Phreodrilidae in northern Australia (Pinder 2008).

Hirudinea subclass has few cave-adapted leeches around the world, and their adaptations to life in caves include depigmentation and lack or reduction of eyes. The slight widening of the oral sucker in *Dina absoloni* was proposed as another cave-specific adaptation by Sket (1986). In the family Haemopidae, *Haemopis caeca* is the only known stygobiont and was found in Movile Cave (see also Chap. 16). Most of the aquatic cave leeches belong to Erpobdellidae in the Northern Hemisphere; within this family the stygobionts belong to *Dina*, *Trocheta*, and *Croatobranchus* which occur in the Dinaric karst, the last with an unique mouth morphology (Sket et al. 2001) (Fig. 8.1f). *Erpobdella borisi* is a possible new stygobiont found in Iran (Cichocka et al. 2015).

Polychaeta class are marine species with few representatives living in anchialine caves (see also Chap. 18) or in freshwater cave habitats. There are two well-known polychaetes from freshwater cave habitats: *Troglochaetus beranecki* and *Marifugia cavatica*. The minute and transparent *T. beranecki* is widely distributed in Europe, and a related species was found in Japan and attributed to *Speochaetes* (although never described according to Uéno 1957; from Juberthie and Decu 1998). *M. cavatica* is depigmented and eyeless, lives in a calcified tube, and probably colonized cave waters during Pliocene or Pleistocene from freshwater lakes in the Dinaric karst region (Sket 1997; Mihevc et al. 2001; Fig. 8.1g). Twelve of the 17 described *Namanereis* species inhabiting subterranean habitats were mentioned from Australia, Yemen, Canary Islands, and Mexico (Williams 2004; Glasby et al. 2014; Conde-Vela 2017).

8.3.11 *Mollusca: Mollusks*

Among several classes of mollusks, some are marine and others only fossils; only two have subterranean representatives: Gastropoda and Bivalvia. Cave adaptations are reflected in features such as a thin and fragile shell, white-depigmented body, fine and semi-transparent tegument, and more or less reduced eyes. The small size of the groundwater species can also be an adaptation (Ginet and Decou 1977).

Gastropoda (snails). Unlike epigean snails, the groundwater species belong to a group that can breathe under water with the aid of gills positioned in front of their internal cavity (Ginet and Decou 1977). Altogether, 350 stygobiont gastropods have been described around the world, with 97% of the taxa belonging to Hydrobiidae (Culver 2012), of which 168 species inhabit caves in the Balkan Peninsula (Sket et al. 2004; Fig. 8.1c). Most of the described species were found in the western Palearctic.

Bivalvia (clams). The cave clams belong to the genera *Congeria* and *Pisidium*. Only one species was assigned to *Congeria* until 2013, when C. *kusceri* was split and two other species added: *C. jalzici* and *C. mulaomerovici* (Bilandžija et al. 2013). They all inhabit groundwater of the Dinaric region (Fig. 8.1d). Four species of *Pisidium* are known to inhabit caves of Caucasus, Turkey, and Japan (Bole and Velkovrh 1986). However, the number of described species underestimates true species richness since various cave populations of a species have different shell shape and organization of the hinge teeth, which are usually specific characters, so that each cave is likely to have at least one endemic species (Chertoprud et al. 2016).

8.4 Arthropoda (see Table 8.1)

8.4.1 *Crustacea*

Crustaceans are the most diverse stygobiont group. Crustaceans live in marine and freshwater environments and their adaptations to groundwater include reduction of eggs number (less than 10 compared to dozens at epigean species), reduction of the reproductive rhythm, longer development, longer life, depigmentation, eye reduction, and reduction of the swimming legs and hairs (see also Chap. 4).

There are only a few stygobiont Cladocera (water fleas) worldwide, and their adaptations to subterranean life include valve depigmentation and eye regression. To date, five stygobiontic chydorid species belonging to *Alona* and *Brancelia* are known (Negrea 1994; Van Damme and Sinev 2011), while other cladoceran species belonging to *Macrothrix*, *Neothrix*, *Moina*, and *Leptodora* require further research.

Stygobiont Copepoda belong to the orders Platycopioida, Calanoida, Misophrioida, Cyclopoida, Harpacticoida, and Gelyelloida, although the number of stygobiont species is not evenly distributed among and within these orders (Galassi 2001; Fig. 8.2). Stygobiont species are particularly common within

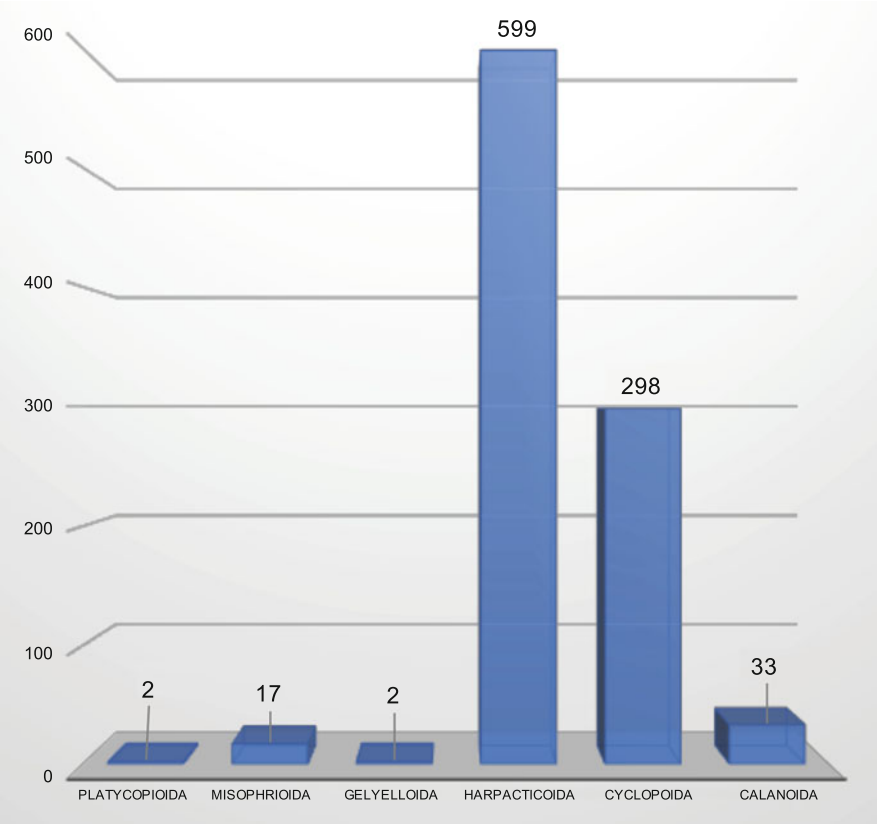

Fig. 8.2 Number of species and subspecies of different orders of cave Copepoda (modified after Galassi 2001)

Harpacticoida, Cyclopoida, and Calanoida. The Cyclopoida and the Harpacticoida have almost 900 species and subspecies (Galassi 2001) distributed worldwide. Most of the stygobiont Harpacticoida (Fig. 8.3e) belong to the families Ameiridae, Canthocamptidae, and Parastenocaridae, with *Praeleptomesochra*, *Pseudoleptomesochrella*, *Parapseudoleptomesochra*, *Nitocrellopsis*, *Stygonitocrella*, *Nitocrella*, *Antrocamptus*, *Spelaeocamptus*, *Gulcamptus*, *Stygepactophanes*, *Ceuthonectes*, *Parastenocaris*, *Forficatocaris*, *Paraforficatocaris*, and *Potamocaris* being exclusively subterranean genera. Chappuisidae has only two exclusively subterranean species (Rouch 1994). The exclusively subterranean Cyclopoida (Fig. 8.3g) belong to genera *Speocyclops*, *Graeteriella*, *Allocyclops*, and *Kieferiella*, with *Speocyclops* as the most specious genus. The 11 known freshwater stygobiont Calanoida belong to Diaptomidae (Bowman 1986; Shu et al. 2017). Freshwater calanoids are distributed from Mexico to Europe and to the Far East, including Australia (Shu et al. 2017), although marine and anchialine cave Calanoida are much more diversified (see also Chap. 18).

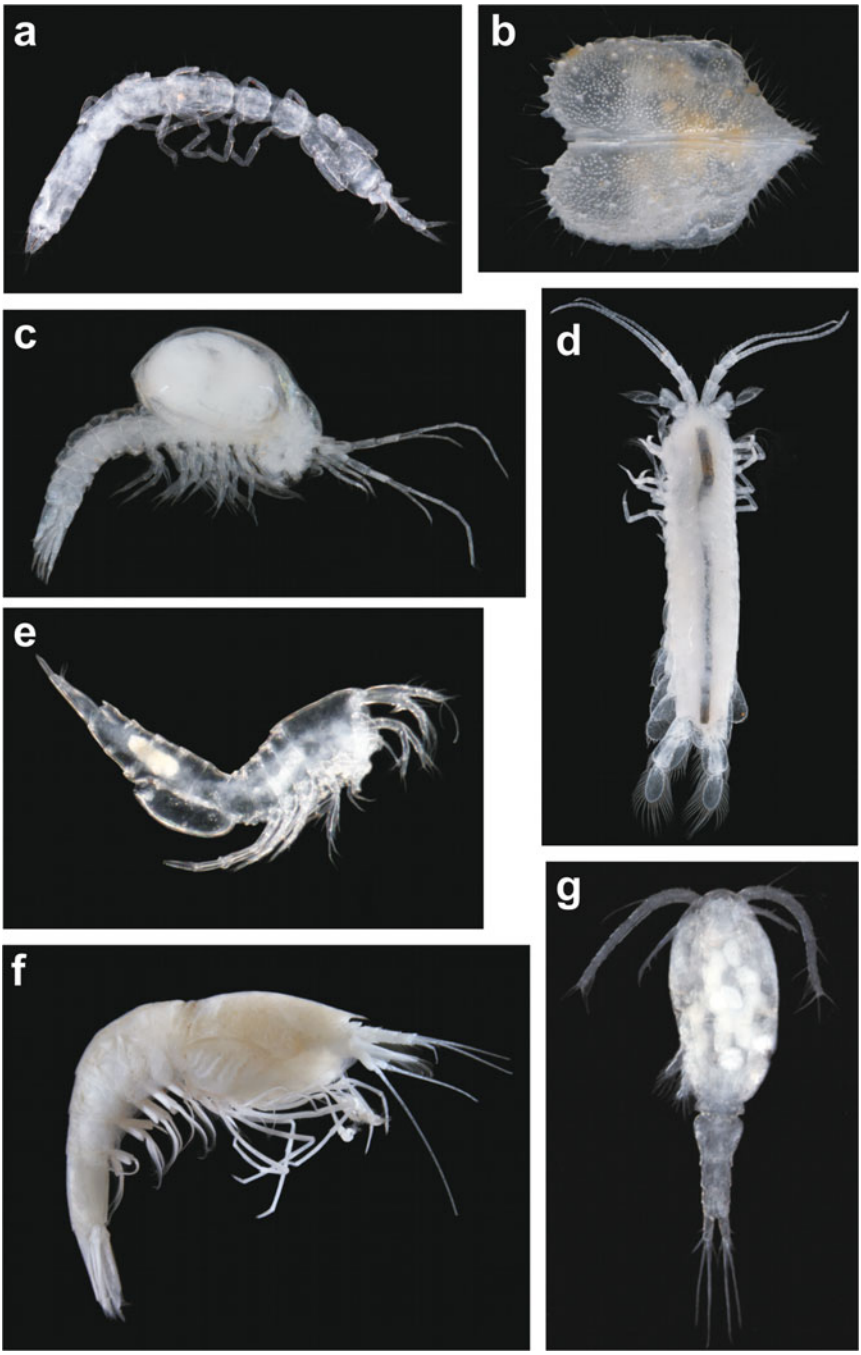

Fig. 8.3 Stygobiont crustaceans from caves and calcrete aquifers; (**a**) Microcerberidae (Isopoda), (**b**) *Gomphodella yandi* (Ostracoda), (**c**) *Mangkurtu* sp. (Spelaegriphacea), (**d**) *Halosbaena tulki* (Thermosbaenacea), (**e**) *Phyllopodopsyllus wellsi* (Harpacticoida), (**f**) *Stygiocaris stylifera*

Stygobiont orders Platycopioida and Misophrioida are found only in marine and anchialine caves (see also Chap. 18). The order Gelyelloida is represented by two species that live in groundwater in France and Switzerland and by another species living in the interstitial sediments of a stream in the USA (Galassi 2001).

The class Remipedia was first described from an anchialine cave (Yager 1981). They lack eyes and are depigmented and have been found only in marine cave systems in the Caribbean Sea, Australia, Canary Islands, Mexico, and Dominican Republic (Koenemann et al. 2018; see also Chaps. 18 and 19). There are 29 described species (Koenemann et al. 2018) and most speciose genera are *Speleonectes*, *Cryptocorynetes,* and *Morlockia*.

According to Danielopol and Hartmann (1985), 310 species and subspecies of the class Ostracoda (seed shrimps) were known from hypogean habitats in 1986, of which only 50 were reported from karst and caves habitats (Fig. 8.3b). Most of subterranean ostracods belong to the order Podocopida and some of the genera have only stygobiont species (i.e., *Mixtacandona*, *Caribecandona*, *Danielocandona*, *Phreatocandona*). Since 1986, dozens of species have been described from freshwater and marine cave habitats. The most notable is the discovery of more than 80 stygobiont ostracods in the Pilbara region of Australia (see also Chap. 20), most of them belonging to endemic genera (e.g., *Deminutiocandona*, *Pilbaracandona*, *Areacandona*; Karanovic 2007). Other interesting discoveries have enlarged not only the number of cave ostracods and their biogeographic distribution but also the knowledge on the origin and history of the group; for example, the discovery of a *Frambocythere* species in a South Korean cave, a genus considered extinct in Eocene (Smith et al. 2017). Subterranean ostracods are mostly blind and depigmented, their size is reduced, and chaetotaxy simplified, while some of the chemosensory aesthetascs are enlarged (Martens 2004).

Groundwater Mysidacea (opossum shrimps) are known from coastal caves, phreatic waters, and anchialine habitats (see also Chap. 18) mostly in the Caribbean region, Mexico, and Mediterranean basin, with only a few species described from south-east Africa and southern India. Stygobiont species belong to *Spelaeomysis*, *Stygiomysis*, *Antromysis*, *Troglomysis*, *Heteromysoides*, *Burrimysis*, and *Palaumysis*. They are blind and depigmented and have a reduced carapace; their sensory setae also show some differences from their epigean relatives in terms of their fine morphology (Crouau 1978, 1980).

Three stygobiont species of Bochusacea (formerly Mictacea) have been described from marine caves of the Caribbean Sea: *Mictocaris halope* and two species of *Thetispelecaris* (Bowman and Iliffe 1985; Ohtsuka et al. 2002).

Eyeless and unpigmented spelaeogriphaceans and thermosbaenaceans are represented by few species from subterranean waters. The Spelaeogriphacea are found only in continental waters, in limestone or sandstone caves, or in calcrete

Fig. 8.3 (continued) (Decapoda), (**g**) *Thermocyclops decipiens* (Cyclopoida). Note that the relative size of the animals is not respected. Photos by © Jane McRae

aquifers where they are represented by three genera, *Mangkurtu* (Fig. 8.3c), *Potiicoara*, and *Spelaeogriphus* (Jaume 2008). Thermosbaenacea are marine crustaceans and most taxa occur in the anchialine environment. Only 18 species of Thermosbaenacea have been recorded in limnic or brackish waters, in caves, or in interstitial habitats (Jaume 2008), and they belong to *Thermosbaena*, *Tethysbaena*, *Limnosbaena*, *Halosbaena* (Fig. 8.3d), *Theosbaena*, and *Tulumella* (Boutin 1998). Subterranean thermosbaenaceans have a larger distribution, matching precisely the area covered by the ancient Tethys Sea (Jaume 2008).

One of the most diverse orders of crustaceans, Isopoda, is found in all subterranean marine and freshwater habitats (see also Chap. 7 for a review of terrestrial isopods). The order contains small individuals that live in interstitial habitats and bigger individuals that occur in larger groundwater bodies. They lack eyes, are depigmented, have relatively longer antennae than their epigean relatives and sometimes very elongated uropods, have slower development and produce fewer eggs, —even one single bigger egg that is richer in vitellus as in Microparasellidae (Coineau 1998). With one exception all suborders have also colonized groundwater habitats. Few species belong to the most primitive suborder of isopods, the Phreatoicidea (Coineau 1998; Knott and Halse 1999; Wilson 2008). The rest of groundwater representatives belong to Asellota [i.e., *Caecidotea*, *Proasellus*, *Synasellus*, *Stenasellus*, *Microcerberus* (Fig. 8.3a), *Microcharon*, etc.], Cymothoida (i.e., *Cyathura*, *Stygocyathura*, *Thyphlocirolana*, *Faucheria*), Sphaeromatidea (i.e., *Monolistra*), and Calabozoida (from Coineau 1998). In the world, the most diverse regions in aquatic isopods are Caribbean and Mediterranean. *Asellus aquaticus* is a special example of a largely distributed isopod inhabiting various aquatic habitats in Europe, with only two subspecies restricted to caves, one in Movile Cave and another in the Dinaric karst caves. The importance of this species is that it shows how surface populations diverge after subterranean colonization and that only about one-third of all changed traits can be considered as troglomorphisms (Konec et al. 2015).

Amphipoda is another diverse order of crustaceans characterized by the lack of both eyes and body pigmentation and a diversity of body and appendage sizes depending on the groundwater habitat it occupies. They also have longer life and lay larger and fewer eggs. More than half of the known species (~750 species) occur in caves (Holsinger 1994; Hobbs 2004). Groundwater amphipods belong to 32 families; among the most speciose genera are *Niphargus*, *Stygobromus*, *Metaniphargus*, *Bogidiella*, *Pseudoniphargus*, *Ingolfiella*, *Gammarus*, *Salentinella*, *Metacrangonyx*, *Paramelita*, etc. Two broad regions are especially rich in amphipods, namely, a region comprising eastern and southern North America and West Indies and the Mediterranean region of Europe. *Niphargus* species are used in biospeleology as models for phylogeographical and evolutionary studies (see a recent paper by Delić et al. 2017).

The most evolved crustacean order, the Decapoda, have numerous cave representatives in the infraorders of Brachyura (crabs), Caridea (shrimps), Astacidea (crayfishes), and Anomura. The cave decapods have thin tegument, fine and long pereiopods and antennae with increased number of aesthetascs and are depigmented,

except for some anchialine shrimps that are orange, red, or pink in color. The visual organs are reduced or animals are completely blind with a slow metabolism and increased longevity (Cooper and Cooper 1978; Hobbs 1998).

More than 30 species of crabs with marine or freshwater origins have been described from caves. *Sesarmoides*, *Trogloplax*, and *Cancrocaeca* are the main cave genera with a marine origin, while the freshwater crabs belong to *Cerberusa*, *Isolapotamon*, *Phaibulamon*, *Stygothelphusa*, *Adeleana*, *Thelphusula*, *Phricothelphusa*, *Sendleria*, *Holthuisana*, *Rouxana*, *Typhlopseudothelphusa*, *Neostrengeria*, *Chaceus*, and *Rodriguezia*. The cave crabs are distributed in Indonesia, Papua-New Guinea-New Britain, Thailand (the species of marine origin), Jamaica, Mexico, Guatemala, Belize, and South America (the species of freshwater origin) (from Guinot 1994).

Cave shrimps belong to different families and some genera are especially speciose: *Procaris*, *Caridina*, *Parisia*, *Troglocaris*, *Typhlatya*, *Macrobrachium*, *Troglomexicanus*, and *Typhlocaris* (Fig. 8.3f). They are distributed in North America, West Indies, Australia, and the Mediterranean regions (Hobbs 1998; Page et al. 2008).

Freshwater crayfishes are considered successful in colonizing caves, with the Cambaridae as the best represented family. *Cambarus*, *Orconectes*, and *Procambarus* are the most diversified genera distributed in North America and north of Mexico (Hobbs 1998).

Syncarida superorder have subterranean representatives in both its orders, Anaspidacea and Bathynellacea. Anaspidacea has families restricted to caves or interstitial habitats, like Psammaspididae and Stygocarididae, that lack eyes and have reduced appendages (Coineau 1998). They were identified in Tasmania, Australia, and South America. Bathynellacea have exclusively groundwater representatives distributed on all continents. They lack eyes and statocysts and have reduced appendages. The order has more than 95 species, most of them belonging to *Bathynella* with more than 50 species and subspecies (Camacho and Valdecasas 2008). *Hexabathynella* has a cosmopolitan distribution being as rich in species as *Iberobathynella* with a limited distribution to the Iberian Peninsula (Coineau and Camacho 2004; Camacho 2003). Most genera have small geographic distribution (Camacho and Valdecasas 2008).

8.4.2 *Hydrachnidia: Water Mites*

Water mites are known only from phreatic and hyporheic zone waters (Fig. 8.1h). Specializations to these habitats include eye reduction or lack of eyes, depigmentation and thinner body cuticle, smaller and elongated body, shorter legs than their epigean relatives, and reduction of the number of eggs (Teschner 1963). Only one of the 10 suprafamilies of this subclass has no subterranean representatives. The most frequent genera in phreatic waters are *Stygotrombidium*, *Cerberotrombidium*, *Wandesia*, *Tartarothyas*, *Bandakia*, *Torrenticola*, *Neomamersa*, *Kawamuracarus*, *Atractides*, *Frontipodopsis*, *Aturus*, *Stygomomonia*, etc. (Schwarz et al. 1998).

Fig. 8.4 Stygobiont beetles from a single calcrete aquifer in the Australian desert (Dytiscidae: Hydroporini), from left to right: *Paroster macrosturtensis*, *P. mesosturtensis*, *P. microsturtensis*. Photo by © Chris Watts

8.4.3 Insecta, Coleoptera aquatica: Aquatic Beetles

The first stygobiont beetle (*Siettitia balsetensis*) was discovered in 1904, in France, by Abeille de Perrin and until the end of the twentieth century only 16 more species and one subspecies were reported from Japan, China, Thailand, Indonesia, and Ecuador (Spangler and Decu 1998). They belong to Dytiscidae, Elmidae, Hydrophilidae, and Noteridae families. The number of stygobiont species increased dramatically with the study of the calcrete aquifers in Western Australia (see also Chap. 20) where approximately 100 dytiscid species with regressed or absent eyes have been found within 45 separate calcrete bodies (Leys et al. 2003; Watts and Humphreys 2009; Watts et al. 2016).

Along with the typical adaptations of subterranean inhabitants, stygobiont beetles have unique adaptations that are not found in their epigean water beetle relatives, such as the change of pupation habitat from terrestrial to the bottom of the subterranean waters (Uéno 1957). Smaller size was also considered as one of the general adaptations of stygobiont beetles until the discovery of calcrete Dytiscidae of very different sizes (Fig. 8.4).

8.5 Chordata

8.5.1 Pisces: Fishes

Fish are the most studied group of cave inhabitants, especially in relation to processes of adaptations. All stygobiont fishes belong to the Teleostei and have a small and slender body. More than 80 taxa were described but new species are added each year. Cave fishes belong to the orders Characiformes, Cypriniformes,

Siluriformes, Gymnotiformes, Percopsiformes, Ophidiiformes, Cyprinodontiformes, Synbranchiformes, and Perciformes. The richest in species are Cypriniformes and Siluriformes. The most diversified genera are *Sinocyclocheilus*, *Triplophysa*, *Rhamdia*, *Trichomycterus*, *Ancistrus*, and *Lucifuga*. Cave fishes are most common in tropical and subtropical caves, but a few have also been described from temperate caves (Weber et al. 1998; Romero 2001; Trajano et al. 2010). The most recent discovery was the first cave fish in Europe, found in the cave labyrinth called the Danube-Aach System, in southern Germany (Behrmann-Godel et al. 2017).

Adaptations of cave fish include the ones common for all stygobiont animals—depigmentation and reduction or lack of eyes, as well as some typical adaptations for the group: reduction of the pineal organ in some species, enhanced olfaction, taste and touch senses, and the development of the lateral line (see also Chap. 4).

8.5.2 Amphibia

Only the order of Urodela (salamanders) has cave representatives. The most advanced adaptations include the development of the lateral line, slender legs, a flat and wide head, and neoteny. *Eurycea*, *Typhlotriton*, *Haideotriton*, and *Gyrinophilus* are known from North America; the species of these genera are depigmented and have reduced eyes. The only European cave salamander is *Proteus anguinus* which reaches sexual maturity at 11–14 years for the males and 15–18 years for the females, while hatching takes place more than 100 days after oviposition (Juberthie et al. 1996; Durand 1998). A first black *Proteus* was found almost three centuries after the description of this species by Von Valvasor in 1689, and described as a subspecies endemic to a small area in Slovenia (Sket and Arntzen 1994).

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