

Class Malacostraca (subclass Eumalacostraca)

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1 Chapter 7: Class Malacostraca (SubClass Eumalacostraca)

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46

48 Abstract

This chapter present an updated taxonomic review of Freshwater Malacostraca. It is organized 49 into an introduction to Malacostraca followed by 7 other sections corresponding to the main 50 orders of freshwater Eumalacostraca (Amphipoda, Bathynellacea, Decapoda, Ingolfiellida, 51 Mysida and Stygomysida, Isopoda, and Thermosbaenacea) present in Mediterranean Basin. 52 Each section contains the ecology and distribution of orders, the necessary material preparation 53 54 methods, the relevant morphological terms, and current limitations in our knowledge of the group. Dichotomous identification keys to family, genus and even species are provided for most 55 of groups (only genera with more than 15 species were not include in keys to species). 56

57

58 Keywords: Crustacea, Mediterranean Basin, taxonomy, biogeography

60 **1. Introduction to Malacostraca**

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65 **INTRODUCTION**

Malacostraca are the most diversified class of Crustacea and represent more than half of total crustacean diversity. They are characterized by the development of ambulatory legs and specializations for benthic life, the absence of free-living larval development (brooding eggs), and the colonization of every kind of fresh and salted aquatic environments. Their body size range is very wide, from a few millimetres up to 3 m, even if the largest freshwater specimens (i.e. the Tasmanian giant freshwater crayfish) do not exceed 80 cm.

Malacostraca are composed of three subclasses (Eumalacostraca, Hoplocarida, 72 73 Phyllocarida); two of them exclusively include marine species, and all the freshwater species of the class belong to the subclass Eumalacostraca. They constitute a very diversified group that 74 includes around 75% of all freshwater crustacean species (Balian et al., 2008), and are 75 76 represented by eight orders and at least 1,086 species in the Mediterranean basin (Table 1). The Mediterranean basin can be considered as a hotspot for Malacostraca: it harbors 18% of the 77 world freshwater species, up to one third of the world known species of almost all orders, and 78 79 up to more than 50% of Thermosbaenacea (Table 1). Only Decapoda are less diversified in this area, with only 2% of the world diversity of this order. 80

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82 ECOLOGY AND DISTRIBUTION

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Among freshwater Malacostraca of the Mediterranean basin, most species (\$73%) inhabit 84 groundwaters, and the remaining species colonize running waters ($\approx 18\%$), lakes or ponds 85 (\approx 5%), and only 3.5% survive in brackish waters. The Mediterranean basin is therefore 86 characterized by a very high proportion of groundwater species, which represent around 24% 87 of freshwater crustaceans in the world (Gibert & Culver, 2009). The proportion of obligate 88 89 groundwater species in the Mediterranean basin is likely related to two major historical events: i) a strong vicariance related to the paleological instability of the Mediterranean Sea and the sea 90 level fluctuations (e.g. Messinian crisis) (Ayati et al., 2019), and ii) the relative long-term 91 climatic stability observed throughout the Pleistocene period, when speciation events 92 93 accumulated over time (Zagmajster et al., 2014).

Malacostraca are widely distributed throughout the Mediterranean basin (Fig. 7.1A), but 94 95 80% of species are endemic (i.e. restricted to one country or one archipelago) (Fig. 7.1B). There also exists a clear positive correlation ($R^2 = 0.91$) between the total number of species in each 96 country and the number of endemic ones. Groundwater species are generally restricted to less 97 98 than two countries, whereas epigean species can be widely distributed, especially species able to survive in brackish waters. However, it is difficult to draw robust conclusions on the species 99 distribution because information is lacking in many countries such as the Middle-East countries 100 101 and about some groups (e.g. groundwater species). For example, countries in the north of the Mediterranean basin harbor a higher diversity than southern countries do, but this difference 102 might be related to poor knowledge about the southern part of the basin (Kayo et al., 2012; 103 104 Zagmajster et al., 2018).

105 106 107 108 109 110 111 112 113 114 115 116 117 118	General diversity patterns can be drawn despite this limitation. If we analyze diversity in the north and in the south separately, total diversity tends to decrease from west to east (Fig. 7.1A). In the Mediterranean islands, the Balearic Islands and Sardinia are the richest as regards total species richness as well as the proportion of endemic species (48% and 37.5%, respectively). The analysis of presence/absence data for all Malacostraca clearly highlights four main groups of faunal assemblages (Fig. 7.2). One group includes countries from the northern part of the Mediterranean basin, and is divided into 4 sub-groups: Iberian countries (sub-group N1); France, Italy and Slovenia (sub-group N2); Balkanian countries from Croatia to Greece (sub-group N3); and Turkey (sub-group N4). The second group includes eastern countries and Egypt (group S1), the third one includes Maghreb (group S2), and finally the fourth one includes the Mediterranean islands and Lybia (group S3).
119	KEY TO ORDER OF EUMALACOSTRACA
120	(Cumcea and Tanaidacea not include in the key)
121	
122	1 Carapace reduced or absent
123 124	1' Carapace well developed (Fig. 7.3B,F)
125	2(1) Thoracopods uniramous, body vermiform or not
126	2' Thorocapods biramous, body vermiform, less than 2 mm (Fig. 7.3E) Bathynellacea
127	
128	3(2) Body laterally compressed (Fig. 7.3A), telson and abdominal segments free
129 130 131	3' Body dorsoventrally compressed (Fig. 7.3C), telson and abdominal segments fused into a pleotelson
132 133 134	4(3) Cephalothorax composed of head and first segment of the mesosome fused together (Fig. 7.10); presence or not of vestigial pedunculate eyes; eyes lacking; pleosome without epimera and with reduced pleopod/uropod appendages
135 136 137 138	4' Head not fused with the first segment of the mesosome (Fig. 7.4); vestigial pedunculate not present; eyes present or lacking; pleosome with three epimera and normally developed appendages
139 140	5(1') Compounds eyes generally present, but absent in some groundwater genera, when present they are pedonculate; pleopods always developed
141 142 143	5' Eyes absent, Pleopods reduced and only on the two first abdominal segments, absent from remaining segments, eight pairs of thoracopods, first modified as a maxilliped
144	6(5) Seven pairs of thoracopods (Fig. 7.3D)7
145 146	6' Five pairs of walking legs, including chelae Decapoda

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182 2. Malacostraca: Amphipoda

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187 **INTRODUCTION**

Amphipoda Latreille 1816 are present in all types of continental waters (springs, rivers, lakes)
 and in groundwaters (subterranean interstitial and cave systems) on all continents. Apart from
 a few exceptions, they are easily recognizable in the field from their shrimp-like habitus.

Biogeographic analysis indicates that amphipods were likely widespread in Pangea, Gondwana, and Laurentia (Väinölä et al., 2008). These studies were confirmed by the discovery of the oldest fossil *Rosagammarus minichiellus* in late Triassic limestone in Nevada (McMenamin et al., 2013). Marine ancestors subsequently colonized very early freshwaters during the Jurassic period before a probable massive diversification during the Cretaceous (Copilaş-Ciocianu et al., 2019) and Paleogene (Hou et al., 2014) periods.

The ancestors of Mediterranean amphipods may have an Atlantic origin around 40 Mya 197 (Hou & Sket, 2016). They conquered its freshwater confluents, like Iberogammarus and 198 Echinogammarus sensu stricto did. Finally, some crossed the proto-Mediterranean sea to the 199 200 lands located at its eastern edges, (the Typhlogammarus group and part of the Sarothrogammarus group), or also spread along the future Mediterranean coasts 201 (Rhipidogammarus). Other groundwater groups (e.g. hadzioid-thalassoid Metacrangonyctidae 202 amphipods) result from ancient continental-level vicariance (Bauzà-Ribot et al., 2012), or from 203 204 more recent vicariance and long-distance dispersal (Pseudoniphargidae; (Stokkan et al., 2018).

Among the 1,870 amphipod species and subspecies recorded from fresh or inland waters worldwide (Horton et al., 2020), more than 31% are present in the Mediterranean basin, where a total of 14 families, 50 genera and 581 species are recorded; most of them are endemic to the region.

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210 GENERAL ECOLOGY AND DISTRIBUTION

Amphipoda are widely distributed and colonize all types of marine and continental waters on all continents. They represent one of the highest invertebrate biomass values and are prey for many other organisms. They also support many functional processes in these ecosystems like organic matter recycling and bioturbation.

In the Mediterranean basin, Amphipods are present in all countries and big islands. We recorded 559 species (96%) restricted to only one type of environment (running water, lake, groundwater, brackish water) and only 22 euryecous species (i.e. present in a least two types of aquatic ecosystems). Euryecous species are present mainly in running waters, lakes and brackish water, and only a few species (e.g. *Niphargus zagrebensis*) can live permanently either in groundwater or in surface waters.

The highest diversity is found in groundwaters, which represent 74% of the total amphipod richness with 429 species, followed by running waters (127 species) and lakes (31 species). Only 17 species live solely in lakes and originally came from Ohrid Lake (8 species) or from Turkey (9 species); the other lacustrine species are euryecous species that also live in running waters (14 species) or in brackish environments (4 species).

Among the 14 families recorded so far, most of them are widespread worldwide, with members 226 fresh and marine waters. Others (Crangonyctidae, Niphargidae, 227 living in both Pontogammaridae, and Typhlogammaridae) have a Eurasian distribution and are only present 228 in the central and eastern parts of the Mediterranean basin, except Crangonyx africanus in 229 Morocco. Metacrangonyctidae and Pseudoniphargidae are mainly distributed in the 230 231 Mediterranean area but also have a few members in the Canary and Caribbean islands. Finally, only two families are endemic to the Mediterranean basin: Salentinellidae with 14 species 232 widely distributed around the Mediterranean Sea between Greece and Algeria, and 233 Sensonatoridae with only one known species in Spain (Sensonator valentienensis Notenboom, 234 1986). 235

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237 TERMINOLOGY AND MORPHOLOGY

Amphipoda are medium/large-size Malacostraca (from 0.1 up to 35 mm in the Mediterranean basin). Their body is typically compressed laterally, though less so for Corophiidae. It is divided into 13 segments that can be grouped into the head, the mesosome, the metasome, and the urosome (Fig. 7.4).

The head is fused to the thorax and bears two pairs of antennae. The upper pair is 242 243 antennae 1, with a basal peduncle composed of three articles and a distal flagellum composed 244 of many articles. The third peduncular article also bears an accessory flagellum on its distal end, usually composed of a reduced number (less than 10) of tiny cylindrical articles. The 245 246 second pair of antennae (antennae 2) has a flagellum composed of several small articles and a peduncle composed of five articles; articles 4 and 5 are much longer than the first 3 articles (the 247 first one is hidden by the head). Most epigean species (with few exceptions like epigean 248 249 Niphargus zagrebensis S. Karaman, 1950) have one pair of more or less developed sessile compound eyes. Eyes are absent in obligate groundwater species. However, we often found 250 eyed species in groundwaters, especially in the Mediterranean basin, where epigean species can 251 be present in a large proportion of groundwaters round the year. The mouthpart is on the ventral 252 surface of the head and is composed of the labrum, labium, mandibles, maxillae I and II, and 253 254 maxilliped.

The mesosome (or thorax or pereon) bears different kinds of legs, but no carapace. It has eight pairs of uniramous appendages, the first of which are used as accessory mouthparts. Two pairs of gnathopods (modified pereopods 1 and 2) are used for grasping, usually with a last subchelate article; the next five pairs (pereopods 3-7) are walking legs. Gnathopods and pereopods 3 and 4 have modified coxae transformed into large coxal plates. Coxal gills are present on mesosome segments in various numbers according to species, and sternal gills are known only in Crangonyctidae.

The metasome (or abdomen or pleion) is divided into two parts – the pleosome and urosome segments. Each segment bears one pair of legs. The pleosome bears three pairs of swimming legs named pleopods, with multi-articulated rami. The urosome bears three pairs of uropods. The length and the shape of uropod 3 can be highly variable among genera. The basal part of the uropod is the peduncle, that branches into an exopodite (with one or two articles, the second one can be short and hidden by the apical spines of article 1) and a medial branch named the endopodite (only one article or no article at all). The telson – the final body segment – is attached above uropod 3.

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274 COLLECTION, PREPARATION, AND IDENTIFICATION

Amphipoda are widely distributed in all aquatic environments, including groundwaters.
Therefore, the sampling methods and devices are numerous and depend on the specific habitats
where the fauna is found.

In surface waters, we can sample them using all kinds of sampling tools and methods (sweep net, kick sampling, grab sampler, dredges, and even artificial substrates) or just by taking stones, leaf litter or macrophyte by hand or with a kitchen colander. There are rarely more than 3 species in any given site. However, it is strongly recommended to sample the different substrates because many species have different microdistribution patterns when they co-occur (Piscart et al., 2007).

- In groundwaters, any kind of specific material for this environment can be used (Malard et al.,
 2002). Baited bottle traps or nets exposed overnight are also very efficient for many
 groundwater organisms.
- Amphipoda can be easily fixed and preserved in 70% ethanol or another fixative for morphological analysis and in 95% ethanol for molecular analysis.

Many species can be identified under a stereomicroscope, but identification at the species 289 level may require dissection, mounting body parts and appendages on slides, and subsequent 290 examination using a 400x or greater magnification microscope. Specimens in glycerol or 291 ethanol can be handled under a low-power microscope with needles. Glycerol is used as an 292 embedding medium for short-term slides. Baths in clearing solution (e.g. soft acids) or 293 permanent mounting media are only required for depositing museum specimens. A same 294 specimen can be used for both studies: the abdomen for DNA extraction and the other parts for 295 dissection and mounting. This procedure ensures that the sequenced genes correspond to the 296 297 same morphotype.

Taxonomic identification to the species level is generally only possible in males, but females can be used for higher taxonomic levels. The most important body parts for identification are the antennae, mouthpart, coxae, gnathopods, pereopods 5 and 7, epimera, telson, and uropods; but additional body parts need to be examined to identify certain species.

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303 LIMITATIONS

Amphipoda are a highly diversified group with almost 600 known species, and even more 304 remain undescribed. The keys below are designed to cover the 14 families and 49 genera; keys 305 at the species level are provided only for the genera with a low number of species (usually less 306 307 than 15). Rare records are included, unless they are insufficiently documented. Taxonomic synonymy has been updated, but taxonomy is not well established for some genera (e.g. 308 Echinogammarus, Laurogammarus, and Typhlogammarus,) and even families (e.g. 309 310 Pontogammaridae), especially following recent molecular studies. For those genera and till a clear consensus is found, we assume the use of the most parsimonious point of view, even if 311 alternate classifications may be found in other keys. As a consequence, some family, genus and 312 species names may change in the future. 313

Finally, even if our keys were designed to be as clear as possible, we should never forget that identifying certain groups of amphipods (especially groundwater species) can be very difficult and requires strong expertise. Do not hesitate to use alternative information or keys to consolidate your conclusions. We should keep in mind that keys, even at the family level, are designed for species of the Mediterranean basin; they are not adapted to other amphipods worldwide.

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322	KEYS TO AMPHIPODA
323	Key to Amphipoda families
324	1 Antenna 1 significantly shorter than antenna 2
325	1' Antenna 1 subequal or longer than antenna 2
326	
327 328 329 330 331	 2(1) Antenna 1 accessory flagellum absent; eyes well developed
332 333	3(2) Antenna 2 enlarged; mandibular palp present; urosomite dorsally flat Corophiidae [North-Eastern Mediterranean, Central Europe]
334 335 336	3' Urosomite enlarged, antenna 2 not enlarged, mandibular palp absentTalitridae [Peri-Mediterranean]
337	4(1) Sternal gills absent
338 339 340	4' Sternal gills present Crangonyctidae [Europe, Morocco]
341	5(4) Mandibular palp normally developed; eyes present or absent
342 343 344	5' Mandibular palp vestigial; eyes absent
345 346	6(5) Coxae 1-3 subequal or size progressively increasing, coxae 4-5 of various size; uropod 1-2 peduncles with lateral spines; eyes present or absent
347 348 349 350	6' Coxae 1-3 small, size progressively decreasing, and coxa 4-5 larger; uropod 1-2 peduncles without lateral spines; eyes absent
351 352	7(6) Antenna 1 longer than antenna 2; maxilla 1 inner plate with at least one apical setae and/or marginal setae, telson notched, emarginate or entire
353 354 355	7' Antenna 1 and 2 equal or subequal in length; maxilla 1 inner plate reduced with only 0 or 1 apical setae; telson entireIschyroceridae (one genus <i>Jassa</i>) [Sicily]
356 357	8(7) Telson lobes almost completely separated, rami of uropod 3 lanceolate
358 359	8' Telson lobes partially fused, even sometime very slightly; uropod 3 rami straight more or less long
360	

361	
362 363 364	9(8) Coxae 1-3 longer than wide or sub-rectangular; gnathopod 2 propodus elongated slightly stronger than gnathopod 1; labium inner lobe vestigial or absent; uropod 3 rami sub-equal
365	[Western Europe]
366 367 368 369	9' Coxae 1-3 small wider than long; gnathopod 2 propodus much stronger than gnathopod 1; labium inner lobe normally developed, except in the genus <i>Gammaropisa</i> ; uropod 3 rami unequal, exopodite much longer than endopoditeEriopisidae [Turkey, Tunisia]
370 371	10(8') Telson entire or slightly emarginate (notch < 30% of the lobe), eyes absent 11
372	10' Telson deeply notched almost entirely, eyes present or absent
373 374 375 376	11(10) Pleopods uniramous or inner ramus reduced or vestigial; uropod 3 rami subequal in length
377 378 379	11' Pleopods biramous, inner ramus well developed; uropod 3 exopodite much longer than endopodite Pseudoniphargidae [Western Europe and North Africa]
380 381 382	12(10') Inner lobe of maxilla 2 with oblique row of facial setae; eyes generally present of various sizes
383 384 385	12' Inner lobe of maxilla 2 without oblique row of facial setae ; Labium without a more or less developed inner lobes, eye absent
386 387 388 389	13(12) Maxilla 1 outer plate with apical spines comb-like with few lateral teeth (except <i>Longigammarus</i>); pereopod 7 longer than 5; uropod 3 endopodite shorter than exopodite; eyes present or absent
390 391	13' Maxilla 1 outer plate with apical spines comb-like with numerous lateral teeth (>10); pereopod 7 subequal in length than 5; uropod 3 sub-equally biramous; eyes absent
392 393	[Balkan and Eastern Europe]
394 395 396 397 398 399	14(13) Antenna 2 peduncle article 1 enlarged, bulbous; antenna 1 longer or sub-equal in length than antenna 2, antenna 1 slender, generally longer than a half of the body length, the diameter of the articles of the peduncle is not much different; uropod 1 with or without basofacial robust setae; urosomite 2 with multiple small robust setae across the somite
400	[Cosmopolitan]
401 402 403	14' Antenna 2 peduncle article 1 subequal than article 3; antennae 1-2 sub-equal in length and short (\leq an half of the body length), antenna 1 stout, shorter than a half of the body length, the diameter of the articles of the peduncle strongly decrease in length and in width from

404 405	article 1 to article 3; uropod 1 without basofacial robust setae; urosomite 2 without dorsal setae
406	[Western Europe (invasive), Eastern Europe and Minor Asia]
407	
408	Key to Bogidiellidae genera
409	1 Molar non-triturative; maxilla 1 palp with 2 articles
410	1' Molar triturative; maxilla 1 palp with 1 or 2 articles
411 412 413 414 415	2(1) Epistomal ridge with a sclerified subcircular area; pleopod rami very long with 9 articles (one species: <i>M. maroccana</i> Diviacco & Ruffo, 1985) [Morocco]
416 417 418	2' Epistomal ridge without slcerified area; pleopod rami with 3 articles
419	
420 421 422 423	3(1) Pleopods 2, ramus article 2 of males with a modified seta <i>Stygogidiella</i> (one species: S. cypria G. Karaman, 1989) [Cyprus]
424	3' Pleopods 2, ramus article 2 of males without modified seta
425	
426 427	4(3) Uropods not sexually dimorphous, uropods without transformed spines, pleopods endopodites small, vestigial or absent
428 429 430 431	4' Uropods sexually dimorphous, uropod 1 or 2 rami with transformed (rasp-like, spoon-like) spines; pleopods endopodites absent
432 433 434 435 436	 5(4) Maxilla 1 outer lobe with 6 distal spines, telson deeply cleft
437	
438	Key to species of Medigidiella
439	1 Lenticular organ \leq a half of the basis width or absent (not visible)
440 441 442	1' Lenticular organ very large, almost as large as the basis of pereopods 3-6, absent on pereopod 7
443	2(1) Lenticular organ absent (not visible)

444	2' Lenticular organ visible on pereopod 3-7
445 446 447	3(2) Pleopod inner rami absent; telson with apical spines only; basis of gnathopods 1 and 2 with only one posterior setae
448 449	3' Pleopod inner rami reduced but present; telson with apical and subapical spines; basis of gnathopods 1 and 2 with 2 posterior setae
450 451 452	4(3) Antenna 2 without groups of setae on peduncle articles; maxilliped outer lobe with 2 spines; gnathopod 1 propodus without short spines; uropod 1 peduncle with one spine 5
453 454 455	4' Antenna 2 with groups of setae on peduncle articles; maxilliped outer lobe with 3 spines; gnathopod 1 propodus with 2 or 3 short spines; uropod 1 peduncle without spine
456 457 458	5(4) Gnathopod 2 propodus with 2 short spines; pereopod 7 propodus with 4-6 anterolateral setae; uropod 3 rami with 7-11 lateral spines
459 460 461	5' Gnathopod 2 propodus with 3 short spines; pereopod 7 propodus with 7-9 anterolateral setae; uropod 3 rami with 3-6 lateral spines
462 463	6(5) Gnathopods 1-2 propodi short; uropods 1-2 rami with short distal spines
464 465	6' Gnathopods 1-2 propodi longer; uropods 1-2 rami with relatively long distal spines
466 467 468 469	7(2') Antenna 1 accessory flagellum ≤ two articles of the flagellum, peduncle articles with two spines; maxilliped outer lobe with bifid spines; gnathopod 1 propodus with 4-5 short spines
470 471 472	7' Antenna 1 accessory flagellum longer than the three articles of the flagellum, peduncle articles without spine; maxilliped outer lobe with simple spines; gnathopod 1 propodus with 7 short spines
473 474 475 476	8(7) Antenna 2 with aesthestascs; maxilla 2 without plumose setae; gnathopod 1 basis with only one long posterior seta; gnathopod 2 propodus with 4 short spines; telson with 4 plumose setae
477 478 479	8' Antenna 2 without aesthestascs; maxilla 2 without plumose setae; gnathopod 1 basis with 2 long posterior setae; gnathopod 2 propodus with 3 short spines; telson with at least 6 plumose setae
480	
481 482 483 484	9(8) Lenticular organ small, about 1/3 of the basis width; labium outer lobe with spines; pereopod 7 propodus with less than 9 anterolateral setae, dactylus equal or longer than a half of the propodus; uropod 2 rami with modified distal spines in males

485 486	9' Lenticular organ large, about 1/2 of the basis width; labium outer lobe with spines; pereopod 7 propodus with at least 9 anterolateral setae, dactylus shorter than a half of the propodus with unmodified distal arings in males.
487 488	
489	
490	Key to Corophiidae genera and species
491 492	1 Antenna 2 article 2 with gland very small
493 494 495 496	1' Antenna 2 article 2 with gland cone large, conspicuous
497 498	2(1) Antenna 2 peduncle article 5 with 1 distal teeth or without teeth
499 500	2' Antenna 2 peduncle article 5 with 2 distal teeth on the lower margin
501 502	3(2) Antenna 2 peduncle article 5 with 1 distal teeth (short or long)
503 504	3' Antenna 2 peduncle article 5 without distal teeth on the lower margin
505	
506 507	4(3) Antenna 2 peduncle article 5 with 1 long distal teeth; uropod 2 outer rami with 6 marginal spines
508 509	4' Antenna 2 peduncle article 5 with 1 short distal teeth; uropod 2 outer rami with 3 marginal spines <i>Ch. curvispinum</i> (Martynov, 1924)
510	
511	Key to Crangonyctidae genera and species
512 513	1 Urosomites coalesced; uropod 3 inner ramus absent
514 515	1' Urosomites free; uropod 3 inner ramus small or scale-like
516 517 518 519 520	 2(1) Body pigmented; pleopods with 2 coupling spines (retinacules); uropod 3 endopodite without terminal "squamous knob"
521 522 523 524 525	 2' Body not pigmented; pleopods with 5-6 coupling spines (retinacules); uropod 3 endopodite with a terminal "squamous knob" Pontonyx (one species: P. osellai (Ruffo, 1974)) [Turkey]

526	3(2) Epimera 2 with spines at distal margin but never setae
527	3' Epimera 2 with numerous setae at distal marginS. longidactylus S. Karaman, 1929
528 529 530	4(3) Females's oostegite broader; Eyes present or absent; pereopod dactyls in males longer and slenderer than in females
531 532	3' Female's oostegite narrow; Eyes absent; pereopod dactyls subequal in shape between males and females
533 534 535	5(4) Eyes present; gnathopod 2 propodus in females is short and broad than in males <i>S. ambulans ambulans</i> (F. Müller, 1846)
536 537	5' Eyes absent; gnathopod 2 propodus in males is strongly dilated
538	
539 540	6(1') Eyes present, epigean species; gnathopod 2 palm with notched spines; pereopod 6 propodus much shorter than basis <i>C. pseudogracilis</i> Bousfield, 1958
541 542	6' Eyes absent, hypogean species; gnathopod 2 palm with simple spines; pereopod 6 propodus longer than basis and carpus
543	
544	Key to Eriopisidae genera and species
545 546 547 548	1 Labium inner lobe absent; gnathopod 1 carpus slightly shorter than propodus; pleopod 3 greatly modified in males
549	1' Labium inner lobe present; gnathopod 1 carpus longer than propodus; pleopod 3 not modified
550 551 552	(one species: <i>T. seurati</i> (Gauthier, 1936)) [Tunisia]
553 554 555	* the position of <i>Gammaropisa</i> in Eriopisidae remains doubtful because it did not match to the revision of Lowry and Myers 2013, who defined Eriopisidae with an internal lobe in the labium but this lobe is not drawn by Ruffo 1987.
556	
557	Key to Gammaridae genera
558	1 Antenna 2 gland cone small, conical and straight 2
559 560 561 562 563	1' Antenna 2 gland cone extremely elongated and recurved going back toward coxae 1

564 565 566	2(1) Pleonites and pereonites without mediodorsal keels; pereopod 7 basal article with or without large posteriodistal lobe, urosome generally not carinate (except in some <i>Gammarus</i> and <i>Echinogammarus</i>)
567 568 569 570 571	 2' Pleonites and some pereonites with mediodorsal keels; pereopod 7 basal article with a large posteriodistal lobe, urosome carinate
572	3(2) Uropod 3 endopodite well developed, overreaching 25% of the exopodite
573	3' Uropod 3 endopodite very reduced, scale like, <25% of the exopodite
574 575 576 577 578	4 Maxilla 1 outer lobe with 17 curved spines; coxal gill 7 absent; eyes absent
579 580	4' Maxilla 1 outer lobe with straight simple or pectinate spines; coxal gill 7 present; eyes present or absent
581 582 583 584	5 Gnathopod 1 propodus in males larger than gnathopod 2; Gnathopod 2 carpus elongated [Spain, France]
585 586 587	5' Gnathopod 1 in male propodus smaller than gnathopod 2; uropod 3 endopodite ≥ 25% exopodite
588 589	6 Uropod 1 reduced, not reaching apices of uropod 2, rami without lateral spines
590	6' Uropod 1 longer than uropod 2
591 592 593 594	7 Maxilla 1 outer lobe with many densely pectinate setae (like Typhlogammaridae), inner lobe wider than long
595 596 597	7'. Maxilla 1 outer lobe with less densely pectinate setae (like Gammaridae), inner lobe longer than wide, pereopod 7 base elongated more than twice as long as wide <i>Rhipidogammarus</i> [Peri-Mediterranean]
598 599 600	8(6') Uropod 1 longer than uropod 2 and reaching its apex, uropod 1 rami with several distal spines
601 602 603	8' Uropod 1 longer than uropod 2 but not reaching its apex, uropod 1 rami with only one strong distal spine
604 605	9(8) Urosomites 1 et 2 without dorsal elevations 10

606 607	9' Urosomites 1 et 2 with dorsal humps or cones with some apical spines Dikerogammarus [Turkey, invasive in Western Europe]
608 609 610	10(9) Pereopod 7 ventroposterior lobe absent or small; uropod 1 outer ramus subequal to the inner ramus
611 612 613	10' Pereopod 7 ventroposterior lobe well developed, uropod 1 outer ramus reaching at least 60% of inner ramus
614	11(10) Setae on at least either on percopods 5 to 7, urosomite and/or epimera 12
615 616 617	11' Setae almost completely lacking on percopods 5 to 7, urosomites and epimeron<i>Chaetogammarus</i> (one species: <i>C. saisensis</i> Fadil et al, 2009)[Morocco]
618 619 620 621	12(11) Gnathopod 1 propodus in males much larger than gnathopod 2, eyes elongate 2x longer than wide
622 623 624	12' Gnathopod 1 propodus in males equal of slightly longer than gnathopod 2, eyes ovoid or 1.5x longer than wide <i>Echinogammarus / Homoeogammarus</i> [Peri-Mediterranean]
625	
626 627 628 629 630	 13(10') Pereopod 7 ventroposterior lobe broad and rounded; uropod 1 outer ramus reaching 60% of inner ramus; uropod 3 with very long setae and marginal spines; telson with marginal spines
631 632 633 634 635	 13' Pereopod 7 ventroposterior lobe rounded-triangular; uropod 1 outer and inner rami subequal in length; uropod 3 with very few setae; telson without marginal spines
636	
637	Key to species of <i>Dikerogammarus</i>
638	1 Antenna 1 peduncle segments long and slender 2
639	1' Antenna 1 peduncle segments short and swollen D. gruberi (Mateus & Mateus, 1990)
640 641	2(1) Pereopod 7 basal segment with setae in the inner surface
642	2' Pereopod 7 basal segment without setae in the inner surface
643 644 645 646	3(2) Antenna 1 peduncle segment 2 and antenna 2 segment 4-5 with few short setae (shorter than the diameter of the segment) on the inferior margin

647 648 649	3' Antenna 1 peduncle segment 2 and antenna 2 segment 4-5 with many long setae (longer than the diameter of the segment) on the inferior margin <i>D. bispinosus</i> Martynov, 1925
650 651 652	4(2') Antenna 2 flagellum with long setae forming a brush, urosomites 1 et 2 with dorsal humps well developed and armed with 3-6 upright apical spines and forming like a crater
653 654 655 656	4' Antenna 2 flagellum with short setae never forming a brush, urosomites 1 et 2 with small dorsal humps armed with 1-3 apical spines slightly oriented towards the telson
657	Key to species of <i>Iberogammarus</i>
658 659	1 Antenna 2 of male with many groups of long and densely implanted curled setae. Third segment of mandible palp with less than 6 terminal setae
660 661	1' Antenna 2 of male with straight setae. Third article of mandible palp with more than 6 terminal setae
662 663 664	2(1) Gnathopod 1 propodus of males without the medial palmar spine. Basis of P7 with strong backward projecting ventro-posterior corner <i>I. macrocarpus</i> (Stock, 1969)
665 666 667	2' Gnathopod 1 propodus of males with a strong medial palmar spine. Basis of P7 with rounded, non-projecting, ventro-posterior corner <i>I. toletanus</i> (Pinkster & Stock, 1970)
668	Key to species of Longigammarus
669	
670 671 672 673 674	 Eyes present; maxilla 1 outer plate with 11 apical spines, slightly recurved
675	Key to species of Rhipidogammarus
676	1 Antenna 1 peduncle article 2 with at least 4 groups of setae
677	1' Antenna 1 peduncle article 2 with 2-3 groups of setae
678	
679 680	2(1) Coxae 1-5 with long ventral setae, anterior margin of carpus of P7 with setae longer than spines
681 682 683	2' Coxae 1-5 with short ventral setae only, anterior margin of carpus of P7 without long setae
684 685	3(1') Antenna 1 flagellum with more than 35 articles; uropod 3 exopodite shorter (no more than 7x longer than endopodite) without sets or few long setae

686 687 688	3' Antenna 1 flagellum with more than 30 articles; uropod 3 exopodite long (10x longer than endopodite) with many long setae (2x longer than spines)
689 690	4(3) Mandibular palp article 2 with long setae reaching the setae type D on the article 3; uropod 3 exopodite without seta
691 692	4' Mandibular palp article 2 with setae never reaching the setae type D on the article 3; uropod 3 exopodite with few setae 2x longer than spines
693	
694	Key to species of Tyrrhenogammarus
695 696	1 Pereopod 3 carpus with a fan of long setae; uropod 1 with sub-equal rami; epimera 3 with a slightly marked ventroposterior corner <i>Th. catacumbae</i> (G. Karaman & Ruffo, 1977)
697 698	1' Pereopod 3 carpus without long setae; uropod 1 inner ramus longer than outer ramus; epimera 3 without distinct ventroposterior corner
699	
700	Key to Hadziidae genera and species
701 702	1 Uropods 1 and 2 with row of 5 plumose setae, exopodite with dorsal setae; telson with only apical spines
703 704 705 706	1' Uropods 1 and 2 with row of 5 plumose setae, exopodite with dorsal setae; telson with marginal spines
707	
708	2 Mandibular palp article 2 as long as article 1
709 710	2' Mandibular palp article 2 longer than article 1
711 712	3(2) Gnathopod 2 propod in females with entire convex palm; gnathopod 2 propod in males as wide as carpus; uropod 3 rami broad
713 714 715	3' Gnathopod 2 carpus in females with excavated, propodus palm concave; gnathopod 2 propodus in males wider than carpus; uropod 3 rami narrow
716	4(3) Pleopods 1-3 each with 2 retinacula accompanied by one strong seta
717 718	4' Pleopods 1-3 each with 2 retinacula without strong seta
719 720 721 722	5 Pereopods 3-7 and antennae long and slender, including dactyl of pereopods 3-7; telson lobes with 2, occasionally 3 distal spines and without outer marginal spines
722	5' Perconode 3-7 and antennae shorter and stouter: telson lobes with 3-4 distal spinos and 0-1
723 724 725	outer marginal spines

726 727	6(3') Pleopod 3 peduncle with 1-2 median spine on posterior margin
728 729 720	6' Pleopod 3 peduncle without median spine on posterior margin
731	7(2') Uropod 2 peduncle distal end with a protuberance
732 733	7' Uropod 2 peduncle without protuberance
734 735	8(7) Uropod 2 endopodite of males with transformed apical spine, peduncle with dorsomedial comb-like spines
736 737 738	8'. Uropod 2 endopodite of males without transformed apical spine, peduncle without dorsomedial comb-like spine
739	9(7') Lobe of telson with spines along both margins 10
740	9' Lobe of telson without spine along outer margin M. minuta Ruffo, 1947
741 742 743	10(9) Maxilla 1 inner lobe long reaching the basis of spines of outer lobe, distally prominent <i>M. adriatica</i> Pesce, 1979
744 745 746	10' Maxilla 1 inner lobe short never reaching the basis of spines of outer lobe
747	Key to Metacrangonyctidae genera and species
748 749 750	1 Gnathopod 2 propodus not modified, palm slightly convex; gnathopod 1 merus without brush; coxae 1-3 sub-equal and longer than coxae 4-5
751 752 753 754 755	1' Gnathopod 2 propodus modified in males, palm strongly concave; gnathopod 1 merus with many short setae forming a brush; coxae 1-5 decreasing progressively in length
756 757	2(1) Uropod 3 exopodite longer than peduncle, marginal spines present
758	2' Uropod 3 exopodite equal or shorter than peduncle, marginal spines absent
759 760 761	3(2) Uropod 1 peduncle basofacial robust setae present
762	3' Uropod 1 peduncle basofacial robust setae absent M. longicaudatus Ruffo, 1954
763 764	4(2') Uropod 3 exopodite with several terminal robust setae
765	4' Uropod 3 exopodite without one terminal robust seta

766	
767	5(4) Antenna 1 accessory flagellum with 2-3 articles
768 769	5' Antenna 1 accessory flagellum with 5 articles <i>M. longipes</i> Chevreux, 1909
770	6(5) Telson with distal spines M. remyi Balazuc & Ruffo, 1953
771 772	6' Telson without apical spines
773	7(4') Uropod 1 peduncle basofacial robust setae present
774	7' Uropod 1 peduncle basofacial robust setae absent <i>M. ortali</i> G. Karaman 1989
775 776	8(7) Mandibular palp with 2 or 3 articles
777 778	8' Mandibular palp with only one article 10
779	9(8) Antenna 1 flagellum with only 10 articles in females (male unknown)
780 781 782	9' Antenna 1 flagellum with 14 articles in females
783	10(8') Antenna 1 flagellum with 11-14 articles 11
784	10' Antenna 1 flagellum with more than 15 articles
785 786 787 788 789	11(10) Uropode 3 endopodite present but reduce, scale-like 12 11' Uropode 3 uniramous, endopodite absent G. ruffoi Messouli, Boutin & Coineau, 1991
790 791	12(11) Antenna 1 article 1 with 2 fines facial spines; uropod 3 peduncle with 1 or 2 spines and one seta on ventral margin <i>M. aroudanensis</i> Messouli, Boutin & Coineau, 1991
792 793 794	12' Antenna 1 article 1 with 3 or 4 facial spines; uropod 3 peduncle with 2 spines and without seta on ventral margin
795 796	13(10') Uropod 1 endopodite without baso-facial seta, telson with 2 apical setae clearly separated to each other, peduncle with one terminal seta
797 798 799	13' Uropod 1 endopodite with a slender baso-facial seta, telson with 2 apical setae very close to each other
800 801 802	14(13) Habitus stocky; antenna 2 peduncle article 1 with 2 sub-terminal spines; uropod 3 peduncle with 1-3 dorso-apical spines ; telson apex flat of slightly emarginate
803 804 805	14' Habitus slender; antenna 2 peduncle article 1 with 2 sub-terminal spines; uropod 3 peduncle with 1 dorso-apical spine; telson apex rounded

807	Key to Niphargidae genera
808 809	1 Urosomite not enlarged, not carminate; uropod 3 biramous, outer ramus with one or 2 articles
810 811 812 813 814	1' Urosomite enlarged, dorsally carinate, hiding urosomites 2 and 3; uropod 3 very short, outer ramus with 1 article, inner ramus absent <i>Carinurella</i> (one species: <i>C. paradoxa</i> Sket, 1964) [Italia, Slovenia]
815	2(1) Uropod 3 exopodite of one article
816 817	2' Uropod 3 exopodite of two articles
818 819	3(2) Uropod 3 exopodite very short, twice as long as its terminal spines; maxilla 1 palp with one article
820 821 822	3' Uropod 3 exopodite long, several times longer than peduncle; maxilla 1 palp with 2 articles
823 824	4(3) Mandibular palp with 3 noticeable articles
825 826 827	4' Mandibular palp very short, reduced to only one small article <i>Chaetoniphargus</i> (one species: <i>C. lubuskensis</i> Karaman G.S. & Sket, 2019) [Croatia]
828	
829 830 831 832	5(4) Antenna 1 accessory flagellum with one article; mandibular palp article 3 with only terminal E-setae; telson slightly cleft
833 834 835 836	5' Antenna 1 accessory flagellum with two articles; mandibular palp article 3 with A, B, C, D and E-setae; telson deeply cleft
837 838	6(2') Maxilliped palp article 4 with one, rarely 2 distal nails
839 840 841	6' Maxilliped palp article 4 with 3 distal nails <i>Exniphargus</i> (one species: <i>E. tzanisi</i> G. Karaman, 2016) [Crete Island]
842 843 844 845 846 847	 7. Maxilliped inner and outer plate short and broad; maxilla 2 both plates are short and broad; maxilla 1 inner plate very strong, broader than palpus, outer plate with 9-10 pectinate spines, palp short, not exceeding basis of outer plate spines

7' Maxilliped inner and outer plate slender; maxilla 2 both plates are slender; maxilla 1 inner

- [peri-mediterranean except North Africa]

Key to Pontogammaridae

854 855 856 857	Urosomites 1 et 2 with dorsal humps armed with apical spines (as in <i>Dikerogammarus</i> , b differing from it by strongly setose margins of coxae 1-4 and percopods 5-7 bas 	out is) ıs)
858 859 860 861 862 863 864 865 866	'Urosomites 1 et 2 without dorsal elevations	ıs)
	(1) Presence of a keel on the dorsum; telson lobes with setae longer than spines; antenna peduncle with short setae, antenna 2 and pereopod 5-7 much less setose <i>T. spandli</i> (Karaman 1931)	1 (S.
	'No keel on the dorsum; telson lobes with setae shorter than spines; antenna 2 peduncle with some long setae; antenna 2 and pereopod 5-7 very setose	i th '4)
867 868	(1') Mandibular palp article 3 with 3 rows of setae type B and articles 2-3 with less and short setae; urosomite 2 with spines	ter . 4
869 870 871 872	^a Mandibular palp article 3 with 5 rows of setae type B and articles 2-3 with very long a numerous setae, much longer than the width of articles; Urosomite 2 without spin	nd les 14)
873 874	(3) Uromosite 1 armed without setae only; coxae 1-4 and pereopods 3-5 bases with dense a numerous long setae	nd :4)
875 876 877	^o Urosomite 1 armed with spines and setae; coxae 1-4 and pereopods 3-5 bases with short and less numerous setae <i>P. robustoïdes</i> (Sars, 189	ter 4)
878	ey to Pseudoniphargidae genera	
879 880 881	Body compressed and strongly curved; head anterior lobe strongly developed; coxa ventrally wide; uropod 3 short, exopodite slightly (1.5 times) longer than pedune <i>Parapseudonipharg</i>	1 cle sus
882 883	(one species: <i>P. baetis</i> Notenboom, 1988) [Spain]	
884 885 886 887	'Body outspread; head anterior lobe weakly developed; coxa 1 sub-rectangular; uropod long, exopodite much longer than peduncle, at least 3 times	. 3

- Key to Salentinellidae genera and species

890 891	1 Uropod 1 longer than uropod 2; epimeral plates 2-3 as long as wide; telson cleft, elongated
892	[Western Mediterranean Basin]
893 894 895 896 897	1' Uropod 1 shorter than uropod 2; epimeral plates 2-3 elongated forming plates; telson uncleft with concave margins
898	2(1) Posterodistal lobe of percopod 7 merus almost reaching end of carpus
899	2' Posterodistal lobe of pereopod 7 merus not reaching beyond half the length of carpus 4
900 901	3(2) Telson partially cleft
902	3' Telson uncleft
903 904 905 906 907	 4(3') Antennae 1 and 2 peduncles without distal spines; pleopod peduncles with coupling spines; telson longer than wide
908 909	5(4) Urosomite 3 lengthened, about 1.5 times as long as high
910	5' Urosomite 3 not lengthened, about as long as high7
911 912	6(5) Telson with dorsal setae implanted near apex of lobes S. petiti Coine!au, 1968
913	6' Telson with dorsal setae not implanted near apex of lobe S. longicaudata Platvoet, 1987
914	
915	7(5') Telson deeply cleft over more than a half of lobes
916	7' Telson not cleft over 1/3 of lobes
917 918	8(7) Uropod 3 endopodite more than 15% of the exopodite9
919	8' Uropod 3 endopodite less than 15% of the exopodite S. meijersae Platvoet, 1987
920 921	9(8) Uropod 1 peduncle without ventrodistal projection10
922	9' Uropod 1 peduncle with a strong ventrodistal projection S. cazemierae Platvoet, 1987
923 924 925 926	10(9) Antenna 1 and 2 sub-equal in length, accessory flagellum shorter than the first peduncle article; Uropod 3 endopodite longer than a half of the exopodite, exopodite article 2 less developed
927 928 929	10' Antenna 1 shorter than antenna 2, accessory flagellum longer than the first peduncle article; Uropod 3 endopodite shorter than a half of the exopodite, exopodite article 2 well developed

930 931	11(10) Uropod 3 short, endopodite egal or less than 2/3 of exopodite; gnathopod 2 propodus
932	palm strongly convex asymmetrically (largest part at 1/3 of the palm) 12
933 934	11' Uropod 3 slender, endopodite around 3/4 of exopodite; gnathopod 2 propodus palm convex symmetrically (largest part in the middle of the palm)
935 936 937	12(11) Pereopod 4 dactylus shorter than a half of the propodus
938	12' pereopod 4 dactylus equal to a half of the propodus S. gineti Balazuc, 1957
939	
940	Key to Typhlogammaridae genera and species
941 942	1 Body not carinate; maxilla 1 palp symmetric; uropod 3 exopodite article 2 vestigial or absent 2
943 944 945 946 947	 1' Body dorsally carinate, third mesosome segment and all metasome segments with one pair of dorso-lateral teeth each; maxilla 1 palp asymmetric (right maxilla different from the left one); uropod 3 exopodite article 2 ordinary
948 949 950 951 952 953	2(1) Antenna 2 gland cone shorter than article 3 of the peduncle; coxae 1-7 short diamond shaped or trapezoïdal; uropod 3 longer, much exceeding the top of uropods 1-2
954 955 956 957 958	 2' Antenna 2 gland cone very long overreaching article 3 of the peduncle; coxae 1-7 elongated sub-rectangular; uropod 3 short, not exceeding the top of uropods 1-2 Accubogammarus (one species: A. algor (G. Karaman, 1973), subspecies not include in the key) [Balkans]
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990 **3. Malacostraca: Bathynellacea**

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1000 INTRODUCTION

1001 Bathynellacea Chappuis, 1915 are obligate groundwater inhabitants (stygobionts) (limnic and oligo- to

1002 polyhaline waters) of all continents except Antarctica. Their interstitial life style would correlate with a

- decrease of the body size as well as with the reduction or loss of appendages and other organs (Coineau
 & Camacho 2013), these features may be interpreted as evidence of an evolutionary process involving
- 1005 progenesis (Schminke 1981a: Schram 1982).
- The origin of Bathynellacea could be pre-Pangean. They might have been highly diversified in the Paleozoic seas, especially during the Carboniferous period. Some of these ancestors may have colonized the continental subterranean freshwaters of the Pangea as early as in the Permian and Triassic periods, and also part of the Gondwana (Camacho *et al.*, 2018c) before the Pangea break up. Thereafter, the
- fragmentation of Laurasia and Gondwana during the Mesozoic period (Golonka 2007) led to the current
- 1011 disjunct distribution of syncarids (Schram, 1977), and induced their independent evolution on each
- 1012 landmass. All the genera belonging to Parabathynellidae Noodt, 1965 from peninsular India show a
- 1013 Gondwanan heritage (Ranga Reddy 2011, Bandari et al., 2016). The most recent common ancestor of
- bathynellaceans can be dated back to the Triassic or Jurassic periods, as showed by our analysis(Camacho *et al.*, 2021).
- 1016 Their current distribution is important, because they are restricted to freshwaters from remote geological 1017 times. They are one of the oldest groups of freshwater fauna and have no marine relatives for future 1018 colonizations, so they serve as indicators of ancient connections between the continents. They are 1019 considered a very suitable group for zoogeography studies, as they are old enough phylogenetically 1020 speaking, their capacity for dispersal is severely limited, and even today they are represented by a high 1021 number of species distributed worldwide. They can provide information on possible dispersal routes in 1022 past and present geological periods.
- 1022 past and present geo

1024 GENERAL ECOLOGY AND DISTRIBUTION

- Bathynellacea exclusively live in groundwater sensu lato (caves, springs, wells and hyporrheic zones of 1025 1026 rivers): they are interstitial stygobionts (they inhabit in the water filling the interstices between sand grains and gravels in sediments). Little is know about their life cycles. They live long, e.g. 1027 1028 Paraiberobathynella fagei (Delamare Deboutteville & Angelier, 1950) can live up to two and a half years. Fertilization is internal, but copulation has not been observed; they are K-strategists, i.e. the 1029 1030 female produces a single large egg that occupies almost its entire abdomen for almost nine months (in 1031 the few cases observed to date), deposits it on the substrate and a larva identical to the adult is immediately born but with only 3 or 4 pairs of legs, depending on the species. Metamorphosis takes 1032 1033 place inside the egg. Due to the absence of a swimming larva, their ability to disperse is very low. The post-embryonic development or parazoeal phase (Schminke, 1981a) (= larval phase 1, Serban, 1985), 1034 1035 which occurs after birth, consists of 8 to 11 stages marked by molts, depending on the species.
- 1036 They do not generally swim, except some species (e.g. Cho & Humphreys 2010 observed 1037 *Brevisomabathynella uramurdaliensis* swimming quite powerfully in an aquarium). They walk with

their thoracopods. Some species show a swimming escape reaction. They touch the sand grains with their antennules, explore the interstices, resulting in discontinuous movements interrupted by frequent stops. Then they flex their pleon and leaning on their uropod and furca, they suddenly launch themselves forward, or change direction and move backwards. Thanks to their body flexibility, they can clean their antennae with the spines of their uropods and furca (personal observation). Their thigmotaxis will generally keep them in contact with the sandy sediment so that they can know their position (they are devoid of statocysts).

They graze and scrape deposits from sediment grains and also eat protists, fungi and bacterial films.
According to Serban (1980), Bathynellidae Grobben, 1905 comprise "filter and large food feeders",
whereas Parabathynellidae would be "large food feeders". Some parabathynellids are carnivorous, eat
harpacticoid copepods (*Iberobathynella* Schminke, 1973) or ostracods (*Brevisomabathynella*).
Cannibalism has been observed by Morimoto (1970), who reported large specimens of *Allobathynella*Morimoto & Miura, 1957 preying on young ones (Schminke & Cho 2013).

1051 Bathynellacea are preyed upon by amphipods and subterranean fish.

1052 They live in freshwater, although some species have been found in brackish groundwater, near the sea1053 coastline. They can be considered cold stenotherms, they do not usually survive above 20°C. However,

the genus *Thermobathynella* Capart, 1951 has been found in a hot spring (water at 55°C) and we found
 Paraiberobathynella cf *fagei* in the Sima de la Higuera (Murcia, Spain) living at 27°C.

1056 Bathynellacea have been found from Alaska (Camacho et al., 2016b) to New Zealand (Schminke 1973) and their distribution is worldwide with high degrees of local endemic species (Camacho 2019) and 1057 cryptic species (Camacho et al., 2011, 2012, 2018c). The order Bathynellacea is composed of three 1058 1059 families (338 species and 89 genera) (Camacho et al., 2021): Parabathynellidae, Bathynellidae and Leptobathynellidae Noodt, 1965. Parabathynellidae (210 species, 45 genera) are currently known in 1060 temperate to tropical zones in both hemispheres; Bathynellidae (110 species, 37 genera) are known 1061 1062 mainly in temperate zones of the northern hemisphere and some areas of the southern hemisphere (they are very frequent in Australia); while Leptobathynellidae (18 species,7 genera) are only known in South 1063

1064 America (Brazil, Argentina, Paraguay and Chile), Africa (Ivory Coast and South Africa), California and

India. Parabathynellidae are most frequently found in samples than members of the other two families
are, perhaps due to their larger size and consistency. Furthermore, their study is easier not only because
of their size, but also because their morphological variability is greater and therefore it is easier to

discriminate between genera and species. All Leptobathynellidae species are very thin and fragile, their
 dissection is very difficult and their identification almost impossible; to date they are not known in the
 Mediterranean area, but perhaps they have gone unnoticed in the samples, or have escaped from the

sampling nets or perhaps they live in areas without sampling coverage, but maybe they will be found

1072 one day. The same happened in India: as soon as the sampling effort intensified, three *Parvulobathynella* 1073 Schminke, 1973 species were found. The Bathynellidae family is characterized by its great homogeneity,

1074 so that it is very difficult to find characters that differentiate morphotypes. Large collections of 1075 specimens from this family collected all over the world have not yet been studied, because they are too 1076 difficult to identify. Morphological studies need to be supplemented with molecular data for researchers 1077 to discriminate species.

Following the emergence of molecular studies, cryptic species are being discovered in the group, both
in Europe and Australia, and show that diversity is even greater than suspected. To this we must add a
significant unexplored and unsampled "underground aquatic world" (in caves and unconsolidated

sediments), which will give many surprises.

1082 In the Mediterranean area in question, 71 species belonging to 20 genera are formally described: 36 1083 Parabathynellidae species (7 genera) and 35 Bathynellidae species (13 genera). The Iberian Peninsula is 1084 the area exhibiting the highest diversity: 41 species altogether, 30 Parabathynellidae species (5 genera) 1085 and 11 Bathynellidae species (5 genera). The *Iberobathynella* genus, with 22 species belonging to 3 sub-1086 genera from the Iberian Peninsula, is one of the most diverse in the world, behind *Allobathynella* with 1087 25 species, and the cosmopolitan *Hexabathynella* Schminke, 1972 with 23 species distributed 1088 throughout the world (5 species in the area and four of them in the Iberian Peninsula) (Camacho, 2019). The greatest Bathynellidae diversity is found in France; thanks to the work of Serban, Coineau &
Delamare Deboutteville (1971, 1972), 17 species (8 genera) are well known; however, only 3 species of
the family Parabathynellidae live in France (several populations of *Parabathynella stygia* Chappuis,
1926 (= phreatica), *Paraiberobathynella fagei* and *Hexabathynella knoepfflery* (Coineau, 1964) from
Corsica). The other findings are sporadic: one species in Israel, one in Morocco, and one in southern
Tunisia.
All known species are short-range endemisms, as recent molecular studies revealed. Some species
considered to be widely distributed in Spain such as *Iberobathynella imuniensis* Camacho, 1987

1096 considered to be widely distributed in Spain, such as *Iberobathynella imuniensis* Camacho, 1987
1097 (inhabitant of the Cantabrian coast, from the Pyrenees to Galicia) and *Paraiberobathynella fagei*1098 (described in France, in the Roussillon regin, and believed to live throughout eastern Spain, in Andalusia
1099 and Mallorca), only live in the type locality and areas nearby, while the rest of the populations is surely
1000 composed of different cryptic species, morphologically indistinguishable from the type species.

A small territory like the Iberian Peninsula is the most diverse area on Earth in terms of bathynellids. The Ojo Guareña Natural Monument (Burgos) (a karst complex with more than 110 km of development), where eight species of Bathynellacea have been found (4 are still undescribed: a new genus, two cryptic species of *Vejdovskybathynella edelweiss* and a cryptic species of *I. imuniensis*), is the most diverse place in the world and the biodiversity hotspot of the group (Camacho *et al.*, 2010).

1106

1107 TERMINOLOGY AND MORPHOLOGY

Microscopic Malacostraca are 0.5-3.0 mm in length, sometimes up to 6.3 mm, e.g. *Billibathynella humphreysi* Cho, 2005. Eumalacostraca do not have a carapace and have biramous thoracopods. Their
body is elongate and more or less straight (Fig. 7.5), worm-like and depigmented, female do not have a

- 1111 brood pouch. Eyes and statocysts are absent.
- 1112 Their body is divided into the: head, eight free thoracic segments with eight pairs of biramous
- thoracopods (thoracopod VIII is modified as a copulatory organ in the male and reduced in the female),
- five free abdominal segments without pleopods or with one or two uniramous pleopods and a pleotelsonwith biramous uropods and furcal rami with spines (Fig. 7.5).
- 1116 Head longer than wide, with a fine cephalic capsule (Fig. 7.5). Anterior part with a couple of antennules 1117 (A.I) (article with sexual dimorphism in some genera) and a pair of antennae (A.II) with a variable
- 1118 number of articles. The five mouth pieces are located ventrally: labrum (single piece), a pair of
- 1119 paragnathes (present in all Bathynellidae species and a few species of genera belonging to
- 1120 Parabathynellidae and Leptobathynellidae) (Camacho *et al.*, 2021), mandibles (Md), maxillules (Mx.I)
- 1121 and maxillae (Mx.II). (Fig. 7.5).
- 1122 The oral opening is located at the posterior end of the rostral third.
- 1123 Thorax (Fig. 7.5), with eight well-defined segments (ancestral structure); circular cross section of
- segments; diameter and length increasing towards the distal end. Eight pairs of thoracopods: the first
- seven ones are used for locomotion and the eighth one is transformed into a copulatory organ (penis) in
- males, and is greatly reduced (or even absent) in females. Limit between thorax and abdomen not very clear. Thoracopod I (Fig. 7.5) is the smallest, thoracopods II to IV or V increasing in length and the last
- 1128 ones of the same length. Biramous thoracopods (ThI, ThII... ThVII), with exopod (1-12 articles in
- 1129 Parabathynellidae, two in Leptobathynellidae, and one in Bathynellidae) and endopod (four articles in
- 1130 Parabathynellidae and Leptobathynellidae, and three or four articles in Bathynellidae) which can exhibit
- 1131 sexual dimorphism on the third article of Th VI (Pacificabathynella Schminke & Noodt, 1988 and
- 1132 Paradoxibathynella Serban, 2000) and on coxa of ThVII (Altainella Camacho, 2020); respiratory epipod
- 1133 (absent on ThI and sometimes on ThII and/or III), connected with coxa and basipod. Usually ctenidiae
- 1134 present at the base of the setae on the exopod and along one of the articles on the endopod.
- 1135 ThVII absent in *Hexabathynella* and *Hexaiberobathynella*.
- 1136 Female ThVIII (Fig. 7.5) smaller than other legs. Very reduced in *Hexabathynella* and *Iberobathynella*
- (Fig. 7.5B), remains of articles indistinguishable. It is still possible to identify the articles in some
 Bathynellidae (Fig. 7.5A) genera, although they are always very reduced.

- 1139 Male ThVIII: massive, more or less rounded or curved; strongly modified but distinguishable articles
- (like lobes) of a typical leg. The terms used to designate each part are equivalent in the three families:
- a) protopod, penial complex and basipod; basal region, outer lobe, inner lobe and dentate lobe constitute
- the penial complex (these last 3 lobes are well distinguishable in Parabathynellidae (Fig. 7.5B)); genital
- opening located between the lobes; some setae usually on basipod; b) endopod, only one article and
- setae; c) exopod, only one article with some setae on ventral edge. Some structures such as basipod and
- 1145 penial complex are complicated in the Bathynellidae family (Fig. 7.5A).
- 1146 Five segments on abdomen and pleotelson with furcal rami and uropods (Fig. 7.5 Habitus). Sometimes
- 1147 vestigial pleopods on first and second segments. Setae smooth, barbed or plumose basidorsally or 1148 basiventrally present on pleotelson. Uropod lateral: sympod (with spines), exopod and endopod, with
- 1149 specific setation. Furcal rami (with spines) located on pleotelson lobes.
- 1150 Anus located in the terminal part of the pleotelson and covered by an operculum (anal operculum) in 1151 some Parabathynellidae species.
- 1152

1153 COLLECTION, PREPARATION AND IDENTIFICATION

1154 The specific methods for collecting samples depend on the specific habitat where the fauna is found in 1155 groundwater *sensu lato*. However, almost all of them are based on substrate removal and on filtration of 1156 the cloudy water with hand nets of *ad hoc* designs and a mesh size < 0.1mm.

1157 The aquatic environments sampled within caves are gours, puddles, pools, drips, lakes and underground

- 1158 rivers. Outside, springs, wells, boreholes, permanent cores (for example in mining surveys) that intersect 1159 aquifers and a hyporheic substratum (in lakes and rivers) are sampled. Bathynelids have recently been
- 1160 found in samples from the Mesovoid Shallow Substratum (MSS) of the Sierra de Guadarrama (Madrid,
- 1161 Spain) arranged for the collection of terrestrial fauna (Camacho & Ortuño, 2019). Therefore, sampling
- 1162 methods and devices are numerous and varied. A comprehensive compilation can be viewed at:
- **1163** Sampling Manual for the Assessment of Regional Groundwater Biodiversity, PASCALIS 2002 (Ed. by
- 1164 F. Malard, Asociate editors: Dole-Olivier, M.-J., J. Mathieu & F. Stoch).
- Field samples can be kept alive in a refrigerator or frozen in absolute or 70% ethanol (this is a 1165 conservative liquid, but not a fixative one, so that the specimens deteriorate over time). In the case of 1166 1167 living samples, it is convenient to wash and separate them as soon as possible. In this way, each type of fauna can be fixed in the most suitable fixative and according to the subsequent study you want to carry 1168 1169 out. For morphological studies it is appropriate to use 4% formalin for 48 hours, while keeping the specimens in a refrigerator at 4°C. After washing, they can be prepared for dissection right away and 1170 assembled in permanent preparations (Perina & Camacho, 2016), or the entire specimens can be 1171 preserved in 70% ethanol for subsequent studies. Bathynels have thin and fragile cuticles. If the 1172 specimens are to be preserved for long-term morphological studies, they must be fixed properly before 1173 being stored in the preservative liquid. When absolute or 70% ethanol is used for field samples, the 1174 specimens should also be washed and processed as soon as possible and thus be suitable for immediate 1175 1176 molecular studies and short-term morphological studies as well. This way, the same specimen can and should be used for both studies: the abdomen for DNA extraction and the other parts for dissection and 1177 1178 mounting in permanent preparations (after dipping in 4% formalin for 48 hours), with the same routine as in the previous case (Perina & Camacho, 2016). This procedure ensures that the sequenced genes 1179 correspond to a given morphotype. Samples frequently contain a mixture of species indistinguishable 1180 under the binocular microscope. If some specimens are used entirely for morphological studies and 1181
- 1182 others are entirely destroyed by DNA extraction, it will be impossible to associate each gene sequence
- to a specific morphotype.
- **1184** Taxonomic identification and the description of new species require a complete morphological study of
- specimens, males and females if possible. Anatomical observations can be performed using an oil
- 1186 immersion lens ($100 \times$ magnification) with an interference microscope equipped with a drawing tube.
- 1187 Photographs are not a substitute for drawings in taxonomic works but can complement them.

1188 Well-prepared permanent preparations ensure good preservation of the specimens in scientific 1189 collections. They guarantee their survival and availability, at least on the medium term just as well-1190 preserved DNA extracts and DNA collections of public institutions ensure access to them for future 1191 scientific studies.

1192

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- 1196

KEYS TO BATHYNELLACEA 1198 1199 1200 Key to Bathynellacea families 1201 1 Lengthened powerfully cephalic capsule; AI with 6 or 7 articles; 6 to 8 articles in AII, directed forward 1202 or perpendicular, with very well developed exopod (Fig. 7.5A); labrum with smooth distal free edge 1203 (Fig. 7.6D); paragnathes present; Md, length/width= 3 (very long) (Fig. 7.6G), prehensile palp with 1 to 3 articles (Fig. 7.6H) in antero-ventral position, reduced pars incisiva (in antero medial part) and 1204 typical lobe (plate like) of *pars molaris* absent; MxII not prehensile (Fig. 7.6K); exopod of thoracopods 1205 with 1 article (Fig. 7.7A,B); male ThVIII remembers "a leg" (Fig. 7.6D); pleopods of 2 articles; 3 or 1206 more oblique spine rows on sympod of uropod (Fig. 7.7F,H); dorsal seta on pleotelson 1207 1208 1209 2 Weakly elongated cephalic capsule; AI with 6 to 10 articles; 1 to 6 articles in AII, directed backwards, without exopod (Fig. 7.6B); labrum with dentate distal free edge (Fig. 10.2.E); paragnathes absent or 1210 rarely present; Md, length/width= 0.8 (high), with palp not prehensile of 1 article (Fig. 7.6I) in antero-1211 1212 dorsal position, large pars incisiva (occupying entire distal part) and typical lobe (plate like) of pars molaris present; MxII not prehensile (Fig. 7.6L); exopod of thoracopods multiarticled (Fig. 7.7C); 1213 male ThVIII different of "a leg" (Fig. 7.7E); when present (rarely) pleopod reduced; 5 to 30 inner spine 1214 1215 row on sympod of uropod (Fig. 7.7G); ventral or dorso-lateral seta on pleotelson 1216 3 Elongated cephalic capsule; AI with 6 articles; 5 to 7 articles in AII, directed backwards, with very 1217 1218 rudimentary exopod (Fig. 7.6C); labrum with poory armed distal free edge (Fig. 7.6F); paragnathes present; Md, length/width= 1.5 (long), palp not prehensile with 1 or 2 articles (Fig. 7.6J), in antero-1219 dorsal position, reduced pars incisiva (occupying antero-distal part) and typical lobe (plate like) of 1220 1221 pars molaris absent; MxII prehensile (Fig. 7.6M); exopod of thoracopods with 2 articles; male ThVIII not remembering "a leg"; absent pleopods; 2 similar distal spines on sympod of uropod; no seta on 1222 1223 pleotelson Leptobathynellidae (Fig. 7.7) 1224 1225 Key to Bathynellidae sub-families 1226 1227 1 Penial region of male ThVIII with 3 lobes; AI with 7 articles; AI > = or < AII; 3 articles in mandibular palp without sexual dimorphism; endoped of ThI to VII with 4 articles; female ThVIII with 1 article; 1228 4 spines as minimum on sympod of uropod; 3-4 claws on endopod of uropod (Fig. 7.7H) 1229 1230Bathynellinae 1' Penial region of male ThVIII with 1 lobe; AI with 6 or 7 articles; AI > or = AII; 1 to 3 articles in 1231 mandibular palp with or no sexual dimorphism; endopod of ThI to VII with 3 or 4 articles; endopod 1232 of female ThVIII with 1 or 2 articles; 4 spines as maximum on sympod of uropod; 2-4 claws on 1233 1234 1235 1236 Key to Bathynellinae genera 1 Six similar spines on sympod of uropod (Fig. 7.7I); 4 claws on endopod of uropod; 1st & 2^d spines of 1237 furca the largest (Fig. 7.7J); mandibular palp without sexual dimorphism with 3 articles; 7 articles in 1238 1239 AII; AI=AII; seta on medial segment of exopod of AII; 4 articles in endopod of ThI to VII 1240Bathynella 1' Four different spines on sympod of uropod (Fig. 7.7H); 3 claws on endopod of uropod; 2^d spines of 1241 1242 furca the largest (1.1 times 3th) (Fig. 7.7K); mandibular palp with sexual dimorphism and 3 articles; 7

1243 1244	articles in AII; AI=AII; seta on medial segment of exopod of AII; 4 articles in endopod of ThI to VII
1244 1245 1246	(one species: A. stammeri (Jakobi, 1954)) [Slovenia]
1247 1248	Key to Gallobathynellinae genera
1249 1250	1 AI with 6 articles; AII with 6 or 7 articles; AI>AII; Md palp with 3 articles without sexual dimorphism; ThI endopod with 4 articles
1251 1252 1253	1' AI with 7 articles; 7 or 8 articles in AII; AI>, < or =AII; Md palp of 3 articles, with or without sexual dimorphism; ThI endopod with 3 or 4 articles
1254 1255 1256	2(1) AI with 6 articles; medial seta absent on exopod of AII; 3 articles on Md palp; ThI endopod of 4 articles; ThII to V endopod with 3 articles and ThVI-VII endopod with 3 or 4 articles; female ThVIII of 1 simplified article, without epipod
1257 1258 1259 1260	2' AII with 7 articles; medial seta present on AII exopod; Md palp of 3 articles; endopod ThI to VII with 4 articles; large female ThVIII epipod with 2 articles
1261 1262	3(2) ThII to VII with 3 articles; 5 spines on furca, the second longest
1263 1264 1265 1266	3' ThII to V endopod with 3 articles; ThVI-VII endopod with 4 articles; 5 spines on furca, the second very, very long
1267 1268 1269	4(1) AI with 7 articles; AII with 7 articles; AI> or =AII; Md palp sexually dimorphic with 3 articles; ThI-V four-segmented endopod
1270 1271 1272	4' AI with 7 articles; AII with 7 or 8 articles; AI>, < or =AII; Md palp sexually or not dimorphic with 1 to 3 articles; ThI-VII endopod with 4 articles or ThI to V endopod with 3 articles
1273 1274 1275	5(4) ThI-VII with 4 articles on endopod; epipod present on female ThVIII; 4 spines on sympod and 2 claws on endopod of uropod; 5 spines of different size on furca
1276 1277 1278 1279	5' ThI-V endopod with 4 articles and ThVI and VII endopod with 3 articles; female ThVIII without epipod; 3 spines on sympod and 4 claws on endopod of uropod; 5 spines of similar size on furca <i>Sardobathynella</i> (one species: <i>S. cottarelli</i> Serban, 1973)
1280 1281	[Italy: Sardinia]
1282 1283 1284	6(4') AI with 7 articles; AII with 7 or 8 articles; ThI to V endopod with 3 articles; 1 to 3 articles on Md palp (dimorphic or not)

1285 1286	6' AI with 7 articles; AII with 8 articles; ThI-VII endopod with 4 articles; Md palp sexually dimorphic with 3 articles
1287 1288 1289 1290 1291 1292	7(6) AI with 7 articles; AII with 7 articles; AI=AII; Md palp with 2 articles; well developed endopod and exopod of female ThVIII; 4 spines on sympod and 2 claws on endopod of uropod; 5 spines of different size on furca
1293 1294 1295	7' AI with 7 articles; AII with 8 articles; AI> or < AII; Md palp with 1 to 3 articles; endopod and exopod of female ThVIII well developed or endopod absent; 3 or 4 spines on sympod and 2 or 3 claws on endopod of uropod; 5 spines of similar or different size on furca
1296 1297 1298 1299	8(7) AI>AII; medial seta of AII exopod absent or present; Md palp with 2 or 3 articles; female ThVIII with well developped endopod and exopod; 4 spines on sympod and two or three claws on endopod of uropod; 5 spines of similar or different size on furca
1300 1301 1302 1303 1304	 8' AI<aii; 1="" 2="" 3="" 5="" absent;="" aii="" and="" article;="" claws="" endopod="" exopod="" female="" furca<="" md="" medial="" of="" on="" palp="" present;="" seta="" similar="" size="" spines="" sympod="" td="" thviii="" uropod;=""></aii;>
1305 1306 1307 1308	9(8) Medial seta of exopod of AII absent; Md palp not dimorphic with 2 or 3 articles; female ThVIII with large endopod and exopod; 4 spines on sympod and 2 or 3 claws on endopod of uropod; 5 spines of similar or different size on furca
1309 1310 1311	9' Medial seta of exopod of AII present; Md palp dimorphic or not, with 3 articles; very small endopod of female ThVIII; 4 spines on sympod and 2 claws on endopod of uropod; 5 spines of similar size on furca
1312 1313 1314 1315 1316 1317	10(6) Medial seta of exopod of AII present; sexual dimorphism on mandibular palp; very short basipodal seta and well developed endopod and exopod of female ThVIII; 3 or 4 spines on sympod and 4 claws on endopod of uropod
1318 1319 1320 1321	10' Medial seta of exopod of AII absent; sexual dimorphism on labrum and mandibular palp; <i>pars molaris</i> of Md with complex morphology; very long basipodal seta and well developed endopod and exopod on female ThVIII; 4 spines on sympod and 2 claws on endopod of uropod
1322	
1323	Key to species of Delamareibathynella
1324 1325	1 One dentate lobe on <i>pars molaris</i> of Md D. debouttevillei Serban, 1989 [France: Ardéche]
1326 1327 1328	1' Two dentate lobes on <i>pars molaris</i> of Md

1329	Key to species of Gallobathynella
1330	1 Three or 4 teeth on <i>pars molaris</i> of Md
1331 1332 1333	1' Two teeth on <i>pars molaris</i> of Md <i>G. hispanica</i> (Delamare Deboutteville, 1954) [Spain: Tarragona]
1334 1335	2(1) Pars molaris of Md with 3 teeth and 2 setae on mandibular palp of Md; 2 claws and 3 or 4 setae on endopod and 3 or 4 setae on exopod of uropod
1336 1337 1338	2' <i>Pars molaris</i> with 4 teeth and 3 setae on mandibular palp of Md; 2 claws and 4 setae on endopod and 2 setae on exopod of uropod; second spine three times longer than first spine which is twice as long as dorsal spine and similar to fourth of furca
1339 1340	[France: Pyrénées-Orientales]
1341 1342 1343	3(2) Similar 3 or 4 spines on sympod of uropod; 3 setae on exopod of uropod; epipod longer than basipod of female ThVIII
1344 1345 1346	3' Uropod sympod with 4 spines, first the longest; 4 setae on exopod of uropod; epipod as long as basipod and exopod similar to endopod of female ThVIII; second spine 2.5 times longer than first spine which is as long as dorsal and fourth spines of furca
1347 1348 1349	<i>G. boui</i> Serban, Coineau & Delamare Deboutteville, 1971 [France: Hérault]
1350 1351 1352 1353 1354	 4(3) Three spines on sympod of uropod; 4 setae on endopod of uropod; longer than basipod seta of the coxopod and exopod >> than endopod of female ThVIII; very small endopod of male ThVIII; second spine 4 times longer than first spine which is as long as dorsal spine of furca
1355 1356 1357 1358 1359 1360	4' Four spines on sympod of uropod; 3 setae on endopod of uropod; no seta on coxopod and exopod > than endopod of female ThVIII; distal mamill on frontal projection of basipod and small endopod of male ThVIII; second spine almost as long as first spine which is longer than third and fourth, similar length of dorsal spine of furca <i>G. tarissei</i> Serban, Coineau & Delamare Deboutteville, 1971 [France: Aude]
1361	Key to species of Paradoxiclamousella
1362 1363 1364 1365 1366 1367	1 Barbed terminal claws of Md palp; two barbed setae on basipod of ThI-II; 12 setae on endopod of ThI; 4 setae on third article of endopod of ThII to IV; 5 setae on exopod of ThI to VII; almost square basipod of male ThVIII without seta; epipod and coxal seta smaller than basipod of female ThVIII; exopod as long as basipod of female ThVIII; 2 setae on endopod of female ThVIII (Fig. 7.7L); 6 setae on pleopod; third spines twice as long as the first and second on furca
1368	[Spain: Cantabria]
1369 1370 1371 1372 1373 1374	1' Smooth terminal claws (very long on male) of Md palp; 2 smooth setae on basipod of ThI-II; 10 setae on endopod of ThI; ThII to IV endopod with 3 setae on third article; ThI to VII exopod with 4 setae; rectangular basipod of male ThVIII with one seta; epipod and coxal seta longer than basipod of female ThVIII; exopod as long half basipod of female ThVIII; one seta on very small endopod of female ThVIII (Fig. 7.7M); 5 setae on pleopod; third spines slightly longer than others of furca
- 1375 [Spain: Asturias]
- 1376

1377

Key to species of Vejdovskybathynella

- 3(2) AII exopod with medial seta; exopod > endopod of female ThVIII; large endopod of male ThVIII;
 5 or 7 setae on pleopod; 4 similar spines on sympod of uropod; 2 claws on endopod of uropod 4

1397 1398 3' AII exopod without medial seta; exopod >> endopod of female ThVIII; small endopod of male 1399 ThVIII; six setae on pleopod; uropod sympod with distal spines longer than other three spines; 3 claws 1400 on endopod of uropod V. caroloi Camacho, 2007 1401 [Spain: Cantabria]

- 4' Male ThVIII basipod with large frontal projection; exopod of male ThVIII three times longer than
 wide; 7 setae on pleopod *V. espattyensis* Serban & Leclerc, 1984
 [France: Ardèche]

- 1418
- 6 (5) Fourth article of AII with one seta and no seta on first article; AII exopod with medial seta; exopod
 = endopod of female ThVIII; male ThVIII with small frontal projection on basipod and large endopod;

1421 1422 1423	exopod of male ThVIII two times longer than wide; 4 similar spines on sympod and 3 claws on endopod of uropod
1424 1425 1426 1427 1428	6' Fourth article of AII with two setae and one seta on first article; AII exopod without medial seta; exopod >> endopod of female ThVIII; male ThVIII with large frontal projection on basipod and very large endopod; exopod of male ThVIII three times longer than wide; 4 different spines (the basal smallest) on sympod and 2 claws on endopod of uropod
1429	
1430	Key to Parabathynellidae genera
1431 1432	1 Six pairs of thoracopods 2 1' Seven pairs of thoracopods 3
1433 1434 1435	2(1) AI with 6 articles; AII with 5 articles (Fig. 7.8A)
1436 1437 1438 1439	3(1) AI with 6 or 7 articles; AII with 4 or 5 articles (Fig. 7.8C)
1440 1441 1442 1443	4(3) AI with 6 articles; AII with 5 articles (Fig. 7.8C); Furca with 3 spines (Fig. 7.8E) <i>Cteniobathynella</i> (one species: <i>Ct. Calmani</i> (Por, 1968)) [Israel: Tiberias Lake]
1444	4' AI with 7 articles; AII with 4 or 5 articles; furca with 5 or 6 spines (Fig. 7.8F) Parabathynella
1445 1446 1447	5(3') AI with 6 or 7 articles; 2 articles on exopod of ThII to V
1448 1449 1450 1451 1452	 6(5) AI with 6 or 7 articles; labrum with hook-like teeth (Fig. 7.8G); claws very curved on distal endite of MxI (Fig. 7.8I)
1453 1454	6' AI with 7 articles; labrum with "normal teeth" (Fig. 7.8H); "normal claws" on distal endite of MxI (Fig. 7.8J)
1455 1456	Key to species of <i>Hexabathynella</i>
1457 1458 1459 1460	1 Md <i>pars molaris</i> with 5 or 6 teeth; 4 teeth on distal endite of Mx; 1 or 2 setae on first article of MxII; article fourth of ThI endopod with 2 or 3 setae; first pleopod absent or present; uropod inhomonomous or homonomous with 3 to 7 spines on sympod; uropod with 3 or 4 setae on exopod and 2 or 3 on endopod; 3 or 9 to 13 spines on furca
1461 1462 1463	1' Md <i>pars molaris</i> with 4 teeth; distal endite of Mx with 5 teeth; one setae on first article of MxII; fourth article of ThI endopod with 3 setae; first pleopod present; 2 spines on sympod of inhomonomous uropod; uropod with 2 setae on exopod and 2 on endopod; 6-7 spines on furca

1464 1465	
1466 1467 1468 1469	2(1) Md <i>pars molaris</i> with 5 or 6 teeth; 2 setae on first article of MxII; fourth article of ThI endopod with 2 setae; first pleopod absent or present; 6 or 7 spines on inhomonomous or homonomous sympod of uropod; 3 spines on furca
1470 1471 1472 1473	2' Md <i>pars molaris</i> with 5 teeth; 1 setae on first article of MxII; fourth article of ThI endopod with three setae; first pleopod present; 3 spines on inhomonomous sympod of uropod; 3 setae on exopod and 3 on endopod of uropod; 9 to 13 spines on furca
1474 1475 1476	3(2) Fourth article of AII without seta or 1 seta; Md <i>pars molaris</i> with 5 teeth; first pleopod absent; sympod of uropod inhomonomous
1477 1478 1479 1480	3' Fourth article of AII with 2 setae; Md <i>pars molaris</i> with 6 teeth; first pleopod present; sympod of uropod homonomous; 3 setae on exopod and 2 on endopod of uropod
1481 1482 1483 1484	4(3) Fourth article of AII with 1 seta; distal spine of Md not modified; second article of MxII with 3 setae; 4 setae on exopod and 3 on endopod of uropod <i>H. valdecasasi</i> Camacho, 2003 [Spain: Toledo]
1485 1486 1487	4' Fourth segment of AII without seta; distal spine of Md modified; second segment of MxII with 4 setae; 3 setae on exopod and 2 on endopod of uropod
1488 1489	Key to species of Hexaiberobathynella
1490 1491 1492 1493	 1 Mandibular palp not exceeding distal part of Md <i>pars incisiva</i>; 1 tooth on female ThVIII (Fig. 7.8K); 5 to 8 spines on sympod of uropod; 5 to 8 spines on furca
1494 1495 1496 1497	1' Mandibular palp exceeding distal part of Md <i>pars incisiva</i> ; 3 teeth on female ThVIII (Fig. 7.8L); 10 to 13 spines on sympod of the uropod; 8 to 10 spines on furca
1498 1499	Key to species of Parabathynella
1500 1501 1502	1 AII with 5 articles; 9 teeth on labrum; 5 teeth on distal endite of MxI; 1 seta on first article of MxII; 2 setae on second and third articles of endopod of ThI; 5 spines on furca
1503	[Slovenia]
1504 1505 1506 1507	 1 All with 4 articles; 12 teeth on labrum; 6 teeth on distal endite of MxI; 2 setae on first article of MxII; 3 setae on second and 1 on third article of ThI endopod; 6 spines on furca

1508 1509

Key to species of Paraiberobathynella

1 Labrum with 8 main teeth; Md *pars incisiva* with 6 to 8 teeth; Md *pars molaris* with 6 to 11 teeth;
inhomonomous sympod of the uropod; 7 or 8 spines on furca; exopod of ThI with 2 or 3 articles... 2

- 1512 1' Labrum with 9 to 11 teeth; Md *pars incisiva* with 5 to 9 teeth; Md *pars molaris* with 12 teeth;
 1513 homonomous sympod of the uropod; 8 to 12 spines on furca; exopod of ThI, II, VI and VII with 3
 1514 articles (Fig. 7.7C), and ThIII to V with 4 articles *Pi. notenboomi* (Camacho, 1989)
 1515 [Spain: Alicante]
- 1516

- 1524 1525

Key to species of Iberobathynella

1537

3(2) First article of ThII to VII endopod without dorsal seta; 2 setae on first article of ThII to VII exopod; 2 or 3 setae on second article of ThI endopod; 1 or 2 articles on ThI exopod; cuticle of female ThVIII smooth (Fig. 7.8R) or wrinkled (Fig. 7.8S); (Fig. 7.8T) uropod sympod inhomonomous or homonomous; 4 to 6 setae on exopod and 0, 1 or 3 on endopod of uropod *Iberobathynella* (*Espanobathynella*)

3' First article of ThII to VII endopod with 1 dorsal seta; 3 setae on first article of ThII to VII exopod;
3 setae on second article of ThI endopod; ThI exopod with 2 articles; cuticle of female ThVIII smooth
(Fig. 7.8U); uropod sympod homonomous (Fig. 7.8V); 4 to 8 setae on exopod and 3 on endopod of
uropod *Iberobathynella (Iberobathynella)*

15471548Key to species of Iberobathynella (Asturibathynella)

1551	1' AI with 7 articles
1552 1553 1554 1555 1556	 2(1) First article of MxII with 1 seta; first article of ThI endopod with 2 setae; cuticle of female ThVIII smooth; 5 spines on sympod of uropod; 5 setae on exopod and 3 on endopod of uropod
1557 1558 1559 1560	2' First article of MxII without seta; first article of ThI endopod with 1 seta; cuticle of female ThVIII wrinkled; 9 spines on sympod of uropod; 4 setae on exopod and 2 on endopod of uropod
1561 1562 1563	3(1') First article of MxII with 1 seta; first article of ThI endopod with 2 setae; cuticle of female ThVIII smooth or wrinkled; anal operculum protuded or not
1564 1565	3' First article of MxII without seta; first article of ThI endopod with 1 or 2 setae; cuticle of female ThVIII smooth or wrinkled; anal operculum protuded
1566 1567 1568 1569	4(3) Md <i>pars molaris</i> with 7 teeth; Md <i>pars distales</i> with 6 or 7 teeth; cuticle of female ThVIII smooth or wrinkled; 7 or 8 spines on sympod of uropod; 4 or 5 setae on exopod and 1 or 3 on endopod of uropod; 6 to 10 spines on furca; anal operculum not protuded
1570 1571 1572 1573	4' Md <i>pars molaris</i> with 5 teeth; Md <i>pars distales</i> with 4 teeth; cuticle of female ThVIII smooth; 6 spines on sympod of uropod; 5 setae on exopod and no seta on endopod of uropod; 5 spines on furca; anal operculum protuded
1574 1575 1576 1577 1578	5(4) Md <i>pars distalis</i> with 7 teeth; cuticle of female ThVIII wrinkled; 7 spines on sympod of uropod; 4 setae on exopod and 3 on endopod of uropod; 7 to 10 spines on furca
1579 1580 1581 1582	5' Md <i>pars distalis</i> with 6 teeth; cuticle of female ThVIII smooth; 8 spines on sympod of uropod; 5 setae on exopod and 1 on endopod of uropod; 6 or 7 spines on furca
1583 1584 1585 1586	6(3') Md <i>pars molaris</i> with 6 to 7 teeth, <i>pars distalis</i> with 5 to 7 teeth; first article of ThI endopod with 1 setae; cuticle of female ThVIII wrinkled or smooth; 5 to 9 spines on sympod of uropod; 3 or 4 setae on exopod and 1 or 2 on endopod of uropod
1587 1588 1589 1590	6' Md <i>pars molaris</i> with 5 teeth, <i>pars distales</i> with 4 teeth; first article of ThI endopod with two setae; cuticle of female ThVIII wrinkled; 9 or 10 spines on sympod of uropod; 4 setae on exopod and 2 on endopod of uropod <i>I. (A) parasturiensis</i> Camacho & Serban, 1998 [Spain: Asturias, Cantabria]
1591 1592 1593 1594	7(6) Md <i>pars molaris</i> with 7 teeth, <i>pars distalis</i> with 5 to 7 teeth; cuticle of female ThVIII smooth or wrinkled; 5 to 7 spines on sympod of uropod; 3 or 4 setae on exopod and 2 on endopod of uropod

1595 1596	7' Md <i>pars molaris</i> with 6 teeth, <i>pars distalis</i> with 5 teeth; cuticle of female ThVIII smooth or wrinkled; 5 to 9 spines on sympod of uropod; 3 or 4 setae on exopod and one or two on endopod of uropod
1597	
1598 1599 1600 1601 1602	8(7) Cuticle of female ThVIII wrinkled; setules on distal end of inner lobe of male ThVIII present; 6 to 7 spines on sympod of uropod; 4 setae on exopod and 2 on endopod of uropod
1603 1604 1605	8' Cuticle of female ThVIII smooth; distal part of inner lobe of male ThVIII without setules; 5 to 6 spines on sympod of uropod; 3 setae on exopod and 2 on endopod of uropod
1606	[Portugal: Barcelos. Spain: León, Pontevedra]
1607 1608 1609	9(7') Cuticle of female ThVIII smooth; 5 to 7 spines on sympod of uropod; 3 or 4 setae on exopod and 1 or 2 on endopod of uropod
1610 1611 1612	 9' Cuticle of female ThVIII wrinkled; 9 spines on sympod of uropod; 4 setae on exopod and 2 on endopod of uropod
1613 1614 1615	10(9) Five spines on sympod of uropod; 4 setae on exopod and 2 on endopod of uropod
1616	[Spain: Lugo]
1617 1618 1619	10' Seven spines on sympod of uropod; 3 setae on exopod and 1 on endopod of uropod
1620 1621	Key to species of <i>Iberobathynella</i> (<i>Espanobathynella</i>)
1622 1623 1624	1 ThII to VII exopod with 2 articles; ThI with 1 or 2 articles; ThI endopod with 2 or 3 setae on second article; setules on distal part of inner lobe of male ThVIII present or absent; cuticle of female ThVIII smooth or wrinkled; sympod of uropod inhomonomous or homonomous
1625 1626 1627 1628 1629	1' ThII, III and VI, VII exopod with 2 articles and ThIV and V exopod with 3 articles; ThI exopod with 2 articles; second article of ThI endopod with 3 setae; no setules on distal part of male ThVIII inner lobe; cuticle of female ThVIII smooth; 12 or 13 spines on homonomous sympod, 6 setae on exopod and 1 seta on endopod of uropod <i>I. (E) magna</i> Camacho & Serban, 1998 [Spain: Asturias, Cantabria]
1630 1631 1632	2(1) Uropod with sympod inhomonomous; 1 or 2 articles on exopod of ThI; 3 setae on second article of ThI endopod; cuticle of female ThVIII smooth; anal operculum not pronounced
1633 1634 1635	2' Sympod of the uropod homonomous; 1 or 2 articles on exopod of ThI; second article of ThI endopod with 2 setae; cuticle of female ThVIII smooth or wrinkled; anal operculum pronounced or not
1636 1637 1638	3(2) ThI exopod with 2 articles; setules on distal part of male ThVIII inner lobe present; 5 or 6 setae on exopod and 1 seta on endopod of uropod; anal operculum not pronounced

1639 1640	
1641 1642 1643	3' ThI exopod with 1 article; no setules on distal part of male ThVIII inner lobe; 5 setae on exopod and 3 setae on endopod of uropod; anal operculum pronounced <i>I. (E) andalusica</i> Camacho, 2007 [Spain: Córdoba, Sevilla]
1644 1645 1646 1647	4(2') ThI exopod with 1 article; cuticle of female ThVIII smooth; 7 to 9 spines on sympod, 5 setae on exopod and 1 seta on endopod of uropod <i>I. (E) cantabriensis</i> Camacho & Serban, 1998 [Spain: Asturias, Cantabria]
1648 1649 1650 1651 1652	4' ThI exopod with 2 articles; cuticle of female ThVIII wrinkled; 10-12 spines on sympod, 4 setae on exopod and no seta on endopod of uropod <i>I. (E) burgalensis</i> Camacho, 2005 [Spain: Burgos]
1653	Key to species of Iberobathynella (Iberobathynella)
1654 1655	1 Md <i>pars incisiva</i> with 9 to 12 teeth, <i>pars molaris</i> with 6 to 16 teeth; 2 or 3 setae on first article of ThI exopod; 9 to 27 spines on sympod, 5 setae on exopod and 3 seta on endopod of uropod
1656 1657 1658	1' Md <i>pars incisiva</i> with 6 teeth, <i>pars molaris</i> with 10 teeth; 2 setae on first article of ThI exopod; 12 or 13 spines on sympod, 6 to 8 setae on exopod and 3 setae on endopod of uropod
1659	[Portugal: Areinho de Valbom, Spain: Salamanca]
1660 1661 1662	2 (1) Md <i>pars incisiva</i> with 7 or 8 teeth, <i>pars molaris</i> with 6 to 10 teeth; 2 or 3 setae on first article of ThI exopod; 9 to 12 spines on sympod of uropod
1663 1664 1665	2' Md <i>pars incisiva</i> with 7 to 12 teeth, <i>pars molaris</i> with 8 to 16 teeth; 3 setae on first article of ThI exopod; 16 to 27 spines on sympod of uropod
1666 1667	3 (2) First article of ThI exopod with 2 setae; Md <i>pars incisiva</i> with 7 teeth, <i>pars molaris</i> with 6 to 8 teeth; 9 to 12 spines on sympod of uropod; 9 to 13 spines on furca
1668 1669	
1670 1671	3' First article of ThI exopod with 3 setae; Md <i>pars incisiva</i> with 7 or 8 teeth, <i>pars molaris</i> with 8 to 10 teeth; 9 to 11 spines on sympod of uropod; 10 spines on furca
1672 1673 1674	[Portugal: Barcelos]
1675 1676 1677	4 (2) First article of ThVI exopod with 3 setae; Md <i>pars incisiva</i> with 10 teeth, <i>pars molaris</i> with 8 to 10 teeth; 16 to 19 spines on sympod of uropod; 6 or 7 spines on furca <i>L</i> (<i>I</i>) gracilines (Braga 1960)
1678	[Portugal: Beira-Baixa]
1679 1680 1681 1682	4' First article of ThVI exopod with 2 setae; Md <i>pars incisiva</i> with 9 to 12 teeth, <i>pars molaris</i> with 8 to 16 teeth; 18 to 27 spines on sympod of uropod; 9 to 12 spines on furca

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1732 **4. Malacostraca: Decapoda**

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- 1737

1738 INTRODUCTION

Decapoda Latreille 1802 is the most species-rich order within Malacostraca with nearly 15,000 1739 species (De Grave et al., 2009). The order includes many familiar groups such as crabs, shrimps, 1740 crayfish, lobsters and hermit crabs that live in an impressive diversity of marine, freshwater, 1741 subterranean and terrestrial habitats. The majority of decapod species are found in marine 1742 habitats, whereas approximately 3,000 species live exclusively in freshwater habitats on almost 1743 1744 all continents (Cumberlidge et al., 2015). These include over 1,450 species of brachyuran crabs (Cumberlidge et al., 2015), about 800 species and subspecies of caridean and sergestoid shrimps 1745 (De Grave et al., 2015), around 669 species of crayfish (Crandall & De Grave, 2017) and 75 1746 species of anomuran crabs (Cumberlidge et al., 2015; Bueno et al., 2016). 1747

Freshwater crabs have a circumtropical distribution restricted to warm habitats covering five 1748 zoogeographical regions, from the Neotropical region to the Australasian region (Cumberlidge 1749 et al., 2015). Evolutionary studies suggest that freshwater crabs diverged early in the 1750 brachyuran phylogenetic tree. They are thought to have at least two independent origins, with 1751 four of the five freshwater crab families sharing common ancestry (Klaus et al., 2011; Tsang et 1752 al., 2014). Freshwater crabs are estimated to have diverged from their closest marine sister taxa 1753 1754 after the break-up of Pangaea (~200 Mya), around 135 Mya (Tsang et al., 2014). Although the origin of Mediterranean crabs (Potamon spp.) still remains unknown, their species diversity 1755 argues in favor of an East Asian origin (Jesse et al., 2011). Freshwater crayfish and anomuran 1756 crabs are distributed in temperate parts of the two hemispheres (Cumberlidge et al., 2015; 1757 Bueno et al., 2016). The oldest crayfish fossils date back to the Permian and early Triassic 1758 periods, suggesting a widespread Pangaea distribution followed by a number of vicariance 1759 events that allowed the ancient crayfish population to diversify and spread throughout the 1760 continents of Laurasia and Gondwana (Crandall et al., 2000; Cumberlidge et al., 2015). 1761 Freshwater anomuran crabs, which mostly include Aegla species, seem to have a more recent 1762 origin - the early Tertiary period, about 60 Mya (Pérez-Losada et al., 2004). Finally, freshwater 1763 shrimps occur in both tropical and temperate freshwater habitats. Phylogenetic studies have 1764 shown a distant affinity among freshwater shrimp families implying that each family 1765 independently invaded continental and subterranean waters from an ancestral marine stock at 1766 different times (De Grave et al., 2008). The Mediterranean basin was colonized through 1767 multiple ancient transoceanic dispersal or vicariance events (von Rintelen et al., 2012; Carvalho 1768 et al., 2016). 1769

Three groups of freshwater decapods are found in the Mediterranean basin, namely crabs, shrimps, and crayfish. They belong to six families, 15 genera and 63 species (1 family, 3 genera and 3 species are non-native), representing about 2.1% of global diversity; most species are endemic to the region.

1774

1775 GENERAL ECOLOGY AND DISTRIBUTION

Freshwater decapods successfully colonized a very diverse array of epigean and hypogean freshwater habitats reflected by a wide range of life histories as well as morphological and physiological adaptations. Because of their abundance and high biomass, they are integral components of food webs, represent a food source for a wide range of predators and play an important role in nutrient recycling in freshwater ecosystems (Cumberlidge *et al.*, 2015; De Grave *et al.*, 2015).

1782 A rich and highly endemic decapod fauna is found in the freshwater habitats of all countries and most islands of the Mediterranean basin (Jesse et al., 2011; Kouba et al., 2014; 1783 Christodoulou et al., 2016). Their diversity comprises six families (15 genera, 63 species and 1784 subspecies) in this region. The freshwater crab family Potamidae (1 genus, 15 species) is found 1785 1786 in the surface waters of North Africa and the eastern Mediterranean basin (Brandis et al., 2000; Jesse et al., 2011). Crayfish are represented in the Mediterranean basin by one native family -1787 Astacidae (4 genera, 7 species) – and one non-native family – Cambaridae (2 genera, 2 species). 1788 Native crayfish species are distributed in the northern Mediterranean basin but are absent from 1789 continental North Africa (Kouba et al., 2014; Cumberlidge et al., 2015). The distribution of 1790 crayfish in the Mediterranean basin has been under great anthropogenic influence, resulting in 1791 three invasive species currently found in the western Mediterranean region, while numerous 1792 translocations of the native species took place across Europe (Kouba et al., 2014). The largest 1793 shrimp family is Atyidae (6 genera, 26 species and subspecies) with representatives in epigean 1794 and subterranean systems throughout the Mediterranean basin (Christodoulou et al., 2016), 1795 while Palaemonidae (1 genus, 9 species) are restricted to epigean systems throughout the basin 1796 (Christodoulou et al., 2016). Both families occur in all biogeographical regions, except 1797 Antarctica, but are most diverse in the Indo-Malayan region where the majority of palaemonid 1798 species live in marine and brackish waters whereas Atyidae almost exclusively live in 1799 1800 freshwater (De Grave et al., 2015). The areas immediately surrounding the Mediterranean Sea 1801 harbour the world highest stygobiotic species diversity within Atyidae (16 species and subspecies) (Sket & Zakšek 2009; Christodoulou et al., 2016). Finally, Typhlocarididae (1 1802 genus, 4 species) are strictly subterranean and are the only endemic decapod family in the basin 1803 1804 (Christodoulou et al., 2016), with species distributed in Israel, Italy and Libya.

1805

1806 TERMINOLOGY AND MORPHOLOGY

1807 Decapods exhibit a great variability in size and body form. Their size in freshwaters can vary
1808 from 1.0 cm for the bee shrimp (*Caridina cantonensis*) to more than 80 cm and 6 kg for some
1809 of the largest and heaviest freshwater invertebrates such as Tasmanian giant crayfish
1810 (*Astacopsis gouldi*). Mediterranean basin decapods are small- to medium-sized, from about 2
1811 cm (e.g. Atyaephyra orientalis) to about 20 cm (e.g. Pontastacus leptodactylus).

1812 The general decapod body is composed of a head, thorax, and abdomen (Fig. 7.9). The 1813 body is compressed laterally in shrimps, compressed dorsoventrally in crayfish, but strongly 1814 depressed and flattened in brachyuran crabs. The first three of the eight thoracic segments of 1815 shrimps, crayfish, and crabs are fused with the head to form a cephalothorax covered by a shield 1816 – the carapace that extends over the whole head and thorax. The carapace extends laterally 1817 along the sides of the cephalothorax forming branchial chambers that enclose the gills.

1818 The anterior part of the cephalothorax (head) carries a pair of compound stalked eyes, 1819 two pairs of antennae (antenna and antennula), and three pairs of mouth parts (mandible, 1820 maxillula, maxilla). The carapace of freshwater shrimps, crayfish and aeglids (not present in 1821 the Mediterranean basin) protrudes between the eyes and forms a rostrum, while it forms a front

in freshwater crabs. The carapace can be ornamented with various spines, grooves and 1822 depressions. The first three abdominal segments bear three pairs of maxillipeds - specialized 1823 appendages for feeding and locomotion. The next abdominal segments bear five pairs of 1824 pereiopods (ambulatory legs) modified either as walking legs or as chelate limbs (equipped 1825 with pinchers or setal brushes) termed chelipeds. In crayfish, the first three pairs of pereiopods 1826 1827 are chelate, while in caridean shrimps only the first two pairs are chelate and in brachyuran crabs only the first pair is chelate. The name of the group Decapoda (=ten legs) derives from 1828 the presence of ten pereiopods. The pereiopods have the typical biramous form of a crustacean 1829 limb composed from their proximal-most end to their distal-most end of a protopod with two 1830 podomeres (basis and coxa), an endopod with five podomeres (ischium, merus, carpus, 1831 propodus and dactylus), and an exopod that can be fully developed, vestigial or absent. A small 1832 process – the epipod – and multidenticulate setae – setobranch setae – can be present on coxae. 1833

The abdomen (pleon) follows the thorax. It is folded beneath the body in crabs, or extends posteriorly in shrimps and crayfish. Pleopods, modified for swimming, brooding eggs, ventilation and burrowing appendages extend in pairs from the first five abdominal segments. The abdomen terminates in a telson, with a uropod on each side. Both the pleopods and the uropods are biramous, composed of a basal peduncle bearing two branches – the endopod and the exopod. The first two pleopods are sexually modified in male decapods.

1840

1841 COLLECTION, PREPARATION, AND IDENTIFICATION

Freshwater decapods are found in lotic, lentic, and subterranean environments. Different 1842 1843 sampling methods are utilized depending on the species and the habitat. The freshwater shrimps that dwell in epigean waters are usually collected using strong, long-handled, fine-meshed dip 1844 nets, while dredges, seine nets and sweep net electrofishing have also been reported as sampling 1845 techniques. In subterranean habitats, shrimps are caught with baited (e.g. with strips of raw 1846 beef) traps or by hand or with short hand nets and torchlight to illuminate the animals while 1847 scuba diving (Jaume & Brehier, 2005). Freshwater crayfish in shallow waters are collected by 1848 hand by turning rocks over. A dip net can be used in deeper waters while snorkeling or scuba 1849 diving, and seine nets or fyke nets can be used too. Finally, baited wire traps have proven 1850 especially efficient in deeper waters, especially at night. Crabs can be caught during the day by 1851 1852 turning flat rocks over in rivers and streams. In deeper waters, baited traps or fyke nets can be 1853 used.

After collection, shrimps, crayfish, and crabs should be preserved in 70% ethanol for 1854 morphological analyses and in 95% ethanol for molecular analyses. Mediterranean decapods 1855 can be identified under a stereomicroscope down to the genus level. However, determination at 1856 the species level most often requires dissection and mounting of the mouthparts and appendages 1857 on slides and examination using a microscope (10x-40x magnification). Specimens or body 1858 parts can be dyed using different stains or cleared by submersion in weak acid (HCl, chlorine). 1859 The morphological identification of shrimps at the species level requires adult individuals; as 1860 for freshwater crabs, only males can be identified at the species level. Key morphological 1861 characteristics include among others rostrum armature, mouthparts, male pleopods, gonopods, 1862 1863 telson armature, and pereiopod armature. Once the appendages are dissected, they are kept in smaller vials in the vial containing the specimen. It should be noted that many decapod species 1864 of the Mediterranean basin can only be identified with certainty by DNA barcoding (Sket & 1865 Zakšek 2009; Jesse et al., 2011; Christodoulou et al., 2016). 1866

1868 LIMITATIONS

1869 The taxonomy of freshwater decapods in the Mediterranean basin has been somewhat neglected in the past and has only recently grown more stable, as collections include more remote 1870 locations and molecular data are taken into account. Furthermore, high intra- and interspecific 1871 variability and sexual dimorphism complicate the morphological identification of decapods 1872 (Sket & Zakšek 2009; Jugovic et al., 2010). Primary and secondary sexual characters in many 1873 decapods (Atyidae, Potamidae) are taxonomically important, but these characters are poorly 1874 developed in young animals (Sket & Zakšek, 2009; Jugovic et al., 2010; Christodoulou et al., 1875 2016). Moreover, reliable identification of many species requires examining adult males 1876 because characters of taxonomic value have not been observed so far in females (Brandis et al., 1877 2000; Jugovic et al., 2010). The current increased interest in Mediterranean epigean and 1878 hypogean decapods is based on more comprehensive sampling, molecular studies, and a 1879 posteriori examination of morphological characters that altogether improved taxonomy. Over 1880 the past two decades, the number of epigean freshwater shrimp species in the Mediterranean 1881 region has more than doubled, although controversies still remain about the precise number of 1882 species (e.g., Atyaephyra spp.), while new species may well still be awaiting discovery. 1883 Likewise, the number of troglobitic species has more than tripled, and more species are still 1884 awaiting description (Sket & Zakšek, 2009). Despite the increased interest in Mediterranean 1885 epigean and hypogean atyids and the new available methods, the taxonomy of these shrimps 1886 still remains unsettled. 1887

A number of Mediterranean decapods are cryptic species. Although they are genetically quite distinct, they appear morphologically identical to other species. Our keys can identify most species, but for some of them the key concludes to a species complex that molecular and geographical data can further distinguish. Finally, the keys are designed for Mediterranean freshwater decapods, they are not adapted for a global use.

1894	KEY TO DECAPODA
1895	
1896	Key to Decapoda infraorders
1897	1 Abdomen projecting posteriorly
1898 1899	1´Abdomen folded beneath body, tightly pressed to thorax Brachyura, Potamidae [North Africa, Italian and Balkan Peninsulas, Middle East]
1900	
1901	2(1) Abdomen laterally compressed; pleuron of second abdominal somite overlapping pleura
1902	of second and third somite
1903	[Mediterranean basin]
1904	2' Abdomen compressed dorsoventrally; pleuron of second somite not overlapping pleura of
1905	second and third somite Astacidea
1906	[Europe]
1907	
1908	Key to Potamidae genera and species

1909 1910 1911 1912 1913 1914	This <i>Potamon</i> key relies on the morphology of male first gonopod thus not suitable when only female specimens are present (Brandis <i>et al.</i> 2000). The key includes a total number of 15 species presented in Brandis <i>et al.</i> (2000) and Jesse <i>et al.</i> (2010, 2011). Four cryptic species exist within the genus where no morphological characters have been found yet to distinguish them and COI gene nucleic acid sequence differences are required to distinguish them to species level (*).
1915 1916 1917	1 Terminal article of first gonopod broad, more or less oval; mesial portion distinctly tumid; apex long and slightly curve
1918 1919	1´ Terminal article of first gonopod conical or slender; mesial part not tumid
1920 1921 1922 1923	2(1) Flexible zone of first gonopod V-shaped
1924 1925 1926	2´ Flexible zone of first gonopod distinctly bilobed Potamon algeriense Bott, 1967 [Algeria, Morocco, Tunisia]
1927	3(1') First gonopod with conical, cylindrical or triangular terminal article
1928 1929	3' First gonopod with very slender and elongated fusiform terminal article; flexible zone of first gonopod broad or only narrowed only in its lateral part
1930 1931 1932 1933	(<i>P. ibericum</i> , <i>P. kretaion</i> *) [Greece, Turkey]
1934	4(3) Terminal article of first gonopod elongated and conical, mesial edge slightly bulging 5
1935 1936 1937	4´Terminal article of first gonopod stout and triangular; subterminal part with projecting mesial edge
1938	5(4) Flexible zone of first gonopod flexible not symmetrically bilobed
1939	5' Flexible zone of first gonopod symmetrically bilobed
1940 1941 1942 1943	(<i>P. hippocratis</i> , <i>P. karpathos</i> , <i>P. potamios</i> *) (Cyprus, Greece, Israel, Turkey]
1944	6(5) Flexible zone of first gonopod not distinctly V-shaped7
1945 1946 1947	6' Flexible zone of first gonopod distinctly V-shaped Potamon rhodium Parisi, 1913 [Greece, Turkey]

1948 1040	7(6) Flexible zone of first gonopod with only one linguiform elongate lobe
1949 1950	[Lebanon, Syria, Turkey]
1951 1952 1953 1954	7´ Flexible zone of first gonopod slender, terminal article subcylindrical and narrow
1955	8(4) Flexible zone of first gonopod V-shaped or with one mesial or lateral lobe
1956 1957 1958 1959	8' Flexible zone of first gonopod bilobed; terminal article of first gonopod asymmetric in shape, mesial margin bulging in its proximal half <i>Potamon magnum</i> Pretzmann, 1962 [Turkey]
1960	9(8) Flexible zone of first gonopod distinctly V-shaped 10
1961 1962 1963 1964 1965	9' Flexible zone of first gonopod with one lateral located linguiform elongated lobe; subterminal part of first gonopod with low mesial edge
1966 1967 1968 1969	10(9) Terminal article of first gonopod almost triangular; anterolateral margin of carapace broad, serrated with unequally large teeth
1970 1971 1972 1973 1974	10' Terminal article of first gonopod proximal half with straight mesial margins, in distal half becoming sharply deflected; anterolateral margin of carapace narrow serrated with very small regular teeth Potamon persicum Pretzmann, 1962 [Turkey]
1975	Key to Caridea families
1976	1 First and second pereopod with chelae fingers lacking dense apical setal tufts
1977 1978	1' First and second pereopod with chelae bearing dense apical setal tufts Atyidae [peri-mediterranean]
1979	
1980 1981 1982	2(1) Carapace lacking longitudinal sutures; flagellum of first antenna with rami fused basally Palaemonidae, <i>Palaemon</i> [peri-mediterranean]
1983	
1984 1985 1986	2' Carapace bearing pair of straight, longitudinal, dorsolateral sutures; cavernicolous

1987	
1988	Key to Atyidae genera
1989	1 At least first three pereiopods bearing exopods
1990 1991 1992	1' Only first and second pereiopods bearing exopods
1993 1994	2(1) Appendix masculina of male second pleopod bearing spines longer than appendix diameter
1995 1996 1997	2' Appendix masculina of male second pleopod bearing spines much shorter than appendix diameter
1998 1999	3(2) Supraorbital spines on carapace present; exopods of fifth pereiopods absent or reduced 4
2000	3' Supraorbital spines on carapace absent; exopod of fifth pereiopods well developed
2001 2002 2003	[France, Spain]
2004 2005 2006 2007	4(3) Eyes reduced, pigment absent; pterygostomian spine absent; rostrum short unarmed; dactylus of fifth pereiopod with less than 10 spiniform spines
2008 2009 2010 2011	4' Eyes developed and pigmented; pterygostomian spine present; rostrum long and armed; dactylus of fifth pereiopod with more than 10 spiniform spines (comp-like) <i>Dugastella</i> [Morocco, Spain]
2012 2013 2014	5(2') Endopod of male first pleopod as a slightly bent plate, its appendix interna vestigial
2015 2016 2017	5' Endopod of male first pleopod shaped as '9', i.e. with a long, subapically-laterally positioned appendix interna
2018	
2019	Key to species of Atyaephyra
2020 2021 2022 2023 2024 2025	This <i>Atyaephyra</i> key it is based on Christodoulou <i>et al.</i> (2012) and Jablonska <i>et al.</i> (2018) and it refers to individuals of carapace length ≥ 5.0 mm (≥ 3.5 mm for <i>A. orientalis</i>) but the reader should keep in mind that this genus is still under taxonomic revision. Two cryptic species exist within the genus where no morphological characters have been found yet to distinguish them and COI gene nucleic acid sequence differences are required to distinguish them to species level (*).

2026	
2027	1 Propodite of third maxilliped bearing 8–38 (rarely 8) strong mesial spiniform setae
2028 2029	1' Propodite of third maxilliped bearing 0–8 (rarely 8) strong mesial spiniform setae
2030 2031 2032	2(1) Endopod terminal part of first male pleopod slender, tapering; merus of third pereiopod with 4–6 (rarely 3–9) spiniform setae; merus of fourth pereiopod with 3–5 (rarely 2–7) spiniform setae
2033 2034 2035 2036 2037	2' Endopod terminal part of first male pleopod broad; merus of third pereiopod with 7–9 (rarely 6–10) spiniform setae; merus of fourth pereiopod with 6–8 (rarely 5–9) spiniform setae
2038 2039 2040 2041	3(1') Absence of post orbital teeth, leaving an unarmed proximal gap on dorsal surface of rostrum; basal endite of first maxilliped failing to reach or reaching distal end of exopod
2042 2043 2044 2045 2046 2047	 3' Post orbital teeth present without an unarmed proximal gap on dorsal surface of rostrum; basal endite of first maxilliped over-reaching distal end of exopod
2048 2049	4(2) Propodite of third maxilliped bearing 16-30 (rarely 11-38) strong mesial spiniform setae 5
2050 2051 2052 2053	4' Propodite of third maxilliped bearing 9-12 (rarely 8-20) strong mesial spiniform setae
2054 2055 2056 2057	5(4) Stylocerite length 1.02-1.19 (rarely 0.97-1.19) times first antenullar segment length; fifth pleuron distal end pointed with acute angle
2058 2059 2060 2061 2062	5' Stylocerite length 0.82-1.0 (rarely 0.82-1.08) times first antenullar segment length; fifth pleuron distal end rounded, pointed with abtuse angle (rarely with acute)
2063	Key to species of <i>Typhlatya</i>

2064 2065 2066 2067	1 Rostrum scarcely developed, shorter than reduced eye stalks; dactylus of fifth pereopod with row of 36 slender spiniform setae on flexor margin
2068 2069 2070	1´ Rostrum length subequal to reduced eye stalks; dactylus of fifth pereopod with row of 19 – 28 stout spiniform setae on flexor margin <i>Typhlatya arfaea</i> Jaume & Bréhier, 2005 [France]
2071	
2072	Key to species of <i>Dugastella</i>
2073	1 Rivers and springs in Morocco Dugastella marocana Bouvier, 1912
2074 2075	1' Rivers, springs and lagoons in southern Spain
2076	
2077	Key to species of <i>Troglocaris</i>
2078 2079 2080	This <i>Atyaephyra</i> key it is based on Sket & Zaksek (2009). Two cryptic species exist within the genus where no morphological characters have been found yet to distinguish them and COI gene nucleic acid sequence differences are required to distinguish them to species level (*).
2081 2082 2083 2084	1 Endopod of male first pleopod with more than 30, partially grouped, and long, inner marginal setae; rostrum with usually 15 ventral teeth
2085 2086 2087 2088	 1' Endopod of male first pleopod with shorter and scarcer marginal setae; rostrum with fewer than ten ventral teeth
2089	
2090	Key to Spelaeocaris species
2091 2092 2093	This <i>Spelaeocaris</i> key it is based on Sket & Zaksek (2009) with the addition of one more species (<i>Spelaeocaris hercegovinensis</i>) according to the genetic study of Marin (2017).
2093	1 Supraorbital spines on carapace absent; pereopod chelae and dactyli very stout
2095 2096 2097 2098	1' Supraorbital spines on carapace present; pereopod chelae and dactyli very narrow
2099 2100	2(1) Dactylus of fifth pereopod with more than 15 spines, comb-like; at least third and fourth mature male pereopods differentiated

2101 2102 2103 2104 2105	2' Dactylus of fifth pereopod with fewer than 15 spiniform setae, not comb-like; mature male pereopods not differentiated; rostrum reduced, not serrated
2106 2107 2108	3(2) Rostrum long or very short, but always with dorsal teeth; in mature males, only third and fourth pereopods differentiated; endopod lamina of first male pleopod apically strongly lobate
2109 2110 2111 2112 2113 2114 2115 2116	 3' Rostrum very short and not serrated; in mature males, apical parts of third, fourth and fifth pereopods widened; endopod lamina of male first pleopod apically and obliquely cut and not (or feebly) lobate
2117 2118 2119 2120 2121	 4´ Appendix masculina of male second pleopod nearly twice as long as appendix interna; in adult males, propodi of third and fourth pereopod strongly differentiated Spelaeocaris prasence Sket & Zakšek, 2009 [Bosnia Herzegovina, Montenegro]
2122	Key to species of Palaemon
2123 2124 2125	This <i>Palaemon</i> key it is based on a recent revision (Tzomos & Koukouras 2015) of the freshwater members of the genus in the Mediterranean basin.
2125	
2125	1 Fifth pleuron distal end not rounded
2125 2126 2127 2128	1 Fifth pleuron distal end not rounded
2125 2126 2127 2128 2129	1 Fifth pleuron distal end not rounded
2125 2126 2127 2128 2129 2130 2131	1 Fifth pleuron distal end not rounded 2 1' Fifth pleuron distal end rounded 7 2(1) Fifth pleuron distal end strongly pointed 3 2' Fifth pleuron distal end subquadrate and not pointed 6
2123 2126 2127 2128 2129 2130 2131 2132 2133 2134	 1 Fifth pleuron distal end not rounded

2180	Key to species of <i>Typhlocaris</i>
2175 2176 2177 2178 2179	 8' Telson posterior margin with 4–7 plumose setae; third maxilliped exopod equal or longer than ischiomerus; outer margin of scaphocerite straight
2171 2172 2173 2174	8(7) Telson posterior margin with 10–12 plumose setae; third maxilliped exopod shorter than ischiomerus; outer margin of scaphocerite concave
2166 2167 2168 2169 2170	 7(1') Telson posterior margin with 4–12 plumose setae
2161 2162 2163 2164 2165	6' Telson posterior margin with 4–6 plumose setae; endopod of male first pleopod clearly shorter than the exopod; appendix masculina shorter than the endopod of male second pleopods
2157 2158 2159 2160	6(2') Telson posterior margin with two plumose setae; endopod of male first pleopod almost as long as exopod; appendix masculina longer than the endopod of the male second pleopods
2152 2153 2154 2155 2156	5' Telson with 0–6 pairs of marginal lanceolate setae only on its proximal part; endopod of male first pleopod lightly concave on the mesial portion of inner margin; endopod of female first pleopod lanceolate
2148 2149 2150 2151	5(4) Telson with 40–50 pairs of marginal lanceolate setae; endopod of male first pleopod deeply concave on the mesial portion of inner margin; endopod of female first pleopod with concave inner margin and rounded tip
2143 2144 2145 2146 2147	 4' Telson plumose setae over pass the inner spiniform setae; first maxilliped endites arranged almost in a straight line forming just a notch between them; branchiostegal tooth marginal
2140 2141 2142	4(3) Telson plumose setae fail to overpass the inner spiniform setae; first maxilliped endites separated with their inner edges forming an obtuse angle; branchiostegal tooth originating just before anterior margin of carapace

2181	The genus Typhlocaris is in	need of a revision as th	e descriptions of the	genus species are based
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2182 mainly on historical papers and the key characteristics are not well defined.

2183

2184 Key to Astacidea families

For the Astacidea we follow the classification of Crandall & De Grave (2017). The reader should keep in mind that some controversary exist on the status and validity of species which is further complicated with the presence of invasive species and the many human translocations of native species.

- 2189
- 2193 Astacidae
- 2194

2203

2195 Key to Cambaridae genera and species

- First pleopod of mature males terminating in two rounded lobes and spiniform structure;
 females with movable annulus ventralis, not fused anteriorly to sternum
 Procambarus clarkii (Girard, 1852)
 [Invasive: Cyprus, Egypt, France, Israel, Italy, Malta, Morocco, Spain, Tunisia]
- 1' First pleopod of mature males terminating in two triangular or elongate lobes; females with
 annulus ventralis fused anteriorly to sternum *Faxonius limosus* (Rafinesque, 1817)
 [Invasive: France, Italy, Spain]
- 2204 Key to Astacidae genera
- 2205 1' Telson without transverse suture Pacifastacus 2206 (One species: Pa. leniusculus (Dana, 1852) 2207 [Invasive in Europe] 2208 2209 2(1) Two pairs of postorbital ridges; first pleopod distal lobes unequal; second pleopod 2210 exopodite length subequal to endopod; third maxilliped merus with one medial spine, 2211 2212 2' Only one pair of postorbital ridges, or (rarely) with extremely reduced second pair; first 2213 pleopod distal lobes subequal; second pleopod exopod length distinctly smaller than 2214
- 2218

2219	3(2) Second to fourth abdominal somites with pleura bearing acute spines; second pleopod with
2220	ventral process (talon) Pontastacus
2221	(one species: Po. Leptodactylus (Eschscholtz, 1823))
2222	[Despis Harrageving Creatic France Crease Italy Typicay]

- 2222 [Bosnia Herzegovina, Croatia, France, Greece, Italy, Turkey]
- 2220

2228 Key to species of Austropotamobius

This *Austropotamobius* key it is based on Souty-Grosset *et al.* (2006) but the reader should keep in mind that this genus is under constant revision. The separation of *A. fulsianus* which was considered a subspecies of *A. pallipes* is not clear. COI gene nucleic acid sequence differences are required to distinguish the two species (*).

- Area behind cervical groove smooth, cervical spines absent; rostral borders triangle; chelae
 surface granulation very strong and rough; lower surface of antennal scale with denticulation
 Austropotamobius torrentium (von Paula Schrank, 1803)
 [Italian and Balkan Peninsulas]
- (Lerebounet, 1858) species complex (A. paup
- 2242

2233

2243 Key to species of Astacus

The key of *Astacus* is based on Storobogatov (1996). There is controversy whether *A. balcanicus* is a species or a subspecies of *A. astacus*.

2246

- 2254 groove Astacus astacus (Linnaeus, 1758)
 - 2255
 - 2256 **REFERENCES**

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2344 **5. Malacostraca: Ingolfiellida**

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2348

2349 INTRODUCTION

Since their first discovery by Hansen at the beginning of the 1900's (Hansen, 1903) and until recently, Ingolfiellids had been considered as a suborder of Amphipods. Several authors objected, and Lowry and Myers (2017) proposed to raise Ingolfiellids to the order status only recently, after a large revision of Amphipoda. This Ingolfiellida order is a sister group of Amphipoda characterized by the lack of a carapace and coxal gills and the presence of vestigial pedunculate eyes ("eye-stalks" noticed by Hansen), a pleosome composed of six segments devoid of epimera, and reduced pleopod/uropod appendages.

This small order remains largely unknown and includes only two families – Ingolfiellidae (51 species) and the very rare Metaingolfiellidae (one species) –, among which 20 are present in freshwaters (Horton et al., 2020). Species of this group are known on all continents and confirm that Ingolfiellida is a very old lineage that emerged around the Triassic Pangea (237 Mya) and diversified in interstitial freshwaters before further colonizing brackish and marine environments following evolutionary processes (Vonk and Schram, 2003).

The presence of the sole representative of Metaingolfiellidae – *Metaingolfiella mirabilis* – in Italy and species of the *Ingolfiella* genus with ancestral morphological characteristics (Vonk and Schram, 2003) suggests ancient colonization of the Mediterranean basin by species of this order. The two Ingolfiellida families are present in this region and are represented by 9 species belonging to two genera (*Metaingolfiella* and *Ingolfiella*) that represent 45% of the total number of known freshwater Ingolfiellida.

2369

2370 GENERAL ECOLOGY AND DISTRIBUTION

Their ecology remains almost unknown, and most of the species are know from only one specimen (Vonk and Jaume, 2013). Despite a wide distribution in fresh and marine waters, a few species have a euryhaline distribution, and only *Ingolfiella manni* was observed both in fresh and brackish water environments in Chile.

Despite the small number of known species, Ingolfiellida are one of the most widespread groups in the crustacean world and have colonized an exceptional diversity of groundwaters and interstitial habitats ranging from deep sea water (-3,521 m on the deep sea bottom for *Ingolfiella abyssi*) to the top of mountainous freshwater streams (2,000 m asl. in the Andes Mountains for *Ingolfiella uspallatae*).

All Mediterranean species are distributed among the northern countries located between Spain and Greece. They have been found either in river sediments (*I. catalanensis, I. macedonica, I. thibaudi* and *I. vandeli*), or in wells (*M. mirabilis, I. acherontis, I. petkovskii*), and caves (*I. cottarellii, I. beatricis*). The distribution of many species is restricted to a very small area, and

- 2384 several species are known only from one river or one well.
- 2385

2386 TERMINOLOGY AND MORPHOLOGY

2387 Ingolfiellida are small/medium-sized Malacostraca ranging from 1.5 up to 23 mm in length worldwide but less than 2.5 mm in the Mediterranean basin, except M. mirabilis which can 2388 reach 18.7 mm. Females are generally larger than males (when they are known). Their body is 2389 2390 vermiform and adapted to life in interstitial environments such as those of bathnynellacean and bogidiellid amphipods. Their body is divided into 13 segments, which can be grouped into the 2391 head, the mesosome, the metasome, and the urosome (Fig. 7.10). The cephalothorax is 2392 composed of the head fused either with the first segment of the mesosome for Ingolfiellidae or 2393 with segments 1 and 2 of the mesosome for Metaingolfiellidae (Fig. 7.10). Their general 2394 morphology is similar to that of Amphipoda (cf. section Amphipoda of the book). However, 2395 Ingolfiellida differ from Amphipoda by the absence of eyes in all species. A vestigial 2396 pedunculate eye can be present is many Ingolfiellid species but is rarely observed in European 2397 species. Mouthparts are also similar, but the maxilliped does not have the ischial endite (outer 2398 plate). The shape of their gnathopods strongly differs from the shape of Amphipoda 2399 gnathopods: the "hand" of their gnathopods is formed by the 5th article (carpus) and the "finger" 2400 consists of two articles (propodus and dactyl) instead of one, whereas the "hand" of Amphipoda 2401 gnathopods consists of the 6th article (propodus) and the "finger" corresponds to the sole dactyl. 2402 2403 Their mesosome also differs by the absence of coxal gills on their percopods, unsegmented and 2404 uniramous pleopods and the absence of epimera on their urosome.

2405

2406 COLLECTION, PREPARATION, AND IDENTIFICATION

Ingolfiellida are distributed worldwide but are very rare locally. In the Mediterranean basin, all
species are obligate groundwater species and can be sampled using any kind of sampling
method adapted to hypogean species. Several kinds of specific materials (pumps, nets, traps)
for this environment can be used (Malard et al., 2002).

- Ingolfiellida can be easily fixed and preserved in 70% ethanol or another fixative formorphological analysis, and in 95% ethanol for genetic analysis.
- The family and the genera can be identified under a stereomicroscope, but identification at the 2413 species level requires dissection, mounting of body parts and appendages on slides, and 2414 subsequent examination using a 400x or higher-magnification microscope. Specimens kept in 2415 glycerol or ethanol can be handled under a low-power microscope with needles. Glycerol is 2416 used as an embedding medium for short-term slides. Baths in clearing solution (e.g. soft acids) 2417 2418 or permanent mounting media are only required when depositing museum specimens. The same specimen can be used for both studies: the abdomen for DNA extraction and the other parts for 2419 dissection and mounting. This procedure ensures that the sequenced genes correspond to the 2420 2421 same morphotype.

Taxonomic identification at the species level is generally possible using males, but only females
are known for some species (*I. acherontis*, *I. beatricis*, *I. macedonica*). The most important
body parts for identification are the head, mouthparts, gnathopods, pleopods and uropods.
Additional body parts need to be examined to identify certain species.

2426

2427 LIMITATIONS

The key below is designed to cover all currently recognized freshwater ingolfiellid species of the Mediterranean basin. Taxonomic synonymy has been updated. Rare records are included,

2430 2431 2432 2433 2434 2435 2436	unless they are insufficiently documented. For example, <i>Ingolfiella (Balchanella) acherontis</i> is included in the key, but it is not clearly described and its identification key should be used with caution. Species-specific secondary sexual characteristics (modified gnathopods or uropod 2, oostegites, etc), are important for the taxonomy of Ingolfiellida but limited because several species are only known based on one sex (male or female). Another limitation of the key is that most species are only known from a small number of specimens, so that intraspecific variability generally remains unknown.
2437	
2438	KEY TO ORDER INGOLFIELLIDA
2439	Key to Amphipoda families
2440 2441 2442	1 Cephalothorax composed of head and first and second segment fused together; uropod 3 peduncles of right and left uropods fused together
2443 2444	1' Cephalothorax composed of head and first segment fused together; uropod 3 peduncles free
2445 2446	Key to species of Ingolfiella
2447	1 Cephalic ocular lobes developed
2448 2449	1' Cephalic ocular lobes absent
2450 2451	2(1) Gnathopods 1 and 2 with 4 denticles on posterior margin of dactylus
2452 2453 2454	2' Gnathopods 1 and 2 with 3 denticles on posterior margin of dactylus
2455	3(1') First pereonite (second thoracic segment) free
2456 2457	3' First pereonite (second thoracic segment) fused to cephalon <i>I. vandeli</i> Bou, 1970
2458	4(3) Maxilla 1 palp sub-equal to outer lobe, inner lobe with 1 or 2 setae
2459 2460 2461	4'Maxilla 1 palp longer than outer lobe, inner lobe with 3 setae
2462 2463	5(4) Maxilla 1 inner lobe with 2 setae; gnathopods 1 and 2 with 3 denticles; pleopods 1-3 absent in females
2464 2465 2466	5' Maxilla 1 inner lobe with one seta; gnathopods 1 and 2 with 4 denticles on posterior margin of dactylus, pleopods 1-3 present in females <i>I. macedonica</i> S. Karaman, 1959
2467 2468	6(5) Uropod 1 outer ramus less than half of inner ramus length; uropod 2 longer than uropod 1; pereopod 3-4 claw simple

 6' Uropod 1 outer ramus more than half of inner ramus length; uropod 1-2 3-4 claw dentate or bifid <i>I. catalan</i> 	sub-equal; pereopod aensis Coineau, 1963
 2472 7(6) Antenna 1 accessory flagellum hardly longer than the first article 2473 peduncle uropod 2 with 6-7 rows of setae	es of the flagellum; /igna Taglianti, 1989
 2475 7' Antenna 1 accessory flagellum longer than the two first articles of the uropod 2 with 5 rows of setae	flagellum; peduncle <i>baudi</i> Coineau, 1968
2477	

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2493 6. Malacostraca: Isopoda

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2501

2502 INTRODUCTION

Isopoda Latreille, 1817 are a very diverse order both in the number of species and in their morphology. About 10% of all isopods – more than ten thousand described species – live in continental waters, mostly in groundwater (Wilson 2008). They are easily recognizable in the field from their typical dorsally and ventrally flattened body shape, even if some groups of groundwater isopods (e.g. Microcerberidae) differ from this general habitus with a more or less thin and vermiform body.

Biogeographic analysis indicates that isopods, like Amphipoda, were likely widespread in 2509 Pangea, Gondwana, and Laurentia (Wilson 2008). Freshwater colonization by isopods likely 2510 2511 resulted from successive events, with the oldest events occurring during the Palaeozoic period (540-250 Mya) and involving ancestors of a few Asellota families and the entire suborder 2512 Phreatoicidea (not present in the Mediterranean basin nowadays). The most ancient fossil 2513 records - Hesslerella shermani, a Phreatoicidea - dates back to 307 Mya (Schram, 1970). This 2514 hypothesis is congruent with molecular studies suggesting diversification events in freshwaters 2515 400 to 500 Mya (Lins et al., 2012). 2516

Among the 1,000 species described in freshwaters, 336 are present in the Mediterranean basin. The main taxonomic groups are Cirolanidae (8 genera), Asellidae (5 genera), Stenasellidae (5 genera), and Sphaeromatidae (5 genera). A few taxa belonging to Janiridae, Lepidocharontidae, Microcerberidae and Microparasellidae are also present (Boyko et al. 2008).

2522

2523 GENERAL ECOLOGY AND DISTRIBUTION

Mediterranean freshwater isopods inhabit streams, rivers, ponds, lakes, and temporary pools 2524 where they can be found on the substrate or in the interstitial systems beneath the river bed 2525 (hyporheon). Most of the 299 described species are obligatory inhabitants of groundwaters 2526 (stygobionts), found in caves or other habitats where subterranean waters flow through; they 2527 are strictly endemic. Some taxa inhabit thermal waters (Rogers & Lewis 2019). Only the 2528 epigean genus Proasellus (Asellidae) is widely distributed along the entire Mediterranean 2529 basin; one species -P. *coxalis* - is represented by various subspecies whose taxonomic rank 2530 should be accurately revised. 2531

The suborder Asellota includes the highest number of described freshwater species, mostly in the Asellidae and Stenasellidae families. Out of the five genera composing Stenasellidae, which are all strictly subterranean without any epigean relative, *Stenasellus* has the widest distribution: it is present in the groundwaters of the Far East, Middle East, East Africa and the western Mediterranean basin, showing a biogeographic pattern linked to the ancient Thetys sea (Henry & Magniez 1983, Messana et al 2019). Some genera are much diversified but geographically restricted, e.g. *Bragasellus* (20 species), *Synasellus* (35 species), both restricted to the Iberian Peninsula. The janirid *Jaera sarsi*, originally from the Ponto-Caspian fauna but widely distributed in Western Europe has been included, even if it is invasive and present only in the largest rivers.

The five genera of the 'Flabellifera' *sensu lato* group (e.g. Cymothoidea and Sphaeromatidea) 2542 present in the Mediterranean basin are the result of multiple colonizations of continental 2543 groundwater habitats (Thalassostygobionts) during several ancient marine ingressions (Baratti 2544 et al. 1999, Wilson 2008). The genus Sphaeromides has a north Mediterranean distribution, 2545 Typhlocirolana a south-western one, while Turcolana has an eastern one. Botolana and 2546 Moroccolana are confined to Moroccan groundwaters with a strict relationship with 2547 Typhlocirolana, while Faucheria and Kensleylana are found in the groundwaters of southern 2548 France and the northern Iberian Peninsula, respectively. 2549

The subterranean taxa are represented by several mostly scavenger or omnivorous taxa, with a carnivorous tendency. Epigean taxa feed on the periphyton or on detritus.

2552

2553 **TERMINOLOGY AND MORPHOLOGY**

Freshwater taxa include the typical dorso/ventral flattened isopods or narrow-bodied forms, and a few vermiform ones (Fig. 7.11). Adaptations mostly depend on colonized habitats.

Epigean species are variously pigmented, while their subterranean counterparts are unpigmented and whitish. Likewise, eyes are present in the surface species and vary from reduced to completely absent in subterranean species.

The body is composed of three main sections (Fig. 7.12). In epigean taxa, the globular head (cephalon) has a couple of big composed dorso-lateral sessile eyes and two pairs of unramous antennae (A1 and A2); antenna 2 bears a rudimental exopodite (squama) in the more primitive taxa. The mouthpart is on the ventral surface of the head and is composed of the labrum, labium, mandibles, maxillae I and II, and maxilliped. The first thoracic segment is always fused to the cephalon and bears a couple of modified legs (maxillipeds).

The thorax (or pereon) is formed of 7 very similar thoracic metamers (2 to 8) bearing 2566 seven pairs of walking legs (percopods). The first pair is usually modified for grasping in most 2567 species. A couple of genital openings are present on the sternal face of pereionite 7 in males 2568 (genital papillae) and 6 in females. The abdomen (pleon) has 6 well-developed segments. The 2569 first 5 segments are usually free, the sixth one is fused to the telson to form a pleotelson. The 5 2570 couples of appendices (pleopods) are biramous and mostly identical in the two sexes. Their 2571 rami have a respiratory and potential swimming role. The second pair of pleopods is modified 2572 into a copulatory organ in males (Fig. 7.13), to transfer sperm to the female genital opening. It 2573 has a unique construction in each species, and is frequently surrounded by accessory processes. 2574 The identification of most Isopoda, particularly Asellota, relies on the examination of this 2575 structure. The sixth pair (uropods) is variously modified in the diverse taxa. 2576 2577

Fertilized eggs develop in a ventral marsupium of the female, formed by the imbrication of lamellae originating from the coxopodites of pereiopods: the oostegites. Isopoda have a typical biphasic moulting: the rear part of the body moults before the anterior part.

2582 COLLECTION, PREPARATION, AND PRESERVATION

2583 Collection methods vary depending upon the habitat. For surface and cave species, small hand nets with an appropriate mesh dimension or baited traps can be used. For interstitial 2584 hyporheic taxa, the most effective methods are the Bou-Rouch pump and the Karaman-2585 Chappuis method (Malard et al. 2004). Isopods can be easily fixed and preserved in 70% 2586 ethanol or another fixative for morphological analysis and in 95% ethanol for molecular 2587 analysis. If many specimens are taken, ethanol should be replaced after a few days to prevent 2588 dilution by the animal's body water content. For conservation purposes, an ethanol (70/75°) 2589 plus a 5% glycerol mix is best suited to avoid articulations hardening, and also avoids accidental 2590 desiccation. 2591

2592 Specimens are best examined and viewed under low magnification for family or sometimes genus level identification. Species identification requires dissecting various parts of 2593 the body, which can be done by handling the specimen with fine forceps and pins. The simplest 2594 procedure consists in transferring the appendages into a drop of glycerin on a microscope slide. 2595 To see the fine details in heavily chitinized specimens, a semi-permanent slide with a clearing 2596 liquid such as Hoyers medium can be prepared (the slide should stay a few days at 35°C and 2597 2598 then the cover should be sealed). Once dissected, the specimen is ready for examination, which 2599 may require a magnification of 100/1,000x for detailed examination depending on the size of the specimen. Scanning electron microscopy (SEM) observation is the best examination tool 2600 for fine details. 2601

2602

2603 LIMITATIONS

2604 Isopoda are a much diversified group of taxa with almost 1,000 known freshwater species, and many more that remain undescribed. The keys proposed here are designed to cover the four 2605 sub-orders, the 8 families and the 33 genera. Oniscidea are not dealt with, although a few aquatic 2606 and several amphibious species are present in the Mediterranean basin. Keys at the species level 2607 are only provided for genera with a low number of species (usually less than 15). Rare records 2608 are included, unless they are insufficiently documented. Taxonomic synonymy has been 2609 2610 updated, but taxonomy remains unclear for some genera. However, several cirolanid, sphaeromatid and asellid genera are badly described and need revision. As a consequence, some 2611 family, genus and species names may change in the future. 2612

Finally, even if our keys were designed to be as clear as possible, we should never forget that identifying certain groups, especially groundwater species, can be very difficult and requires strong expertise. Do not hesitate to use alternative information or keys to consolidate your conclusions. We should keep in mind that keys, even at the family level, are designed for species of the Mediterranean basin, they are not adapted to other isopods worldwide.

- 2618
- 2619

2620

KEYS TO ISOPODA

2621		
2622	Key to Isopoda suborders and Families	
2623	1 Uropods styliform, inserted terminally on pleotelson	. 2
2624	1' Uropods lamellar, inserted at pleotelson base	. 8

2625 2626 2627	2(1) Antennules normal, or if reduced not minute; pleon variable, with or without fused pleonites
2628 2629	2' Antennules vestigial, minute; pleon always of 5 free pleonites, plus the pleotelson
2630 2631 2632 2633 2634	3(2) One or two, free pleonites; body length variable; antenna peduncle usually with a scale; antennule rarely reduced, peduncle and flagellum distinct; maxilliped almost always with coupling setae on endite; female pleopod 2 uniramous; male pleopod 2 endopod large and geniculate
2635 2636 2637 2638 2639	3' Two long pleonites, and a pleotelson, all cylindrical; body length at least six times width; antenna peduncle without a scale; antennule reduced, peduncle indistinguishable from flagellum; maxilliped without coupling setae on endite; female pleopod 2 biramous; male pleopod 2 endopod not geniculate; interstitial
2640 2641	4(3) Two free pleonites
2642	4' One or zero free pleonites
2643 2644 2645	5(4) Antenna 2 with an exopod; pleonite 1 and 2 wide, pronounced in dorsal view; pleopods 2 bi-articulated Stenasellidae
2646 2647	5' Antenna 2 without exopod; pleonite 1 and 2 short and narrow, not pronounced in dorsal view; pleopods 2 with one article
2648 2649 2650	6(4') Pleotelson lateral margins parallel; uropods longer than pleotelson; body elongate, length at least 6 times width
2651 2652	6' Pleotelson lateral margins converging; uropods shorter than pleotelson; body broad, length less than four times width Janiridae (one genus: <i>Jaera</i>)
2653 2654 2655	7(6) Uropods biramous, large; antennal podomeres shorter than flagellum; rostrum small or absent Lepidocharontidae (one genus: <i>Microcharon</i>)
2656 2657	7' Uropods uniramous; antennal podomeres longer than flagellym; head with prominent rostrum
2658 2659	8(1') Uropods not modified as a ventral operculum9
2660 2661 2662	8' Uropods modified as opercula, covering the entire pleopodal chamber; males with penes arising on sternum of pleonite 1, or on articulation between pereonite 7 and pleonite 1; mandibular molar process a stout, flattened grinding structure
2663	

2664 2665	9(8) Uropods articulating mediolaterally; pleon dorsally with four or five free pleonites plus the pleotelson Cymothoida (one family: Cirolanidae)
2666 2667 2668	9' Uropods, particularly the peduncle/protopod, articulating dorsoventrally; pleon dorsally with four or fewer free pleonites plus the pleotelson
2669	
2670	Key to Asellidae genera
2671	1 Coxae not obscured by pereonite, visible dorsally
2672 2673	1' Coxae reduced not visible dorsally Bragasellus [Iberian Peninsula]
2674 2675	2 Pleopod 1 peduncles fused at base on at least 20%
2676	2' Pleopod 1 peduncles free attached by at least 2 coupling hooks4
2677 2678 2679	3 Mandibular palp absent Synasellus [Iberian Peninsula]
2680 2681 2682	3' Mandibular palp present Chthonasellus (one species: C. Bodoni Argano & Messana, 1991) [Italy]
2683 2684 2685	4 Pleopod 2 endopod with basal spur and pronounced basal apophysis
2686 2687	4' Pleopod 2 endopod without basal spur and without pronounced basal apophysis Proasellus
2688	[Peri-Mediterranean]
2689	
2690	Key to species of Jaera
2691 2692	1 Maxilliped palp article 2 wider than long; uropod exopodite and endopodite well developed, overlapping more than a half of the propodite
2693 2694	1' Maxilliped palp article 2 almost as long as wide; uropod exopodite and endopodite minute, not overlapping a half of the propodite width
2695 2696	2(1) Pleopod 1 δ praeoperculum narrow and pointed
2697	2' Pleopod 1 👌 praeoperculum T-shaped J. italica Kesselyak, 1938
2698 2699 2700	3(2) Pereopods 1 and 7 not sexually dimorphic; pleopods 1 praeoperculum wider at its distal end

2701	3' Pereopod 1 and 7 sexually dimorphic; pleopods 1 praeoperculum restangular		
2702 2703 2704	(super-species including 3 sub-species <i>J. n. nordmanni</i> , <i>J. n. balearica</i> , <i>J. n. brevicaudata</i> not included in this key)		
2705 2706	Key to Microparasellidae genera and species		
2707 2708	1 Somite lateral margins with denticles		
2709 2710 2711	1' Somite lateral margins smooth		
2712 2713	2(1) Uropods visible dorsally		
2714	2' Uropods not visible dorsally		
2715			
2716 2717	3(2) Pleopod 1 \circlearrowleft sub-triangular distally; transverse section of the pleotelson ovoid		
2718 2719	3' Pleopod 1 ♂ rounded distally; transverse section of the pleotelson sub-circular		
2720 2721 2722	4(3') Lateral expansion of the first thoracic segment lacking; uropods exopodite reduce, scale like		
2723 2724	4'. Lateral expansion of the first thoracic segment present; uropods exopodite developed 		
2725			
2726	Key to Stenasellidae genera and species (except Stenasellus)		
2727	1 Body thinner than the preceding; uropods longer than 1/3 of Pleotelson		
2728 2729 2730	1' Body short, length around 2.5 width; uropods short, less than 1/5 of Pleotelson 		
2731 2732 2733	2(1) Pleopod 2 endopodite ♂ composed by two article free, the proximal well developed, the distal never jointed on its internal margin		
2734 2735 2736	2' Pleopod 2 endopodite d' composed by two articles fused, proximal article very small, the distal furrowed <i>Metastenasellus</i> (one species: <i>M. leysi</i> Magniez, 1986) [Algeria]		
2737 2738	3(2) Pleopod 1 👌 propodite subquadrangular and well developed, exopodite flat		

2739 2740 2741 2742	3' Pleopod 1 d exopodite externally curved
2743 2744 2745 2746 2747	4(3) Pleopod 2 endopodite ♂, distal article as a flat oval lamina, with a similar external appendix; pleopod 1 ♂ sympodite without coupling hooks
2748 2749 2750 2751	4'. Pleopod 2 endopodite \Diamond , distal article long and thin, longitudinally folded with proximally divergent margins, sometimes distally fused; pleopod 1 \Diamond sympodite with or without coupling hooks
2752	
2753	Key to species of Stenasellus
2754	1 Pleopod 2 $\stackrel{\scriptstyle ?}{\scriptstyle \bigcirc}$ endopodite, proximal article of the long and thin
2755	1' Pleopod 2 $^{\wedge}$ endopodite, proximal article short and stubby
2756	
2757 2758 2759	2(1) Pleopod 1 3 protopodite without coupling hooks or with simple seta; pleopod 2 3 endopodite almost isodiametric with a large and denticulate terminal part; pleopods 4 and 5 exopodites ovoids, larger than endopodite
2760 2761 2762 2763	2' Pleopod 1 \circ protopodite with coupling hooks; pleopod 2 \circ endopodite, distal article fusoïd with acute apex; distal article of exopodite medially bented and bearing about 15 marginal setae; pleopods 4 and 5 exopodites varying from large and lamellar to thin or styliform
2764 2765	3(2) Pereopod 1 propodite robust
2766	3' Pereopod 1 propodite thin and fragile
2767	
2768 2769	4(3) Pleopod 2 sympodite subquadrangular, endopodite distal article falciform with about 20 sternal setae
2770 2771	4' Pleopod 2 sympodite subpentagonal, endopodite distal article strong with a disto-externak expansion
2772 2773	5(4) Pereopods 2-7 dactyli with one sternal spine S. escolai Magniez, 1977
2774	5' Pereopods 2-7 dactyli with two sternal spines S. magniezi Escola, 1975
2775	
2776 2777 2778	6(4') Pleopod 2 d exopodite subovoid with 7 distal marginal plumose setae, endopodite distal article with a disto-external rounded expansion bearing 4 tiny spines
--------------------------------------	--
2779 2780 2781	6' Pleopod 2 ♂ exopodite rounded with 18 distal marginal plumose setae, endopodite distal article with an external expansion bearing 8 spines and an internal lobe covered by tiny setae
2782 2783	7(2') Pleopod 2 \bigcirc endopodite distal part stretched but not as an elongated beak
2784	7' Pleopod 2 💍 endopodite distal part stretched as an elongated beak S. buili Remy, 1949
2785 2786 2787	8(7) Pleopod 5 exopodite large almost totally covering endopodite and distally rounded
2788 2789	8' Pleopod 5 exopodite styliform, 5-6 times longer than large, always thinner than endopodite
2790 2791 2792	9(1') Pleopod 2 ♂ distal article almost isodiametric, with an obtuse ending and a large terminal orifice, distal external part more or less pointed <i>S. nuragicus</i> Argano, 1968
2793 2794	9' Pleopod 2 🖒 distal article almost isodiametric, with an obtuse ending and a large terminal orifice, distal external part large
2795 2796	Key de Cirolanidae genera
2797	1 Eyes absent
2798 2799	1' Eyes minute; body length 5 mm Saharolana (one species: S. seurati Monod, 1930) [Tunisia]
2800 2801 2802	2(1) Pleotelson completely fused to pleon; uropods with one terminal ramus; body length ≤ 5 mm
2803 2804	2' Pleotelson not as above; five free pleonite; uropods with two terminal rami; body length variable
2805 2806 2807 2808 2809	 3(2) Pleotelson with two sutures visible laterally for the fused segments; uropod peduncle flattened dorsoventrally
2810 2811 2812 2813	3' Pleotelson with only one suture visible laterally; uropod peduncle elongate and cylindrical, with a single, minute ramus
2814	

2815 2816 2817	4(2') Pleonite 5 covered by pleonite 4; body length 1-10 mm		
2818 2819 2820	5(4) Not rolling into a ball; pleopods 1 not forming an operculum; pleotelson somewhat produced		
2821 2822 2823	5' Adapted to roll into a ball; pleopods 1 forming an operculum; pleotelson never produced . 		
2824			
2825	6(5) Cephalon not laterally overlapped by pereonite 1		
2826 2827 2828	 6 Cephalon posterior 50% embraced by pereonite 1; body length 7 mm Marocola (one species Ma. delamarei Boutin, 1993) [Morocco] 		
2829	7(6) Chronic not projecting algority 5 evenlaged by plaquity 4		
2830	7(6) Crypeus not projecting; preomte 5 overhapped by preomte 4		
2831 2832 2833	(one species: <i>Me. ponsi</i> Jaume & Garcia, 1992) [Spain]		
2834 2835 2836 2837	8(7) Uropod rami dorsoventrally flattened, triangular, subequal in length to peduncle, and shorter than pleotelson		
2838	8' Uropod rami subcylindrical, styliform, length/width 1.5x peduncle, longer than pleotelson .		
2839 2840 2841			
2842			
2843	Key to species of Sphaeromides		
2844	1 Pleonite 3 wider than others		
2845	1' Pleonite 3 not wider than the others		
2846			
2847	2(1) Fifth antennal article with straight margins S. bureschi Strouhal, 1963		
2848	2' Fifth antennal article with inflate margins S. polateni Angelov, 1968		
2849 2850	3(1') Pleotelson apex truncate		
2851	3' Pleotelson apex acute		
2852			

2853	Key de Sphaeromatidae genera and species (except Monolistra)			
2854	1 Pleopod 4 and 5 endopods smooth lacking pleats or fold			
2855 2856	1' Pleopod 4 and 5 endopods with pleats or fold			
2857	2(1) Pleotelson preceded by two or more pleonites fused at least dorsomedially			
2858 2859 2860	2' Pleotelson preceded by two free and articulated pleonites			
2861 2862	3(2) Uropod short, around 0.25x the pleotelson length <i>Merozoon vestigatum</i> Sket, 201 [Croatia]			
2863 2864 2865	3'Uropod length around 0.5x pleotelson length 4 (<i>Caecosphaeroma</i>) [France]			
2866 2867	4(3) All pleonite fused with telson; pleopods short; uropod short, exopodite distinct			
2868 2869 2870	4' First pleonite partially free; pleopod well developed; uropod reduce scale like, exopodite not visible <i>C. burgundum</i> (<i>Vireia</i>) <i>burgundum</i> Dollfus, 1898			
2871 2872 2873	5(1') Maxilliped articles 2-4 lacking lobes, inferior margins with dense fringes of plumose setae 			
2874 2875 2876 2877	5' Maxilliped articles 2-4 more or less lobed, inferior margins with simple setae only 			
2878	6(5) Pereopod 1 propodus with few to many distal setae next to rostrodistal spine			
2879 2880 2881	6' Pereopod 1 propodus without distal setae next to rostro-distal spine			
2882 2883	7(6) Pereopod 1, setae on ischium and merus smooth or sparsely plumose only on their dist part			
2884 2885	7' Pereopod 1, setae on ischium and merus entirely plumose, ending with long setules on their distal part <i>L. monodi</i> (Arcangeli, 1934)			
2886				
2887 2888 2889	8(7) Pereopod 1 propodus with more than 3 setae inserted distally in transverse row next to rostro-distal spine. Antenna flagellum articles with fringe of long setae at distal interior angle seta 2-3 times length of article			
2890 2891 2892	8' Pereopod 1 propodus with 2-3 setae inserted distally in transverse row next to rostro-dista spine. Antenna flagellum articles with fringe of few short setae, seta 1.5 times length of articl			

- 2899 *L. panousei* (Daguerre de Hureaux, Elkaïm & Lejuez, 1964)
- 2900

2901 Key de Microcerberidae genera and species

- 2902 1 Coxae of pereiopods 2-4 ring-shaped; male pleopod 2 with saber-shaped endopod with
 2903 pointed and laterally curved apex; Pleopod 4 with elongate sympod, with 3 rami of similar
 2904 size, only proximally covered by pleopod 3...... *Microcerberus stygius Karaman, 1933*
- 2905 1' Coxae of pereiopods 2-4 more or less pointed; male pleopod 2 with elongate rectangular sympod, tiny rounded exopod, and apically bifid; Pleopod 4 well covered by pleopod 3, biramous, without articulations *Coxicerberus ruffoi* (Chappuis, 1953)
- 2908

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2934 7. Malacostraca: Mysida and Stygiomysida

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2938

2939 INTRODUCTION

2940 Mysida

Peracarid crustaceans of the order Mysida are recognizable by their shrimp-like habitus, by 2941 2942 separate, stalked eyes, fused cephalothorax, well-developed carapace and tail fan, by swimming and respiratory currents driven by rotating movements of their thoracic exopods, and by the 2943 2944 absence of gills and of true chelae. The author's own global census (19 Feb. 2021) yielded a total of 178 genera and 1,190 species considered valid. Doubtful cases excluded, an additional 2945 three genera and nine species are known from the Miocene down to the Triassic (Voicu 1974; 2946 2947 San Vicente & Cartanyà 2017). The main taxonomic groups are the family Petalophtalmidae with the subfamilies Petalophthalminae and Hansenomysinae, and the family Mysidae with ten 2948 subfamilies, namely Boreomysinae, Erythropinae, Gastrosaccinae, Heteromysinae, 2949 2950 Leptomysinae, Mysidellinae, Mysinae, Palaumysinae, Rhopalophthalminae, and Siriellinae.

Most extant species inhabit marine waters of all major sea basins from the shore down to 2951 the deep sea, usually with greatest species diversity in sublittoral habitats. Most marine and 2952 freshwater species live on or closely above the bottom, often in swarms; a few are pelagic. 2953 Some species burrow just below the sediment surface, others are associated with benthic 2954 2955 invertebrates. Many species hide during the daytime and emerge at night to feed, mate, moult, and release young. Most species are omnivorous, some are micro-phytophagous, saprophagous, 2956 or carnivorous; none is parasitic. Dense populations can have marked effects on near-bottom 2957 plankton communities. High individual densities occur in turbid, meso- to oligohaline waters 2958 of lagoons and estuaries. Such habitats can provide main pathways for immigration and 2959 adaptation to freshwater. Quantitatively less important pathways involve marine and brackish 2960 groundwater. Reddell (1981) assumes a marine origin of the troglobitic mysids (i.e. 2961 Stygiomysida and Mysida) of Mexico, mainly found in brackish groundwater, less frequently 2962 in fresh groundwater. Such a distribution also holds true for the two Mediterranean 2963 Stygiomysida species (see below); however, the only troglobitic Mysida species (Troglomysis 2964 2965 vjetrenicensis) of the Mediterranean lives exclusively in fresh groundwater.

A total of 26 genera and 75 species of Mysidae (and no Petalophthalmidae) are recorded in freshwater globally, in part based on single freshwater records of euryhaline species. Within Mysidae, as many as 71 species belong to the subfamily Mysinae, two to Leptomysinae (*Americamysis almyra* and *Tenagomysis chiltoni*), one to Heteromysinae (*Deltamysis holmquistae*), and one to Rhopalophthalminae (*Rhopalophthalmus chilkensis*). The remaining six subfamilies have not been recorded in freshwater.

The bulk of freshwater records includes 24 Ponto-Caspian endemics, followed by 12 species from Amazonia and adjacent freshwater systems, nine Mexican, Central American and Caribbean endemics, nine boreo-arctic species including extrazonal glacial relicts, and six Mediterranean endemics.

Including species of NE-Atlantic and Ponto-Caspian origin, ten species (adult body size
 3–13 mm) have been recorded in Mediterranean freshwaters so far: all belong to the subfamily

Mysinae within the family Mysidae. Among these, four Mediterranean endemics are restricted to freshwater, and two other endemics occur in fresh as well as brackish water. Among these six species, as many as four are stenoendemic in the Adriatic Sea, another one in the Eastern Mediterranean including the Adriatic. The predominance of Adriatic endemics in Mediterranean freshwaters may have been favoured by alternating marine, lagoonary, and terrestrial phases (Correggiari *et al.*, 1996) of the shallow N-Adriatic shelf during Pleistocene sea-level changes.

One brackish to marine NE-Atlantic species of Mysidae (*Neomysis integer*) occurs marginally in freshwaters of the Mediterranean basin. Two freshwater Ponto-Caspian endemics (*Hemimysis anomala* and *Limnomysis benedeni*) have recently expanded to the Rhône Delta on the Mediterranean coast of France. Finally, the details of when and how a third Ponto-Caspian endemic (*Paramysis lacustris*) arrived in an isolated freshwater lake without natural surface drainage in the highlands of Anatolia remain unknown.

2991

2992 Stygiomysida

Two families (Stygiomysidae and Lepidomysidae), only two genera, and 16 species of Stygiomysida are known globally. They show a Tethyan distribution, extending from Central America and the Caribbean to Mediterranean and Indian basins (Porter *et al.*, 2008). Both known Mediterranean species (adult body size 6-13 mm) are stenoendemic in brackish groundwater in SE- Italy and are rarely found there in freshwater.

2998

2999 GENERAL ECOLOGY AND DISTRIBUTION

3000 Stygiomysida

This order is represented by only two species in European waters. Both are stenoendemic of brackish groundwater in SE-Italy and are rarely found in freshwater. Although their eyes are rudimentary, unpigmented, *Spelaeomysis bottazzii* and to a minor extent also *Stygiomysis hydruntina* are not strictly photophobic: the former species is regularly found in the dimly lit zone of wells, where it feeds on photoautotrophic organisms (Ariani & Wittmann 2010).

3006 *Stygiomysis hydruntina* has been reported from a few caves and wells near the Adriatic and 3007 Ionian coasts of the Salento Peninsula (SE-Italy). It occurs mainly in deep brackish 3008 groundwater, rarely in near-surface low-salinity waters. Pesce *et al.* (1978) published three 3009 potential freshwater records without indication of salinity; however, a salinity of "0.3‰" is 3010 labelled on the slide containing parts of a male specimen from station PU/23 (own inspection 3011 of material kept at the Museo Civico di Storia Naturale, Verona). Besides, Pesce *et al.* (1978) 3012 indicated Monte Mario coordinates instead of Greenwich coordinates.

Spelaeomysis bottazzii has been reported from a number of caves, dolinas, wells, and 3013 springs near the Adriatic and Ionian coasts of the Salento Peninsula and from the Adriatic coast 3014 of Apulia (SE-Italy). It occurs in deep brackish groundwater up to various near-surface 3015 mesohaline to anhaline waters (Inguscio 1998). Breeding females are rare near the surface; most 3016 of them probably inhabit deep groundwater for more than three months of incubation. 3017 Laboratory females assume strongly reduced brood lamellae at the moult following incubation. 3018 3019 This is interpreted as a strategy to replenish the trophic reserves required for sustaining a long incubation period in deep and trophically poor groundwater (Ariani & Wittmann 2010). 3020

3021 Mysida

Only ten species have so far been found in true freshwater (0.0–0.5 psu) of the Mediterranean.
The other two species given in the key below are expected but have not yet been recorded there
in freshwater. Only four Mediterranean endemics are restricted to freshwater habitats:

3025 Diamysis lacustris is stenoendemic in Lake Scutari on the SE-coast of the Adriatic Sea, altitude 6 m; Troglomysis vjetrenicensis is stenoendemic in subterranean waters in the 3026 Vjetrenica cave system in Herzegovina, near the E-Adriatic coast, altitude about 224 m; 3027 Paramysis (Longidentia) adriatica is known only from tributaries along the northern and 3028 eastern coasts of the Adriatic Sea, altitude 0-2 m. Paramysis (Serrapalpisis) kosswigi was 3029 reported from Lake Isikli and associated running waters of W-Anatolia draining into the Aegean 3030 3031 Basin, altitude 135–1,007 m; previous records from tributaries of the Black Sea were referred to the sister species P. (S.) lacustris by Wittmann et al. (2016). 3032

An additional Mediterranean endemic, *Diamysis fluviatilis*, occurs mainly in freshwater and to a lesser extent in brackish running waters, wells and estuaries along the northern coasts of the Adriatic Sea, altitude 0–16 m. Freshwater populations of *D. mesohalobia heterandra* are confined to the Adriatic basin, altitude 0–3 m. Nonetheless, many more populations inhabit brackish waters of the E-Mediterranean and Marmora seas.

The Mediterranean endemic *D. hebraica* has not yet been reported from true freshwater. It has been found in three oligohaline streams and their springs on the coast of Israel (salinity 0.7– 5 psu). An occurrence in the anhaline range appears plausible during potential periods of strong freshwater input.

Paramysis (Serrapalpisis) lacustris is indigenous in anhaline to mesohaline waters of the 3042 Ponto-Caspian and Marmora basins. Within the boundaries of the Mediterranean climate, it is 3043 3044 found in the freshwater lakes Kus Gölü and Uluabat Gölü near the southern coast of the Marmora Sea. Material from the isolated freshwater Lake Beysehir in the highlands of Anatolia, 3045 altitude 1,115 m, was described as a separate subspecies, the here not acknowledged Paramysis 3046 lacustris turcica Băcescu, 1948. The hydrological situation is quite complex: according to 3047 Günay (2010), at least part of the runoff enters the Mediterranean catchment through 3048 underground connections. This provides sufficient support for attributing this population to the 3049 Mediterranean fauna. Intensive intentional introductions of P. lacustris were made in the 3050 3051 1960s-1970s in waters of Eastern Europe, wherefrom it established in Lithuania and the Gulf 3052 of Finland (Audzijonytė et al., 2017). Non-intentional expansion occurred from the lower to the middle reach of the Danube River (Borza et al., 2019). If this expansion continues, this 3053 3054 species may follow the below-discussed route to the Mediterranean coast of France.

Two other Ponto-Caspian endemics, *Hemimysis anomala* and *Limnomysis benedeni*, occur mainly in freshwater but have also been reported in brackish waters. They expanded from the Black Sea westward along the rivers Danube, Rhine, Rhône, and their associated artificial canals, and finally southward down to the delta of the Rhône on the Mediterranean coast of France, where they were first detected in 2007 and 2009, respectively (Wittmann & Ariani 2009; Wittmann *et al.*, 2014).

Two indigenous NE-Atlantic species inhabit brackish to marine waters, and marginally also freshwaters. *Neomysis integer* inhabits the Mediterranean coasts of Spain and France, but not elsewhere in the Mediterranean. It occurs marginally in freshwater of the Rhône River delta. *Mesopodopsis slabberi* is present in great numbers in brackish and marine, rarely in metahaline waters of the NE-Atlantic, Baltic, Mediterranean, Marmora Sea, Black Sea, and the Sea of

Azov. The lowest salinities for the Mediterranean (0.9-1.4 psu) were reported in the estuaries 3066 of the Rhône and Po rivers and in a brackish drain in Corfu Island (Pesta 1935; Aguesse & 3067 Bigot 1960; Brun 1967). True freshwater records stem only from the Black Sea coast in waters 3068 of the delta and 'Predelta' of the Danube (Dedju & Polischtuk 1968; Begun & Gomoiu 2007; 3069 Wittmann et al., 2016). Based on studies in Lake Sinoe, a barrier lagoon of the Predelta, Begun 3070 3071 & Gomoiu (2007) concluded that this species is episodically found in freshwater but cannot form stable populations there. M. slabberi was recorded in this lagoon only under oligohaline 3072 conditions (1.1–2.1 psu) upon own sampling in 1985, 1998, and 2008. 3073

3074

3075 TERMINOLOGY AND MORPHOLOGY

The terminology used here is according to Wittmann *et al.* (2016). Only features using standard microscopy without dissection are considered below. Gross morphology and additional features are available in Daneliya *et al.* (2019), with a focus on Ponto-Caspian species.

3079 Among Malacostraca, the orders Stygiomysida and Mysida were formerly lumped together in the order Mysidacea based on their shared separate, stalked eyes at least in 3080 3081 postnauplioid larvae (known so far), a respiratory carapace fused only with anterior thoracic somites, first and second antennae each with a three-segmented trunk, eight pairs of mostly 3082 biramous thoracopods (including maxillipeds), and the absence of gills. To our knowledge, the 3083 inner rami (endopods) are used for feeding and climbing, generally not for walking, and the 3084 outer rami (exopods) for swimming and driving respiratory currents through rotating 3085 movements. Both orders show five pairs of non-respiratory, non-natatory pleopods. A 3086 3087 marsupium is formed by 1-7 pairs of oostegites (marsupial plates) arising as epipods in continuous series, starting with the ultimate thoracopod. The young pass through one embryonic 3088 (egg) and two non-feeding larval stages in the marsupium, where they receive parental care 3089 3090 rather than being merely stored, at least Mysida do so.

Based on genetic analyses, Meland & Willassen (2007) positioned the family 3091 Stygiomysidae closer to Mictacea than to Mysida, and proposed to establish Stygiomysida and 3092 Mysida as separate orders. The post-larval stages of Stygiomysida are distinguished from those 3093 of Mysida by reduced eyes, the presence of a spiny ventral lobe on the endopod of uropods 3094 (Figs. 7.16A,B; together with the telson forming a strong tail fan), by two laminar lobes flanking 3095 the male genital orifice instead of tubular penes, and by the absence of statocysts. All the 3096 Mysida dealt with here belong to the family Mysidae and are characterized by a large statocyst 3097 at the basis of the endopod of uropods. This organ contains one exceptionally large statolith 3098 (Fig. 7.16C) in the animal kingdom. The statoliths of most freshwater species, here represented 3099 by certain species of Hemimysis, Limnomysis, Diamysis, and Paramysis, are opaque because 3100 they are mineralized with vaterite, a metastable form of calcium carbonate. The statoliths of 3101 most marine and brackish-water species, and of just a few freshwater species (dealt with below: 3102 Troglomysis; rare in freshwater: Mesopodopsis, Neomysis) appear transparent and vitreous 3103 because they are mineralized with fluorite (CaF₂). However, statoliths can be damaged and may 3104 3105 even vanish as fixation and preservation artefacts.

Both Stygiomysida species known in the Mediterranean are readily distinguished by body shape (Figs. 7.14, 7.15) and size of the ventral lobe on the endopod of uropods (Figs. 7.16A, B). Careful inspection of antennal scale (Fig. 7.18) and telson (Fig. 7.19) are sufficient for identification of three Mysida species living in freshwaters of the Mediterranean. Among additional features, the strongly reduced, obviously dysfunctional cornea (Fig. 7.20B) is a key feature to identify *Troglomysis*, whereas the structure of the carapace (Fig. 7.20) and of the thoracic exopods (Fig. 7.21) are important diagnostic features for *Diamysis*. For certain *Paramysis*, inspection of the paradactylary setae (Fig. 7.22; modified setae flanking the dactylus
of thoracic endopods 3–8) is necessary for identification.

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3116 COLLECTION, PREPARATION, AND PRESERVATION

Mysids are sampled during day and night with nets operated from the shore, with diver-operated 3117 nets, bottom nets, and epibenthic sledges. Baited bottle traps exposed overnight, and empty 3118 3119 mollusc shells, stones with holes, discarded bottles etc. collected during the day are treated ex situ with a few drops of clove oil to expel the animals. Fixation and preservation are performed 3120 with ethanol 80% for morphological analysis or 95% for genetic analysis. Identification at 3121 species level may require dissection, mounting of body parts and appendages on slides, and 3122 subsequent examination using a 400x or higher-magnification microscope. Specimens in 3123 propylene glycol, glycerol, or ethanol can be handled under a low-power microscope with 3124 needles. Glycerol is used as an embedding medium for short-term slides, particularly for 3125 inspection of mineral statoliths that can be damaged by other media. The water-tolerant Swan-3126 medium makes minute, superimposed objects well discernible owing to its strong bleaching 3127 power. After hardening at 60°C for about 15 h, it requires very careful sealing within about one 3128 month to obtain multi-annual slides. Canada-Balsam requires dehydration in ascending ethanol 3129 3130 series. It is recommended for permanent slides intended for deposition of museum specimens.

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3132 LIMITATIONS

The key below is designed to cover all currently recognized freshwater mysidacean species of the Mediterranean. Rare records are included, unless they are insufficiently documented. Taxonomic synonymy is updated. Secondary sexual characteristics are crucial for the taxonomy of Mysida, but are restricted here in order to obtain a short-cut key applicable to specimens of any sex and stage of maturity (except juveniles in some cases).

Freshwater is defined as water with a salinity range of 0.0–0.5 practical salinity units (psu). Two species occurring in brackish waters of the Mediterranean (but so far recorded only in near but not pure freshwater) are included for potentially prolonging the validity of the key: *Diamysis hebraica* from a documented lowest salinity of 0.7 psu, and *Mesopodopsis slabberi* found at a minimum of 0.9 psu. The latter species repeatedly found in true freshwaters of the Danube Delta along the Black Sea coast but not elsewhere in freshwater.

3144

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The author is greatly indebted to Salvatore Inguscio (Nardò) for providing photos of Stygiomysida. Sincere thanks to Mikhail Daneliya (Helsinki) and to W. Wayne Price (Tampa) for important information about freshwater distribution of mysids.

3149

3151	KEY TO MYSIDA AND STYGIOMYSIDA					
3152						
3153	Key to orders Mysida and Stygiomysida					
3154 3155 3156 3157	1 Endopod of uropods with very large statocyst; sympod without ventral lobe (Fig. 7.16C); cornea mostly well-developed (Figs. 7.17; 7.20A, C–F), rarely reduced (Fig. 20B)					
	(one family: Mysidae)					
3158 3159	1' Endopod of uropods without statocyst; sympod with spiny ventral lobe (Figs.7.16A,B) cornea reduced (Figs. 7.14, 7.15)					
3160						
3161	Key to species of Stygiomysida					
3162 3163 3164 3165	1 Habitus vermiform (Fig. 7.14), resembling the co-occurring thermosbaenacean <i>Monodella stygicola</i> Ruffo, 1949; sympod of uropods with ventral lobe more than half length of unsegmented exopod (Fig. 7.16A)					
3166 3167	(One species: Stygiomysis hydruntina Caroli, 1937) [SE-Italy; mostly in brackish groundwater, occasionally also in freshwater]					
3168 3169	1' Habitus moderately stout, shrimp-like (Fig. 7.15); sympod of uropods with ventral lobe less than 1/4 length of two-segmented exopod (Fig. 7.16B)					
3170 3171 3172	(One species: <i>Spelaeomysis bottazii</i> Caroli, 1924) [SE-Italy; mostly in brackish groundwater, also in freshwater]					
3173						
3174	Key to Genera of Mysidae					
3175	1 Antennal scale setose all around (Figs. 7.18C-H)					
3176 3177	1' Antennal scale with setose margins except for a proximal bare portion of outer margin (Figs. 7.18A,B)					
3178 3179 3180 3181 3182 3183	2(1') Outer margin of antennal scale with smooth portion ending in setae (Fig. 7.18B)					
3184	2' Outer margin of antennal scale with s					
3185						
3186						
3187 3188	mooth portion ending in a tooth (Fig. 7.18A)					

3189 3190 3191 3192 3193	 3(1) Telson entire, slender, subtriangular (Fig. 7.19A)			
3194	3' Telson rhombohedral to subrectangular, with apical cleft (Figs. 7.19B, D–H) 4			
3195 3196 3197	4(3) Telson without median lobe (Figs. 7.19D–H); eyestalks less than three times length cornea (Figs. 7.20C–F)			
3198 3199 3200 3201 3202	 4' Telson with large median lobe emerging from broad apical cleft (Fig. 7.19B); eyestalks a times as long as cornea (Fig. 7.20A)			
3203 3204 3205	 5(4) Apical segment less than 20% antennal scale length; scale terminally broadly rounded both sexes (Figs. 7.18G, H) 			
3206 3207 3208 3209 3210 3211	 5' Apical segment of antennal scale 25–33% of scale length; scale terminally rounded females (Fig. 7.18F), bluntly pointed in males (Fig. 7.18E) <i>Limnomy</i> (One species: <i>L. benedeni</i> Czerniavsky, 1882) [Ponto-Caspian endemic; introduced in Lake Balaton, Lake Aral, and waters Turkmenistan; expansion to large parts of Europe, including the Rhône Delta at Mediterranean coast; mainly in freshwater, also brackish] 			
3212 3213 3214 3215	 6(5) Cornea rudimentary, without pigment (Fig. 7.20B)			
3216	6' Cornea normal, well pigmented (Figs. 7.20 C–F) Diamysis			
3217				
3218	Key to species of <i>Diamysis</i>			
3219	1 Rostrum well rounded or forming a wide convex angle with rounded tip (Figs. 7.20 D–F) 2			
3220	1' Rostrum angular, with acute or narrowly rounded tip (Fig. 7.20 C)			
3222	[freshwater Lake Scutari at the SE-coast of the Adriatic Sea]			
3223				
3224 3225	2(1) Basal plate of thoracic exopods 1–3 terminally ending in a spiniform projection (Fig. 7.21A)			
3226 3227 3228	 2' Basal plate of thoracic exopods 1–3 terminally well rounded (Fig. 7.21B) 			

- 3229 3230 3(2) Rostrum well rounded; male carapace with fringes arranged in only one pair of submedian stripes (Fig. 7.20D); female carapace without fringes 3231 Diamysis fluviatilis Wittmann & Ariani, 2012 3232 [tributaries of the N-Adriatic; mainly in freshwater] 3233 3' Rostrum forms a wide convex angle with rounded tip; male carapace with fringes arranged 3234 in 1-2 pairs of submedian stripes plus a transverse row shortly in front of the posterior 3235 margin (Fig. 7.20E); female carapace without fringes 3236 Diamysis mesohalobia heterandra Ariani & Wittmann, 2000 3237 [Adriatic, Ionian, and Marmora Seas; fresh and brackish waters] 3238 3239 Key to species of *Paramysis* 3240 3241 1' Telson with strong, subrectangular cleft (Fig. 7.19H) 3242 Paramysis (Longidentia) adriatica Wittmann, Ariani & Daneliya, 2016 3243 [freshwater tributaries of the Adriatic Sea] 3244 3245 2(1) Denticulate paradactylary setae of thoracic endopods 5–8 'serrated' only along proximal 3246 50-65% length (Fig. 7.22A); cephalic region swollen (if well preserved) 3247 Paramysis (Serrapalpisis) kosswigi Băcescu, 1948 3248 [freshwaters of W-Anatolia draining into the Aegean Basin] 3249 2' Denticulate paradactylary setae of thoracic endopods 5–8 'serrated' over 70–80% length (Fig. 3250 7.22B); cephalic region not swollen 3251 3252 [expansive Ponto-Caspian endemic, also in (near)-Mediterranean freshwater lakes of 3253 Turkey] 3254
- 3255

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8. Malacostraca: Thermosbaenacea 3312

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3316

INTRODUCTION 3317

Thermosbaenacea Monod 1927 are an obscure group of small crustaceans living in 3318 groundwaters. Their taxonomic position was debated over for a long time before they were 3319 finally classified with Peracarida (see Wagner, 1994 for details). Their small size makes them 3320 difficult to identify in the field, and their elongate vermiform and somewhat dorsoventrally 3321 flattened body makes them look like microisopods or copepods. However, they are easily 3322 3323 recognizable under a stereomicroscope from the presence of an obvious dorsal carapace. They differ from Mysidacea and Decapoda in that they are eyeless and have reduced pleopods present 3324 only on their first two abdominal segments. 3325

The biogeographic origin of Thermosbaenacea still remains to be elucidated because 3326 available information is very scarce. We already know that their distribution area falls within 3327 the boundaries of the ancient Tethys belt, indicating that they may have had a very old ancestor 3328 in the Mesozoic period (252 to 66 Mya), close to Halosbaenidae that are the only known family 3329 distributed worldwide. 3330

3331 However, the diversification process likely occurred in the Mediterranean basin between the marine regression of the late Miocene period and the Messinian salinity crisis (\cong 5.5 Mya) 3332 for the *Tethysbaena atlantomaroccana* group and the marine transgression during the Pliocene 3333 period (2.5-5 Mya) for the Tethysbaena argentarii group (Wagner, 1994). 3334

Among the 40 Thermosbaenacea species recorded worldwide (Horton et al., 2020), less 3335 than 20 occur in freshwaters, among which 12 are present in the Mediterranean basin. A total 3336 of 3 families, 4 genera and 12 species are recorded in the Mediterranean basin, all of them 3337 endemic to the region. 3338

3339

3340 **GENERAL ECOLOGY AND DISTRIBUTION**

Thermosbaenacea are all obligate groundwater species and colonize all types of marine 3341 and continental waters, even if they are always located close to the sea and are more frequent 3342 in marine and brackish waters. Some species can colonize hot water springs; for example, the 3343 type locality of *Thermosbaena mirabilis* has a temperature ranging from 44.5 to 48°C. They 3344 have a strong affinity to low oxygen concentrations and are resistant to high temperatures and 3345 the presence of hydrogen sulfide (H₂S); near-anoxic conditions are even more favourable to 3346 them (Wagner, 2012). They are mainly found is detritus, but likely feed on bacteria and algae 3347 3348 growing on detritus.

3349

TERMINOLOGY AND MORPHOLOGY 3350

Thermosbaenacea are small-sized Malacostraca, generally less than 5 mm long. Their body is elongate, vermiform and slightly flattened dorsoventrally, except *T. mirabilis* whose body is wider and looks like a flabelliform isopod.

Their body consists of a more or less developed carapace, a thorax formed of 8 segments (thoracomeres 1-8), a pleon with generally 6 segments (except Thermosbaenidae whose sixth pleonite is fused with the telson forming a pleotelson) (Figure 7.23).

The cephalic capsule is fused with the thoracic tergum through the maxillipedal 3357 metamere, and partly fused with the second thoracomere to form the carapace. The upper pair 3358 is antennae 1, with a basal peduncle of three articles and a distal flagellum of several articles 3359 with aesthetascs. The third peduncular article also bears an accessory flagellum on its distal 3360 end, usually composed of a reduced number of tiny cylindrical articles. The second pair of 3361 antennae is shorter than the first one; it has a flagellum of 8-11 small articles and a peduncle of 3362 five articles. Eyes are absent, but ocular scales can be present in some genera (e.g. 3363 Limnosbaena). A dorsal brood pouch is formed in ovigerous females, as an extension of the 3364 carapace, wherein eggs and juveniles are incubated. Their mouthpart is on the ventral surface 3365 below their carapace and is composed of the labrum, labium, mandibles, maxillae I and II, and 3366 maxilliped, all laterally connected to the carapace (see Wagner, 1994 for details). 3367

The thorax bears different kinds of legs generally eight pairs of biramous appendages, except for *Limnosbaena* (uniramous), the first of which are used as accessory mouthparts. One pair of gnathopods (modified pereopod 1) is possibly used for grasping detritus, the next six pairs are walking legs (pereopods 2-7), except in *Thermosbaena* only has 5 pereopods.

The pleon is composed of six segments (only five in *Thermosbaena*), but only three pairs of appendages. The first two pleonites bear a pair of reduced pleopods (pleopods 1-2); the first pair is scale-like in Halosbaenidae, and the last pleonite has a well-developed pair of biramous uropods. In *Thermosbaena*, the uropod is attached to the pleotelson and the endopodite is strongly reduced. Finally, a free telson (or pleotelson) is attached to the last pleonite and corresponds to the last part of the body. The shape and armature of the telson are typical of each genus and of each species to a lesser extent.

3379

3380 COLLECTION, PREPARATION, AND IDENTIFICATION

Thermosbaenacea are very rare and present only in groundwaters (aquifers, caves or springs). Therefore, any kind of specific material for this environment (Malard et al., 2002) can be used to collect them. Some species were even collected using a suction bottle or jars operated by divers in caves. Thermosbaenacea can be easily fixed and preserved in 2% buffered glutaraldehyde or in 95% ethanol for genetic analysis.

Determination at the species level requires dissection, mounting of body parts and 3386 3387 appendages on slides, and subsequent examination using a 400x or higher-magnification microscope or even observation in scanning electron microscopy (SEM) (e.g. Tethysbaena 3388 argentarii group). Specimens in glycerol or ethanol can be handled under a low-power 3389 microscope with needles. Baths in clearing solution (e.g. soft acids) and cuticular staining (e.g. 3390 black chlorazol B) can be helpful. A same specimen can be used for both studies: the abdomen 3391 3392 for DNA extraction and the other parts for dissection and mounting. This procedure ensures 3393 that the sequenced genes correspond to the same morphotype.

Taxonomic identification to the species level is generally based on males (if available), but females can be used too. Chaetotaxy is complex but very important for identification. The most important body parts for identification are the antennae, mouthparts, pereopod, pleopods, uropods and telson, but additional body parts need to be examined to identify certain species.

3399 LIMITATIONS

Thermosbaenacea remain a poorly known order, with only ~ 40 species described worldwide and hardly any molecular study to confirm their taxonomy. As a consequence, some families, genera and species names may change in the future, and many species are still to be found. The keys below are designed to cover the 12 species inhabiting fresh and brackish waters of the Mediterranean basin. Rare records are included, unless they are insufficiently documented.

Even if our keys were designed to be as clear as possible, we should keep in mind that identifying certain groups (e.g. the *Tethysbaena argentarii* group) is difficult and requires strong expertise. Do not hesitate to use alternative information or keys (e.g. Wagner 1994) to consolidate your conclusions. We should remain aware that the keys are designed for species of the Mediterranean basin; they are not adapted to other amphipods worldwide, even at the family level.

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3413

KEYS TO THERMOSBAENACEA

3414 Adapted from (Wagner, 1994)

3415 Key to family of Thermosbaenacea

- 3421
- 3422 2(1) Ocular scales absent; gnathopods with one strong serrate seta forming the unguis; propodus
 3423 of gnathopods with spur; pleopod 1 with basal articulation Monodellidae
 3424 [Peri-Mediterranean]

3430 Key to Monodellidae genera and species

[Italy]

3442 3443 3444	2(1) Telson wider than long; anal lobes protruding beyond the terminal stretch of the telso			
3445 3446 3447	2' Telson longer than wide; anal lobes not protruding beyond the terminal stretch of the telson4			
3448 3449	3(2) Antenna 1 main flagellum with 7 articles; Maxilla 1 palp second article with 9 setules; Uropod endopodite with 18-22 plumose setae <i>T. ophelicola</i> Wagner 2012			
3450 3451 2452	3' Antenna 1 main flagellum with 8 articles; Maxilla 1 palp second article with 4 setules; Uropod endopodite with 18-22 plumose setae			
3452 3453	4(2') Terminal stretch of the telson with one or more protuberances			
3454 3455 3456 3457	 4'Terminal stretch of the telson with one or more protuberances			
3458	The accurate identification of each species of the group needs of the froughter species of the group needs of			
3459 3460 3461 3462	Article 2 of the mandibular palp with 6 plumidenticulate setae; Maxilla 2 outer lobe with rake-like terminal setae; the presence of an additional dorsolateral subplumose seta pleopod 2; Medial margin of the first segment of the exopodite of uropod with 5 s plumose setae			
3463 3464 3465 3466 3467	5'. Article 2 of the mandibular palp with 5 plumidenticulate setae; Maxilla 2 outer lobe with 25 rake-like terminal setae; the absence of an additional dorsolateral subplumose seta on pleopod 2; Medial margin of the first segment of the exopodite of uropod with 4 stout plumose setae			
3468 3469	REFERENCES			

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in the Ophel biome of the Ayyalon Cave, Israel. Crustaceana 85: 1571–1587.
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Table 1. Mediterranean and global species diversity per order belonging to Malacostraca. The

reference values of global diversity are those provided in (Balian *et al.*, 2008) and updated with the World Register of Marine Species (Horton *et al.*, 2020) and the present study.

	Mediterranean basin	Global
Amphipoda	581	1,866
Bathynellacea	71	219
Decapoda	63	2,832
Ingolfiellida	9	20
Isopoda	336	994
Mysida	12	60
Stygiomysida	2	5
Thermosbaenacea	12	20
Total	1,084	6,014



Fig. 7.1. Geographic distribution of Malacostraca in the Mediterranean bioclimatic area. A,
species richness was weighted by the country area (species.km-²); B, the number of endemic
species is given for each country.



3495

Fig. 7.2. Results of the hierarchical cluster analysis of Bray Curtis similarity of faunal lists. Solid lines indicate significant differences (P < 0.05) using SIMPROF tests (Clarke, Somerfield & Gorley, 2008) and dashed lines indicate groups of samples not significantly separated by the test.



3502 Fig. 7.3. General aspect of Malacostraca. A, from left to right Dikerogammarus villosus (Amphipoda, Gammaridae), Chelicorophium robustum (Amphipoda: Corophiidae) and 3503 Niphargus schellenbergi (Amphipoda: Nirphargidae), photogaph courtesy of JF Cart; B, from 3504 left to right Pascifastacus leniusculus (Decapoda: Astacidae), photograph courtesy of J.F. Cart, 3505 Atyaephyra thyamisensis (Decapoda: Atyidae) and Potamon hippocratis (Decapoda: 3506 Potamidae), photograph courtesy of W. Klotz; C, Asellus aquaticus (Isopoda: Asellidae), 3507 photograph credit of C. Piscart; D, Hemimysis anomala (Mysida: Mysidae), photograph 3508 courtesy of J.F. Cart; E, Iberobathynella andalusica (Bathynellacea: Parabathynellidae), 3509 photograph credit of I Camacho; F, Tethysbaena ledoyeri (Thermaosbaenacea: Monodellidae), 3510 photograph courtesy of P. Chevaldonné/CNRS. 3511



3513 Fig. 7.4. General morphology of Amphipoda.





Fig. 7.5. Head of Parabathynellidae and habitus of *Iberobathynella*. Schematic parts ofBathynellacea body. A Bathynellidae family and B Parabathynellidae family.



Fig. 7.6. Habitus: 1, Vejdovskybathynella edelweiss Camacho, 2007; 2, Iberobathynella
andalusica Camacho, 2007 and 3, Parvulobathynella distincta Ranga Reddy, Bandari &
Totakura, 2011. AII: A, Vejdovskybathynella edelweiss; B, Iberobathynella andalusica and C,
Parvulobathynella distincta. Labrum: D, Vejdovskybathynella edelweiss; E, Iberobathynella
andalusica and F, Parvulobathynella distincta. Md: D, E, Vejdovskybathynella edelweiss; I,
Iberobathynella andalusica and J, Parvulobathynella distincta. MxII: K, Vejdovskybathynella
edelweiss; L, Iberobathynella andalusica and M, Parvulobathynella distincta.



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Fig. 7.7. Thoracopods: A, ThIII Gallobathynella coiffaiti (Delamare Deboutteville, 1961); B, 3531 3532 ThIII Vejdovskybathynella edelweiss; C, ThI Paraiberobathynella notenboomi (Camacho, 1989). Male ThVIII: D, Vejdovskybathynella edelweiss; E, Paraiberobathynella notenboomi. 3533 Uropods: F, Vejdovskybathynella edelweiss; G, Paraiberobathynella notenboomi; H, 3534 3535 Antrobathynella stammeri (Jakobi, 1954); I, Bathynella paranatans Serban, 1971. Furca: J, 3536 Bathynella paranatans; K, Antrobathynella stammeri. Female ThVIII: L, Paradoxiclamousella pirata Camacho, Dorda & Rey, 2013; L, Paradoxiclamousella fideli Camacho, Dorda & Rey, 3537 3538 2013



Fig. 7.8. AII: A. Hexabathynella sevillaensis Camacho, 2005; B. Hexaiberobathynella 3540 hortezuelensis Camacho & Serban, 1998 and C, Cteniobathynella Schminke, 1973. Furca: E, 3541 Cteniobathynella and F, Parabathynella. Labrum: G, Guadalopebathynella puchi Camacho & 3542 Serban, 1998 and H, Iberobathynella andalusica. MxI: I, Guadalopebathynella puchi; J, 3543 Iberobathynella andalusica and M, Iberobathynella (Asturibathynella) lamasonensis 3544 Camacho, 2005. Female ThVIII: K, Hexaiberobathynella mateusi (Galhano, 1967); L, 3545 3546 Hexaiberobathynella hortezuelensis Camacho & Serban, 1998; N, Iberobathynella (Asturibathynella) ortizi Camacho, 1989; P, Iberobathynella (Asturibathynella) parasturiensis 3547 3548 Camacho & Serban, 1998; R, Iberobathynella (Espanobathynella) andalusica; S, Iberobathynella (E.) burgalensis Camacho, 2007; U, Iberobathynella (Iberobathynella) 3549 paragracilipes Camacho & Serban, 1998. Uropod: Q, Iberobathynella (Asturibathynella) 3550 cornejoensis Camacho, 2005; T, Iberobathynella (Asturibathynella) burgalensis; V, 3551 Iberobathynella (Iberobathynella) paragracilipes Camacho & Serban, 1998. 3552



Fig. 7.9. A, General morphology of Caridea; B, Mouthparts and Pereiopods of Caridea: a, first pereiopod (Chela); b, fifth pereiopod; c, third maxilliped; d, second maxilliped; e, maxilla; f, maxillula; h, mandible; C, General morphology of Astacidea; D, General morphology of Brachyura.



Fig. 7.10. Habitus of *Ingolfiella cottarellii* Ruffo & Vigna Taglianti, 1989 (modified afterKaraman 1993).



Fig. 7.11. A, a psammic *Microcharon* sp. (Lepidocharontidae); B, a stygobiotic *Stygocyathura milloti* (Anthuridae); C, *Faucheria faucheri* (Cirolanidae); D, scheme of an Oniscidae from
Vandel 1966; E, *Jaera* sp. (Janiridae); F, scheme of an Asellidae; G, scheme of a Stenasellidae;

3565 H, scheme of a Microparasellidae. C = cephalon; P = pleotelson; U = uropod; 2-8 = pereonites;
3566 1-2 = pleonites.



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Fig. 7.12. Schematic left lateral view of a female isopod. A2 = antennae; Abd = pleon; Mxp = maxilliped; Oo = oostegites; P = pleopods; U = uropods. 2-8 = free pereonites bearing pereopods (the first one fused to the cephalon bears the maxilliped); 1-5 = pleonites.



Fig. 7.13. Second pleopod male of three different genera: 1. *Stenasellus*; 2. *Proasellus*; 2. *Typhlocirolana*.





3576 Fig. 7.14. *Stygiomysis hydruntina*. Photograph courtesy of Salvatore Inguscio.



3578 Fig. 7.15. *Spelaeomysis bottazzii*. Photograph courtesy of R. Pepe.



3581 7.16. Uropods of (A) *Stygiomysis hydruntina*, (B) *Spelaeomysis bottazzii*, and (C) *Troglomysis*3582 *vjetrenicensis*; (A–C) ventral view, setae omitted.









7.18. Antennal scale of (A) *Paramysis (Longidentia) adriatica*, (B) *Hemimysis anomala*, (C) *Neomysis integer*, (D) *Mesopodopsis slabberi*, (E) male *Limnomysis benedeni*, (F) female *L. benedeni*, (G) *Diamysis fluviatilis*, and (H) *Troglomysis vjetrenicensis*. Most (B and E) or all
(A, C, D, and F–H) setae omitted, respectively.



- 3592 Fig. 7.19. Telson of (A) Neomysis integer, (B) Mesopodopsis slabberi, (C) Hemimysis anomala,
- 3593 (D) Troglomysis vjetrenicensis, (E) Limnomysis benedeni, (F) Diamysis lacustris; (G)
- 3594 *Paramysis (Serrapalpisis) kosswigi*, and (H) *Paramysis (Longidentia) adriatica.*



7.20. Eyes and carapace of (A) Mesopodopsis slabberi, (B) Troglomysis vjetrenicensis, (C)
Diamysis lacustris, (D) male Diamysis fluviatilis, (E) male Diamysis mesohalobia heterandra,
and (F) Diamysis hebraica.


Fig. 7.21. Third thoracic exopods of (A) *Diamysis fluviatilis* and (B) *Diamysis hebraica*; (A and B) setae omitted.



Fig. 7.22. Dactylus with claw and paradactylary setae of fifth thoracic endopods of (A) *Paramysis (Serrapalpisis) kosswigi* and (B) *Paramysis (Serrapalpisis) lacustris*; (A and B)
other types of setae omitted.



3612 Fig. 7.23. General morphology of Monodellidae (modified after Monod & Cals 1988).