



Systematics And Ecology Of The Isopods: Exploring The Manifold Potential Of A Micro-Arthropod

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Abstract

Isopods include an order of crustaceans including crabs and shrimp, that are marine invertebrates. They support soil fertility and decomposition by chewing and consuming organic debris including fungus, rotting wood, and other decaying plant material. Numerous predators, such as centipedes, spiders, beetles, and tiny animals, consume isopods. Isopods are good for plants as they dig and aerate the soil; they decompose dead plants and other organic debris; and their faeces, known as "frass," fertilises the plants. Isopods are kept in terrariums as pets. The spectacular and most diversified isopod crustaceans are the main topic of this study, along with their usefulness and implications in the investigation of systematics, evolution, biology in general, ecology, and ecosystem services, as well as biodiversity. An auxiliary crucial component of this discussion is the underlying potential for recreation in this sector. This discourse further probes into the multifarious panoramas of the benefits of the isopods vulnerable to the domain of research.

Keywords: Isopoda, malacostraca, systematics, microarthropod, oniscidea.

Introduction

The Isopoda are a collection of exceedingly diverse and successful malacostracan crustaceans (including crabs, lobsters, shrimp, krill, and crayfish) that fall under the subclass Eumalacostraca, superorder Peracarida, and order Isopoda. Isopods live in a variety of settings, including marine, freshwater, and terrestrial environments. More than 10,300 species have been discovered in all realms, from the deepest seas to highland terrestrial ecosystems; around 9% of these species exist in continental waters. Isopods are supposed to be dorsoventrally flattened (wider than deep), and many species meet this morphological stereotype. Diverse taxa found in the deep sea and those found in groundwater, especially those living in aquatic habitats, depart considerably from this generalized body plan, particularly parasitic forms. The body size of isopods ranges from a few micrometers in the interstitial Microcerberidea to 50 cm in *Bathynomus giganteus* which is considered the largest isopod in the world. This study focuses on the magnificent and most wide-ranging isopod crustaceans, as well as their relevance and uses in studies of systematics and evolutionary biology, general biology, ecology and ecosystem services,

and biodiversity studies. The underlying recreational potential in this sector also constitutes a vital part of this discourse.

Systematics and Evolutionary biology

Palaeontological and phylogenetic evidence suggests that the ancestral isopod may have had a narrow vaulted body with legs projecting ventrally. Freshwater taxa include either typically flattened isopods or narrow body forms, along with a few taxa that are thin and vermiform, often with legs that emerge close to the dorsal surface (Wilson and Edgecombe, 2003). Other peculiarities of isopods include respiration using their broad posterior limbs (swimming legs or pleopods) with the heart positioned in the posterior part of the body, and biphasic moulting, wherein the back part of the body is cast off before the anterior region. Limb forms are diverse in the isopods, but most species modify the first walking leg (second thoracic limb) for grasping (Wilson, 2008).

Isopods living in freshwater may be divided into groups based on their presumptive age and adaptation to fresh water. The first group contains exclusively freshwater higher-level taxa (i.e., families) named 'primary freshwater.' Several exclusive freshwater families of Asellota and the entire suborder Phreatoicida are considered 'primary freshwater.' Both subordinate taxa are ancient, with originations in the Palaeozoic (Wilson, 1999), and both are derived basally in most phylogenies of the Isopoda, owing to their lack of specialized broad coxal plates (Brusca and Wilson, 1991) and other derived features that characterize the remainder of the Isopoda (Wagele, 1989). The 'secondary freshwater' group are those higher-level taxa members ranging from marine to freshwater habitats. The secondary freshwater groups are evolving freshwater habits and have marine representatives at a low taxonomic level (i.e. within the same family or genus). The transition from marine to freshwater habitats is repeated independently in all isopod groups, and obligate freshwater adaptations appear at different phylogenetic levels. For example, the Palaeophreatoicidae, an extinct Palaeozoic family of the Phreatoicida, were marine or possibly estuarine. At the same time, the fossil Protamphisopus, classified among the crown group phreatoicidans, appears in freshwater lacustrine Triassic facies (Wilson and Edgecombe, 2003).

The Asellota have freshwater and marine taxa but do not fossilize, so whether the ancestor was freshwater, or marine is not directly determinable. Several diverse higher-level asellote taxa are strictly freshwater (Asellidae, Stenasellidae, Protojaniridae). Henry and Magniez (1995) proposed that independent clades of Asellidae evolved from separate marine ancestors. No marine asellid taxa, however, are known in the modern fauna, so this hypothesis remains untested. The Microcerberidae was argued by Wagele et al. (1995) to be primitively freshwater, but this hypothesis is unparsimonious (Wilson, 1996). Wagele (1983) highlighted similarities between Microcerberidae and Atlantasellidae (known only from insular marine caves; Jaume, 2001), such as the coxal plates or spines on the anterior pereonites. These plates, also found in marine microcerberids, are plesiomorphic at the family level because they are present in both families. Finding interstitial microcerberids with coxal spines on continental Australia suggests that these marine taxa have colonized freshwater independently in different

parts of the world. Their freshwater distribution pattern is similar to 'Flabellifera' sensulato and Oniscidea.

The terrestrial isopods (Oniscidea) and the 'Flabellifera' sensulato are derived much later in phylogenetic estimates (Brusca and Wilson, 1991; Tabacaru and Danielopol, 1999), and the fossil record of modern families does not begin until the middle to late Mesozoic or later, with few peculiar taxa possibly related to modern families appearing in the Triassic (Guinot et al., 2005). The Oniscidea, although terrestrial, have their least derived taxa living on marine seashores and have a few freshwater taxa. Among these later-derived, secondarily freshwater taxa, some genera may be found in either fresh or saline waters or are transitional, like the bopyrid genus *Probopyrus* that parasitizes members of the estuarine and freshwater decapod family Palaemonidae. The peculiar aquatic family Calabozidae is exclusively freshwater but may be derived from terrestrial ancestors (Brusca and Wilson, 1991). The family Tainisopidae, among the higher isopods, lacks known marine or estuarine representatives. Its species are hypogean, narrow range endemics, and retain isopod plesiomorphies lost by other 'Flabellifera' sensulato. Whether this family should be classified as 'secondary' or 'primary' freshwater depends on its phylogenetic relationships relative to the remainder of the Isopoda. These relationships, however, are still controversial, with two competing subordinal placements in the literature (Wilson, 2003; Brandt and Poore, 2003, Sfenthourakis and Taiti, 2015).

Several marine Asellota ancestors may have colonized freshwaters late in Pangean times, and subsequent independent evolution gave rise to two freshwater groups, the Laurasian Asellidae and Stenasellidae and the Gondwanan Protojaniridae. Where the asellotan genus *Heterias*, found on the continents of South America, Australia and New Zealand, fits into this picture will ultimately depend on the resolution of the phylogeny of the Janiridae. The presence of *Heterias* and the Protojaniridae on fragments of Gondwana argues for independent freshwater colonization events, as the two taxa are distinct and not closely related (Wilson, 1987). The ancestral Asellota may have been diverse before the break-up of Gondwana because at least four distinct lineages gave rise to freshwater taxa. If this is the case, the Asellota has a minimum age of Triassic (Wilson, 2008).

Among the completely freshwater isopods, the Asellota has most of the 942 described species, with the largest species in the family Asellidae, followed by the Stenasellidae. The Phreatoicidea have at least four families with many undescribed species that may double the number of described species. Other freshwater families have small numbers of described species, although more species are being discovered as surveys are carried out in the southern hemisphere (Wilson, 2008). The Protojaniridae are tiny and fragile and may require specialized techniques to recover them from hypogean habitats; 12 species in five genera are described, but more remain to be found.

The application of "known to unknown" estimates from the Phreatoicidea to the other freshwater isopods results in 62% more than those known, or approximately a total of 2,630 species. Evidence from molecular studies suggests that this estimate could be highly conservative. RAPD (random amplified polymorphic DNA) studies on both species of Asellidae and Stenasellidae (Verovnik et al., 2003) have uncovered previously

unsuspected diversity in well-known populations of *Stenasellus* and *Proasellus*. Similar results have been obtained from studies of genetic variation using enzymatic loci (*Proasellus*: Ketmaier, 2002) or the mtDNA cytochrome oxidase I gene (COI) (*Stenasellus*: Ketmaier et al., 2003). Cryptic species in the epigean phreatoicidean genus *Mesamphisopus* (Gouws et al., 2004, 2005) could include between 15–20 species in South Africa. Four new Tainisopidae species of the hypogean genus *Pygolabis* (Keable and Wilson, 2006) from the Pilbara region of Western Australia are morphologically similar and difficult to identify, but CO-I studies support their species concepts.

Isopods have developed various kinds of lifestyles, among them free-living (Kensley, 1998), scavenging (Wilson, 2011) or predatory (Wallerstein and Brusca, 1982), but also parasitic forms of varying degrees of specialization (Smit et al., 2014, Athira and Balamurali, 2019)) and this is exemplified by the isopod ingroup Cymothoidea (Wägele, 1989). Within this group, numerous lifestyles have evolved, some quite soon after the group's appearance (Dreyer and Wagele, 2001). Synanthropic species have been reported to damage young buds of fruits, vegetables, and flowers. Hopkin (1991) noted that isopods cause significant economic horticultural damage to greenhouse crops. Losses of up to 80% have been reported in vegetable crops such as lettuce, tomato, beans, and pepper.

Isopods occur in epigean lotic and lentic habitats (e.g. Asellidae like the common European *Asellus aquaticus* and Phreatoicideae in Tasmania), but many live in a variety of subterranean habitats. Microcerberidae is found interstitially in freshwater or marine sands. Many families are limited to cavernicolous or subterranean habitats, such as Stenasellidae, Microparasellidae, or Tainisopidae. North American and European members of the Asellidae can be both epigean and hypogean (Lewis and Bowman, 1981). Some taxa (e.g. Hypsimetopidae or Heterias, Janiridae) could best be described as infaunal, living in near subsurface habitats, either burrowing among submerged roots, residing in submerged burrows of other animals (pholoterans) or the subsurface water of streams (hyporheos). A few isopods occur in unusual habitats, such as *Thermosphaeroma thermophilum* in hot springs of the USA southwest. Some oniscideans, ordinarily terrestrial, have re-invaded the continental saline waters (e.g. *Haloniscus searlei*) or even normal freshwater (e.g. Trichoniscidae and Styloniscidae). Australian collection records suggest that some Philosciidae and Trichoniscidae may be amphibious (Taiti and Humphreys, 2001).

Generic endemism is similarly high, with only a few secondary aquatic taxa like *Probopyrus* (Bopyridae) or *Gnorimosphaeroma* (Sphaeromatidae) appearing on more than one continent. Surprisingly, Australia has the highest number of genera even though the largest number of species is found in the Palaearctic, where more research has been done. This pattern arises because, in addition to different taxonomic styles among asellotan and phreatoicidean workers (such as *Asellus*) are widespread in Eurasia. At the same time, Australian genera have highly restricted ranges on scales of 100 - 2 km. In the northern hemisphere, glaciation, which had much less impact in the south, may have had the dual role of pruning the fauna of rare, unique taxa (thus decreasing genetic diversity)

as well as providing a rich environment for speciation, with multiple opportunities for diversification during the advance and retreat of the ice caps (Magniez, 1974).

Several phreatoicidean genera are more extensive, some of them being the speciose *Colubotelson*, located in most freshwater bodies in Tasmania and upland springs in Victoria, and the genus *Crenoicus*, which is characteristic of highland bogs and springs on the Great Dividing Range. But these taxa are the exception rather than the rule, probably attesting to the geological history of Australia as an arid continent, with patchy epigeal sources of water and extensive marine transgressions during the Mesozoic era that transformed the continent into a series of smaller islands (Wilson and Johnson, 1999). The secondary freshwater taxa seem to be patchily spread across the continents, representing either sampling efforts or peculiarities of the region.

The Amazon and other major rivers of South America (Neotropics) are significant hot spots for the fish-parasitic group Cymothoidae, with more than 40 species in this family alone. This result may reflect the diversity of their hosts in this region. The distribution of the freshwater isopods on the continental scale shows significant non-random patterns among the more ancient groups. The Asellotan families Asellidae and Stenasellidae conversely show a Laurasian pattern, with no species occurring among known terranes of Gondwana. A single species of *Caecidotea* (Asellidae) has been reported from the highlands of Guatemala (Argano, 1977), but this record may be the southern limit of a Nearctic pattern for the genus. The Stenasellidae have numerous African records and scattered research papers among Oriental and south margins of North America. This pattern appears to be Tethyan, but more detail is needed on the phylogeny of the Stenasellidae and Asellidae before a historical biogeographical assessment can be made. The Phreatoicidea have a strictly Gondwanan pattern (Wilson and Edgecombe, 2003) and occur only in the terranes of Gondwana, including South Africa, India and Australia-New Zealand.

Since the ancestors of the freshwater Asellota and the Phreatoicidea were marine and possibly cosmopolitan in the Palaeozoic, these patterns may be interpreted as the result of colonization of freshwaters, with subsequent extinction in marine waters. Some Asellota also shows a Gondwanan pattern. The Janiridae, known to be non-monophyletic (Wilson, 1994), contains a diverse group of transitional freshwater and marine taxa (best exemplified by the European genus *Jaera*). Among these taxa, the southern hemisphere genus *Heterias* occurs in Australia and South America (Wilson & Wagele, 1994). *Heterias* species are diverse in southern Australian hyporheos and pholeteros, and recently they have been found in New Zealand by Dean Olsen. The Protojaniridae are strictly freshwater and occur on terranes derived from Gondwana. These observations could be related to rareness and sampling bias, but the documented effort in the northern hemisphere argues that this pattern is real. Until recently, protojanirids were only known from Sri Lanka and South Africa, but undescribed species have been found recently in Australia and Chile.

General Morphology

Isopods show all the characteristics of a typical crustacean and have a segmented body composed of a head, a pereon (thorax) of 7 somites (segments) with their paired pereopods, all are very similar and a pleon (abdomen) of 6 somites. The fourth thoracic segment is the broadest. The roof of the thorax is formed of broad convex terga which are slightly folded laterally. The carapace is absent. The last abdominal segment, to which the uropods are attached, is fused with the telson (or tail segment) to form a pleotelson. The coxal plates extend out the sides of each segment of the pereon, covering the bases of the legs. The first five pairs of abdominal limbs are flat membraneous gills. The mouth parts are the mandibles, first and second maxillae, hypopharynx and maxilliped. The antennules are rudimentary. Compound eyes are prominent and sessile. The dorsal surfaces of the terga are moist, smooth, and pigmented. The pigments are seen all over the terga which appear as brownish patches.

Feeding Preferences

Isopods have a broad range of feeding types, from omnivory in Sphaeromatidae to carnivory in the Cirolanidae. Oniscideans and Asellidae are well-known as leaf litter shredders and have bacterial endosymbionts to aid digestion (Zimmer, 2002, Zimmer and Bartholme, 2003). Tainisopidae may be carnivorous scavengers because they can be captured using baited traps. Most freshwater isopods (e.g. Asellota or Phreatoicidea) can be characterized as generalized detritivores-omnivores but may facultatively choose other items. Phreatoicideans feed on decaying vegetation and roots, or perhaps the microflora and microfauna associated with these substrates, but occasionally will engage in carnivory. Among the 942 described species found in continental waters, the presumptive feeding types (based on extrapolation from taxa where habits are known) are as follows: 3.2% are carnivores, 6.9% are scavenger-carnivores, 9.9% ectoparasites, 0.4% herbivores, 6.1% omnivores, and the remaining 73.5% are detritivores-omnivores, mostly Asellota and Phreatoicidea (Wilson and Fenwick, 1999). Different isopod species have been observed feeding on green living tissues of several plants even if they have another food source as a choice (Fabri et al., 2011). There are certain discussions related to the nutritional significance of coprophagic behaviour of isopods (Zimmer, 2002).

Reproductive Biology

Isopods, like all peracarid crustaceans, have direct development with the young brooded in a ventral pouch until they are released as miniature adults. Isopods have internal fertilization (Wilson, 1991) that occurs before the release of embryos into the marsupium, unlike other peracarid crustaceans. Brood sizes range from 4–5 young in tiny interstitial isopods to hundreds in the parasitic forms, and lifetime reproduction may be limited to one or several broods in most species (Johnson et al., 2001). Many isopods, especially the suborders Asellota and Oniscidea, have secondary sexual features for intromission in both males and females. Brooding of the young, direct development, and internal fertilization may be significant factors in the high endemism observed in most isopod taxa (Wilson, 1991).

Most isopods exhibit direct development, passing from embryo to manca stages (the latter lacking the posterior pair of thoracopods, called pereopods in these taxa) from juveniles to adults. The oostegites of females are proximal plate-like limb branches of pereopods 2–5, and sometimes the maxilliped (thoracopod 1) for a maximum of limbs 1–6 which, together with the corresponding sternites, form an egg receptacle. These, along with male gonopods (modified first pleopods), are added in the moult (s) before the final moult to adulthood. Isopods moult biphasically, using body and limb movements to shed the anterior half of their exoskeleton before the posterior half (Johnson et al., 2001). Most parasitic isopods (e.g., the Cymothoidea) show direct development. Still, members of the Gnathiidae and the epicarideans (the Bopyroidea and Cryptoniscoidea) have complex life cycles, with one or more juvenile stages differing radically from the adult forms. Before the life cycles were understood, some of these stages (e.g., praniza and microniscus) were once thought to represent taxa distinct from the adults. Additionally, males and females in these groups show the most significant amount of sexual dimorphism among isopods. Some terrestrial isopods (the Oniscoidea), marine arcturid, and antarcturid isopods show parental care for their young after hatching (Boyko and Wolff, 2014). The development of intersex populations in soil isopods has a direct relationship with the nitrogen and phosphorous content of the soil as reported by Balamurali and Sanalkumar (2012).

Ecosystem services

Isopods provide essential ecosystem services, such as leaf litter decomposition (Grosset and Faberi, 2018). Soil biodiversity is critical in regulating soil processes that underlie vital ecosystem services (Bardgett et al., 2005; Bardgett and Wardle, 2010). Soil organisms are the primary driving agents of the nutrient cycle, regulate the dynamics of soil organic matter, soil carbon sequestration, and greenhouse gas emissions, modify soil physical structure, and enhance the level and efficiency of nutrient acquisition by the vegetation (Bardgett and Wardle 2010). Some soil organisms, such as terrestrial isopods, are potentially valuable indicators of soil health because they respond to soil management in time scales (months/years) relevant to land management. On the other hand, the activity level of different species depends on particular management practices. These affect the micro-environmental conditions, including temperature, moisture, pH, and type of food sources. Snyder and Hendrix (2008) discussed large obligate detritivores (earthworms, millipedes, and isopods) have been used to accomplish restoration goals, assess restoration progress, and function as bioindicators. Sanalkumar et al., (2009) pointed out patterns of seasonal variations in population density and distribution patterns in certain particular ecosystems.

In many terrestrial ecosystems, isopods play an indispensable role in decomposition processes through the mechanical and chemical breakdown of plant litter and enhancing microbial activity (Zimmer, 2002). Terrestrial isopods' digestive capabilities and characteristics, directly and indirectly, contribute to decomposition processes (Kautz and Topp, 2000). Due to their utilization of weakly decomposed litter and their digestive capabilities, emphasis is laid on the significance of terrestrial isopods in decomposition processes as compared to other soil animals. Although only approximately 5% of the

annual litter is consumed by *Philoscia muscorum* in British grassland (Hassall, 1977), the contribution of the isopod to ecosystem processes may be substantial. Due to cellulose digestion during gut passage (Kukor and Martin, 1986), the content of recalcitrant compounds is lower in isopod faeces than in leaf litter. Through phenol degradation brought about by isopods or their intestinal microbiota (Zimmer, 1999), isopods play a significant role in soil development (Neuhauser and Hartenstein, 1976). In arid regions, the burrowing activity of *Hemilepistus* appears to be an essential factor in soil formation (Kozlovskaja and Striganova, 1977).

Isopods probably compete with other members of the guild of saprophagous soil animals for 'high-quality food. Some of the digestive capabilities of terrestrial isopods may render them competitively superior to other soil animals. Further, species-specific nutritional requirements and digestive capabilities may reduce interspecific competition among sympatric isopods. The resulting intra-guild coexistence through species specificity appears essential for ecosystem processes by providing biodiversity without functional redundancy (Zimmer, 2002).

Research potential

Ecology, behaviour, nutritional biology, anatomy, functional morphology, neurology, physiology, biogeography, systematics, and phylogenetic analyses based on morphological and molecular data are all topics of current isopod study (Schmalfluss, 2018). Isopods have seen a rise in the rates at which starch and cellulose-based polymers (biodegradable plastics) decompose (Wood and Zimmer, 2014). In laboratory toxicity testing, in-field monitoring, and bioindication investigations, isopods are useful models for understanding soil ecotoxicology (van Gestel et al., 2018).

Recreational scope

Isopods are often kept as pets in the household. Despite their unsettling nature, land isopods are not detrimental to people and do not harm the domestic assets if they get inside. They create a world of their own without disturbing the ecosystem of human beings. They are admired as pets for certain specific reasons like they are interesting to watch, alleged as eccentric pets, incredibly little maintenance, are available in a variety of lovely colours and patterns, are affordable to keep, exquisite social creatures, and are simple to manage. Isopods are definitely the most magical invertebrates to work with.

Conclusion

Isopod plays a crucial part in the ecosystem, maintaining the ecology's kerb and stability system. Isopods have additional ecological value in that they serve as biological markers of the well-being of the environment, assist in the cleanup of decaying organic materials, and provide an essential source of food for other species. Research studies clarify the ecological and economic functions and implications of these parasitic isopods, there are some acclaimed benefits alongside the negative impacts they offer. We often dread things we don't understand or have no control over, and the situation with the isopods clearly illustrates this adage. Most isopods have a negative connotation for humans though the

isopods are not purposefully harmful; rather, it is the process of evolution and adaptation that has created isopods to fulfil their ecological function. With all the facts remaining, the positive affects outweigh the negative. Manifold benefits of isopods and its tracking research will open up new avenues of knowledge on isopods and their locus in the world.

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