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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of gastrotrichs (Gastrotricha) in fresh waters

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Abstract The global diversity of inland water Gastrotricha is poorly known, and information is extremely heterogeneous. Gastrotricha have been studied most widely in Europe and America, whereas data from the other continents are scattered or not even available. This scanty information is related to several reasons, first of which is the technical difficulty in collecting and studying microscopic and soft-bodied species. In addition, the research has been limited mostly to the epibenthos and periphyton in lentic waters, and the gastrotrich taxonomy is still under discussion mainly because of the great intraspecific variability. Three of the five freshwater families are widespread or cosmopolitan, and most genera have been reported from at least two continents. There is strong evidence of a high diversity in genera and species in tropical areas. Nearly a half of the freshwater species are known from only one country or even only from one site, but the insufficient faunistic knowledge does not allow defining them as endemic. The phylogenetic relationships and possible evolutionary trends of inland water species of Gastrotricha are outlined.

Keywords Gastrotricha · Chaetonotida · Freshwater species · Global biodiversity · Geographic distribution

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Freshwater Animal Diversity Assessment

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Introduction

Gastrotricha are aquatic microinvertebrates composing a constant, important component of the benthic communities in marine and freshwater habitats. In spite of the often high number of populations, gastrotrichs are not yet well known, possibly due to their minute size and body fragility, which make studying them very difficult. The phylum consists of nearly 690 named species, grouped into two orders, Macrodasyida and Chaetonotida, greatly different in morphology, reproductive biology and ecology. Macrodasyida are about 240 worm-like species, all interstitial in marine and estuarine habitats except for two freshwater ones. The roughly 450 species of Chaetonotida are tenpin-shaped, interstitial or epibenthic in marine, brackish, but mainly freshwater habitats (Balsamo & Todaro, 2002; Fig. 1). Most of the 318 inland waters gastrotrich species have been

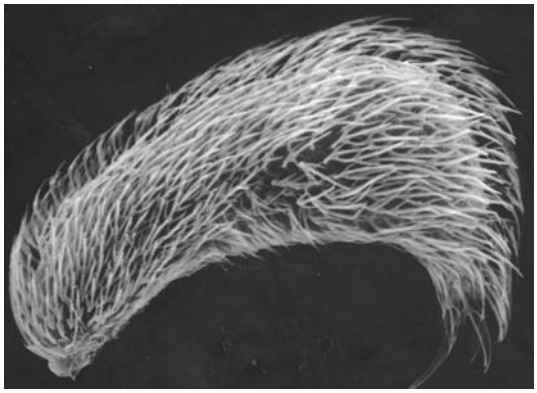

Fig. 1 *Chaetonotus schultzei*, S.E.M

reported from the periphyton and the surface layer of organic sediments in eutrophic, lentic biotopes (Kisielewski, 1998). About 70 species are known from an interstitial habitat, a half of which can be found in lotic waters (see Ricci & Balsamo, 2000). Freshwater Gastrotricha are presently grouped into 21 genera in 5 families of Chaetonotida, and into two genera '*incertae sedis*' of Macrodasyida. Many species have been discovered in the last 50 years, but the list of the species accepted in the current systematization of the group is currently under review following recent extensive and careful faunistic surveys (see for references Schwank, 1990; Kisielewski, 1991, 1998; Naidu & Rao, 2004).

Global species diversity

Past research

First descriptions of freshwater gastrotrich species go back to the XVIII–XIX centuries in detailed studies carried out by famous zoologists, but the systematic research started in late XIX century leading to the first, important monograph by Zelinka (1889) on the European and North American freshwater species. In the beginning of the 1900s scattered faunistic and systematic information was gathered mainly in Europe, but as far away as Africa, India, Ceylon, Tibet, Japan, New Guinea, Jamaica, Paraguay, and America. Since 1970 a significant rise of interest brought about a series of studies mostly in Europe but also in Israel, India, Japan, Korea, US, Argentina and Brazil. Research has touched almost only continental biotopes, but some data are also available for insular fresh waters (Tuscan Archipelago, Italy; Azores, Portugal; Jamaica; see Schwank, 1990; Kisielewski, 1998). The history of the knowledge of brackish-water species is much shorter. Scattered, occasional findings in low-salinity environments have concerned European coastal lagoons, estuaries, deltas, Brazilian mangroves and Amazonian estuaries, even hundreds of kilometres from the sea (see Kisielewski, 1991). Brackish-water gastrotrichs are mostly marine, chaetonotidan species, clearly adapted to great salinity variations. Only a minority of freshwater species can survive salinity, and very few are exclusive to brackish waters and may be endemic of these habitats (Kisielewski, 1991; Tongiorgi et al., 1999).

Estimated global diversity

At a high taxonomical level, the Chaetonotida families Dasydytidae, Neogosseidae and especially Chaetonotidae (subfamily Chaetonotinae) appear to be widely distributed. The other families show a limited distribution: the rare Dichaeturidae have been occasionally found in few European sites, the ditypic Proichthydiidae are only known from South America and Asia, and the subfamily Undulinae (Chaetonotidae) is reported from one site in Amazonia (see Schwank, 1990; Kisielewski, 1991). The only two freshwater monotypic genera of the order Macrodasyida, each recorded in one site, are known only in Europe and South America, respectively (Ruttner-Kolisko, 1955; Kisielewski, 1987). At a super-specific level, almost a half of the genera show an intercontinental distribution. A high diversity of endemic genera in the Brazilian fauna, but not in the European and Levantine ones has been evidenced by Kisielewski (1991). About 1/3 of European species and 1/3–1/2 of South American ones appear cosmopolitan. The distribution of the other species, as well as that of subgenera and genera seems to be restricted to a single continent or, if intercontinental, to the tropical zone. The few studies carried out in the tropical area show a very high generic and specific diversity even of families rare in temperate zones (Kisielewski, 1991). This strongly suggests that freshwater fauna, especially the highly specialized families, will be much richer in the tropical regions. Detailed and reliable faunistic comparisons were

made by Kisielewski (1991, 1999), through exhaustive studies carried out in Poland, Brazil and Israel. About 1/3 (33.7%) of the species found in Brazil was known also in Europe, while the percentage of European species was higher (54.5%) in Israel, probably due to the closer zoogeographical relationships and shorter distance between Levant and Europe.

Aspects of phylogeny and evolution

Gastrotricha for a long time have been placed at the base of the 'Aschelminthes', close to Kinorhyncha, Nematoda, Rotifera or Gnathostomulida (see Boaden, 1985). Recent phylogenetic analyses of the protostomes, based on morphological, molecular, developmental and ecological evidences, have agreed on the basal position of the phylum. Gastrotricha have been included in Cycloneuralia, or linked to Gnathostomulida or to Platyhelminthes (see Zrzavy et al., 2002). The phylum has been considered as the sister-group of Ecdysozoa, included in the Spiralia, and in the 'Platyzoa' (see Zrzavy et al., 2002). Despite the key role generally assigned to Gastrotricha in the protostomes phylogeny, their relationships to other lower metazoans are not yet defined (Schmidt-Rhaesa, 2002). The numerous and great differences between the two orders have given rise to hypothesize that they are paraphyletic to Nematoda, or even that they belong to different phyla (Manylov et al., 2004). The monophyly of the orders and of the phylum has been strongly supported by cladistic morphological and molecular (18S rRNA) analyses (Hochberg & Litvaitis, 2000, 2001; Todaro et al., 2006), but the ancestry of each order and the relationships among families are still open questions. Further efforts in detecting possible plesiomorphies useful to clarify internal phylogeny are needed (Ferraguti & Balsamo, 1995; Hochberg & Litvaitis, 2000, 2001). Among Chaetonotida, Neodasyidae and Xenotrichulidae are marine families, Dasydytidae, Neogosseidae and Proichthydiidae are exclusively freshwater, and Dichaeturidae are freshwater with unclear connections with brackish and marine habitats (Kisielewski, 1990). The largest family Chaetonotidae has three marine genera (*Diuronotus, Halichaetonotus, Musellifer*), three freshwater ones (*Arenotus, Polymerurus*, *Undula*), and five including both marine and freshwater species (*Aspidiophorus, Chaetonotus, Heterolepidoderma, Ichthydium, Lepidodermella*). Hence, most primitive forms were possibly marine, psammic Macrodasyida and Chaetonotida might evolve later, mainly radiating in freshwaters as epibenthic or semipelagic forms. The only two extant freshwater Macrodasyida may represent successful attempts of colonization of inland waters by this marine order. In addition, a few other macrodasyidan species occur in brackish waters, even at salinity, as low as 1‰ (see Kisielewski, 1990). The presence of Macrodasyida far from river mouth, and also in deep beach freshwater springs, suggests a colonization of freshwaters not only through estuarine sediments, but also through water bodies created near beach springs during the marine regression (Kisielewski, 1990). Few, mainly marine Chaetonotida are psammic in brackish waters, but only two species appear exclusive to this habitat, perhaps being rare survivors of the Messinian crisis of the Mediterranean (Tongiorgi et al., 1999). The much greater success of Chaetonotida in colonizing inland waters is proved by the high number of freshwater species, more than 2/3 of the total number of chaetonotidans. The general epibenthic lifestyle is probably related to the organic and muddy nature of these sediments, and appears to have been favoured by particular morphological and biological adaptations [e.g. cuticular sculpturing, parthenogenesis, resting eggs]. Periphytic and semipelagic habitus have possibly developed as adaptations to new, abundant, trophic substrata (vegetation), that are better exploited by this group in lentic waters rather than in lotic ones or in the turbulent, littoral sediments. The primary or secondary presence in the freshwater psammon of the few Chaetonotida cannot be stated with certainty. The radiation of marine Gastrotricha, all interstitial, probably occurred in sandy sediments, whereas the ecological evolutionary trends of inland-water gastrotrichs and the importance of the psammic habitat in this process are still unclear, and could have occurred in different ways in Europe and in South America (see Kisielewski, 1990).

Zoogeography and endemicity

The geographic distribution of the marine gastrotrich fauna is well-known from many world areas (see Hummon, 2001; Naidu & Rao, 2004; Todaro &

Table 1 Total number of inland-water (freshwater + brackish-water) species of Gastrotricha per family and per biogeographical region

Biogeographical Region	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Order/Family									
Chaetonotida	221 + 2	71	91	10	29	8	0	0	316 + 2
Chaetonotidae	192 + 2	60	76	7	25	8	0	0	281
Dasydytidae	21	9	10	0	2	0	0	0	34
Dichaeturidae	3	0	0	0	0	0	0	0	3
Neogosseidae	4	2	4	3	1	0	0	0	8
Proichthydiidae	1	0	1	0	0	0	0	0	2
Macrodasyida	1	0	1	0	0	0	0	0	2
incertae sedis	1	0	1	0	0	0	0	0	2
Total	222 + 2	71	92	10	29	8	0	0	318 + 2

PA: Palearctic; NA: Nearctic; NT: Neotropical; AT: Afrotropical; OL: Oriental; AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

Rocha, 2005), whereas that of freshwater species is still very limited, mainly reflecting researchers nationality. Freshwater Gastrotricha have been studied at extremely different levels in the various parts of the world. In Europe, where most research has been done, 213 species have been identified; 92 species have been reported in South America, 71 in North America, 64 in Asia, 10 in Africa, 8 in Oceania and none in Antarctica (Table 1). Some European countries have been the object of special surveys: France (29 spp.; d'Hondt, 1967), Germany (90 spp.; Remane, 1935-36; Schwank, 1990), Italy (92 spp.; Balsamo & Tongiorgi, 1995), Poland (98 spp.; see Kisielewski, 1998), Romania (90 spp.; see Rudescu, 1967); Russia (91 spp; see Tretjakova, 1991), and United Kingdom (58 species; see Martin, 1990). Single or few records are available for other European countries, or even none at all from Portugal [except for Azores] and Netherlands. Data from North America mainly concerns the US (see Weiss, 2001), and Canada (Schwank, 1990), whilst from Central and South America records regard Argentina (see Grosso & Drahg, 1991), Brazil (Kisielewski, 1987, 1991) and French Guyana (d'Hondt et al., 2006). Some information is available for Colombia, Jamaica, Paraguay, Uruguay (see Schwank, 1990). Of the Asian countries only India (see Naidu & Rao, 2004), Israel (Kisielewski, 1999), Japan (see Sudzuki, 1975) and Korea (Lee & Chang, 2000) have been investigated. Few, scattered records are available for Africa and Oceania: New Guinea and Australia (see de Beauchamp, 1932; Hochberg, 2005; Fig. 2). There is no data available for Antarctica and Pacific Islands. This whole picture points out many gaps in the distribution knowledge, as entire world areas have not yet been explored.

Research has especially focused on the epibenthos and periphyton of mesotrophic and eutrophic lentic waters, in which a rich, diversified fauna is known to exist (Kisielewski, 1998). Some special studies have found a few species in sandy and sandy-silty sediments of lentic and lotic fresh waters, in lagoons and estuarine brackish waters, areas generally considered unsuitable for gastrotrichs for various reasons (water turbulence, substrate perturbation, saline excursion etc.) (see Ricci & Balsamo, 2000). We know almost nothing about gastrotrichs from extreme habitats of biogeographic interest, such as inland saline lakes, deep-sea freshwater springs, river springs, warm springs, oasis springs, cave pools and hyporheic waters. A zoogeographical analysis of the inland-water Gastrotricha is at present very difficult due to a heterogeneous faunistic knowledge in different world regions, and a general insufficiency of data. At least a third of the genera and a half of the species known in inland waters have been recorded from only one country, often from only one site (Table 2). The scanty faunistic information from large areas of the world suggests caution in defining these taxa as endemic ones.

Taxonomic descriptions of freshwater species and iconography have been produced by the authors according to personal, not standardized criteria. Permanent slides useful for comparisons are

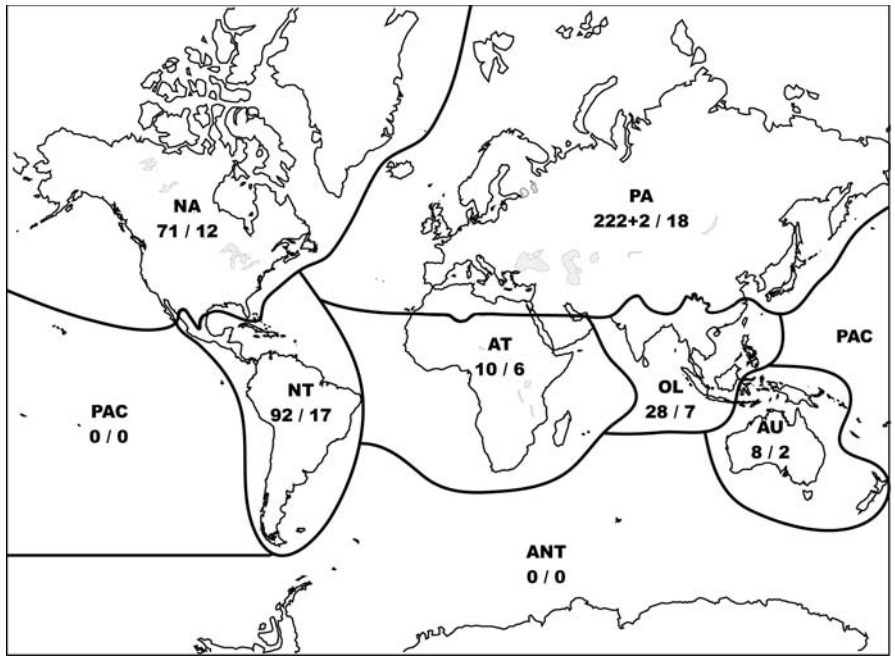

Fig. 2 Total number and zoogeographical distribution of inland water (freshwater + brackish water) species and genera of Gastrotricha. PA, Palearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian, PAC, Pacific Oceanic Islands; ANT, Antarctic

Table 2 Total number of inland-water genera of Gastrotricha per family and per biogeographical region

Biogeographical Region	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Order/Family									
Chaetonotida	17	12	16	6	7	2	0	0	21
Chaetonotidae	7	7	8	4	4	2	0	0	9
Dasydytidae	6	4	5	0	2	0	0	0	7
Dichaeturidae	1	0	0	0	0	0	0	0	1
Neogosseidae	2	1	2	2	1	0	0	0	2
Proichthydiidae	1	0	1	0	0	0	0	0	2
Macrodasyida	1	0	1	0	0	0	0	0	2
incertae sedis	1	0	1	0	0	0	0	0	2
Total	18	12	17	6	7	2	0	0	23

relatively few, often with scarce diagnostic value. Most researchers have only worked in one continent; so that an effective comparison of specimens from different continents, but apparently of the same morphospecies, has been possible in very few cases (see Kisielewski, 1991). Even if some molecular studies have tried to shed light on the relationships of and within the phylum, the current taxonomy is still based on morphological and ultrastructural features. Comparisons are difficult, especially with old species, most of which have been insufficiently described and drawn without details that are now required for identification. Many species show a great morphological variability, and several 'forms', or even subspecies, have been described, but the value of these taxa is questionable. All this makes the gastrotrich taxonomy still unreliable, in spite of the recent systematic revisions by Schwank (1990) and Kisielewski (1991, 1998).

Human related issues

As yet there is a no apparent human related issue for freshwater Gastrotricha but they could be used as bioindicators for the quality of the inland waters, as is

the case of Macrodasyida in marine habitats. Diversity of freshwater gastrotrich communities is highest in mesotrophic-eutrophic unpolluted lentic waters, although some species appear to be relatively tolerant to changes in some abiotic factors.

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