

CHAPTER 3

GASTROTRICHA

Maria Balsamo and M. Antonio Todaro

Introduction

Gastrotrichs are an important component of the benthos and phytofauna of freshwater habitats, where they can reach densities of up to 100 000 individuals m⁻² (Nesteruk, 1996a,b). However, due to their small size and the logistical difficulties met in their study, gastrotrichs, and in particular aspects of their reproductive biology and ecology, are still poorly understood.

Gastrotricha are aschelminthes closely related to acoelomates and form a phylum divided into two orders: Macrodasyida and Chaetonotida (Wirz *et al.*, 1999; Hochberg & Litvaitis, 2000a) (Fig. 1a-c). The Macrodasyida number about 240 species, all but two of which are marine or estuarine; Chaetonotida number 450 species, mainly reported in fresh waters. The ca 300 gastrotrich species commonly found in inland waters inhabit the water-sediment interface and aquatic vegetation, especially in eutrophic biotopes, but can also occur in the interstitial environment (Ricci & Balsamo, 2000). Nearly 70 species have been reported from psammic habitats both in lentic and lotic sediments, although less than half of these have been found in running waters (Hummon *et al.*, 1978; Kisielewski, 1987, 1990; Balsamo & Fregni, 1995; Fregni *et al.*, 1998; Ricci & Balsamo, 2000).

Classification and systematics

All but two freshwater gastrotrich species belong to the order Chaetonotida, which includes seven families and twenty-four genera. Four families, including nine genera, are known exclusively from inland waters, two families (Neodasyidae and Xenotrichulidae) are solely marine and the other includes twelve genera, five of which are exclusively freshwater, seven both marine and freshwater, and two exclusively marine. The most specious genus is *Chaetonotus* with about 150 freshwater species, for which several taxonomical subdivisions have been proposed (Remane, 1936; Schwank, 1990; Kisielewski, 1997). The considerable morphological variability of most freshwater chaetonotids often makes species identification difficult, and consequently the taxonomy is currently unstable. Recently, a freshwater species belonging to the marine Macrodasyida order (*Redudasys fornerisae*) was reported by Kisielewski (1991) in a lentic, interstitial habitat in Brazil. In the

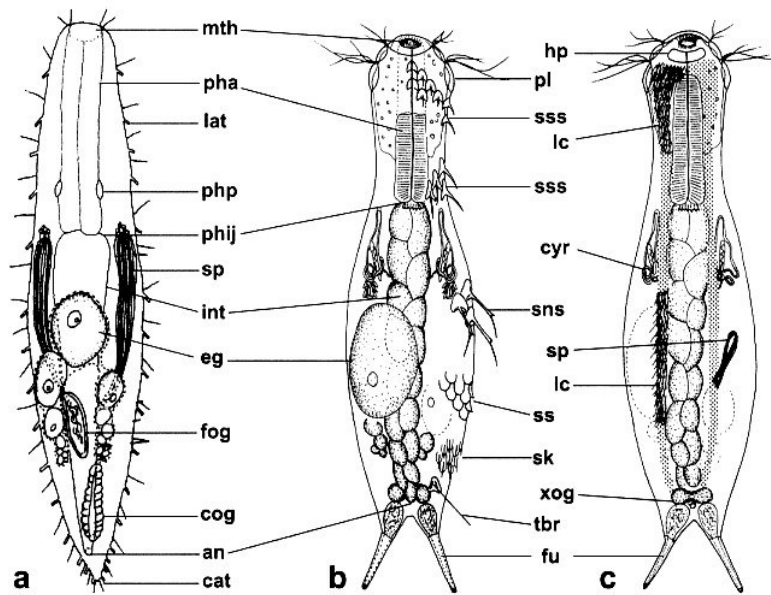


Fig. 1. Scheme of the anatomy of a macrodasyid (a) and of a chaetonotid gastrotrich from dorsal (b) and ventral (c) views: an, anus; cat, caudal adhesive tubes; cog, caudal organ; cyr, cyrtocytes; eg, egg; fog, frontal organ; fu, furca; hp, hypostomion; int, intestine; lat, lateral adhesive tubes; lc, locomotor cilia; mth, mouth; pha, pharynx; phij, pharyngo-intestinal junction; php, pharyngeal pores; pl, pleuria; sk, keeled scale; sns, scales with notched spines; sp, sperm; ss, smooth scales; sss, scales with simple spines; tbr, tactile bristle; xog, X-organ.

same paper, Kisielowski reaffiliates *Marinellina flagellata*, a rare macrodasyid-like species found only once in running waters in Austria (Ruttner-Kolisko, 1955) to Macrodasysida.

Here we provide a taxonomic key to worldwide freshwater gastrotrich genera, modified and simplified from those available in the literature (Balsamo, 1983; Schwank, 1990; Strayer & Hummon, 1991; Kisielowski, 1998).

A key to freshwater Gastrotrich families and genera

1a. Worm-like body, unarmed cuticle or, less frequently, armed with scales and/or spines; several to numerous pairs of adhesive tubes along the body; triradiate pharynx with Y-shaped lumen; pharyngeal pores. Mostly marine and estuarine speciesorder Macrodasysida 2

1b. Tenpin-shaped body, cuticle armed with scales and/or spines or, less frequently, unarmed; two caudal appendages, rarely absent, if present, each appendage generally bears one, rarely two or no, adhesive tubes; no pharyngeal pores. Mostly freshwater species order Chaetonotida 3

- 2a. Body length from 300 to 400 μm ; two pairs of anterior ventral adhesive tubes. Rare. Freshwater, interstitial *Redudasys* (Fig. 2a)
- 2b. Body length up to 220 μm ; one pair of anterior (possibly ventral) adhesive tubes. Rare. Freshwater, interstitial..... *Marinellina* (Fig. 2b)
- 3a. Two caudal appendages, each with/without adhesive tubes 4
- 3b. No caudal appendages; truncated or rounded posterior body end, which may show two protuberances or spines 16
- 4a. Caudal appendages each bearing two adhesive tubes; unarmed body cuticle. Rare. Freshwater, interstitial family Dichaeturidae, *Dichaetura* (Fig. 2c)
- 4b. Caudal appendages each bearing one adhesive tube, or lacking adhesive tube 5
- 5a. No cuticular scales or spines; sickle-shaped caudal adhesive tubes; cephalic cilia not grouped into tufts. Very rare. Freshwater, hyperbenthic or semiplanktonic family Proichthyidiidae 6
- 5b. Cuticular scales and spines generally present; caudal adhesive tubes, if present, mostly straight, long to very short; cephalic cilia grouped into tufts. Common (except *Arenotus* and *Undula*). Freshwater, marine and brackish-water species; periphytic, epibenthic and interstitial family Chaetonotidae 7
- 6a. Short dorsal cephalic cilia arranged in a transverse row; ventral cilia arranged in tufts limited to the head and neck regions. Hyperbenthic *Proichthyidium* (Fig. 2d)
- 6b. No dorsal cephalic cilia; ventral cilia arranged in two longitudinal bands. Semiplanktonic *Proichthyidioides* (Fig. 2e)
- 7a. Caudal appendages bearing adhesive tubes 8
- 7b. Caudal appendages without adhesive tubes *Undula* (Fig. 3f)
- 8a. Very long, segmented caudal furca up to 1/3 of the total body length, which may bear very small scales or spines. Common. Freshwater, epibenthic and periphytic *Polymerurus* (Fig. 2m)
- 8b. Short or very short, unsegmented caudal furca without scales or spines 9
- 9a. Unarmed body cuticle, or armed with numerous scales lacking spines; occasionally a few spines at the furcal base 10

- 9b. Body cuticle with numerous spined and/or keeled scales; spines short to very long, simple or with lateral denticles 15
- 10a. Unarmed body cuticle 11
- 10b. Body cuticle armed with scales lacking spines 12
- 11a. Thin, smooth cuticle which may show very tiny, longitudinal lines; rarely a few spines at the furcal base. Common. Freshwater, brackish-water, rarely marine; epibenthic, periphytic, interstitial *Ichthydium* (Fig. 2f)
- 11b. Very thick, smooth, soft cuticle clearly distinguishable from the epidermis. Rare. Freshwater, interstitial *Arenotus* (Fig. 2g)
- 12a. Small, stalked or keeled scales 13
- 12b. Large, flat, polygonal or circular scales 14
- 13a. Stalked scales. Common. Freshwater, brackish-water, marine; epibenthic, periphytic, interstitial *Aspidiophorus* (Fig. 2h)
- 13b. Keeled scales. Common. Freshwater, brackish-water, marine; epibenthic, periphytic, interstitial *Heterolepidoderma* (Fig. 2i)
- 14a. Numerous polygonal scales. Common. Freshwater, rarely brackish-water and marine; epibenthic, periphytic, interstitial *Lepidodermella* (Fig. 2l)
- 14b. Few circular scales. Rare. Freshwater, periphytic *Fluxiderma* (Fig. 2n)
- 15a. Dorsal scales with double anterior edge, with or without a spine, always without a keel; ventral, interciliary scales similar in shape to the dorsal scales; several pairs of very long and thin spines lateral to the furcal base. Common. Freshwater, epibenthic and periphytic *Lepidochaetus* (Fig. 2o)
- 15b. Dorsal scales with single anterior edge and keel and/or spine; ventral, interciliary scales differ in shape from the dorsal scales. Common. Freshwater, brackish-water, marine; epibenthic, periphytic, interstitial *Chaetonotus* (Figs 3a-e)
- 16a. Two club-shaped, cephalic tentacles; small scales with very short spines on the trunk; truncated or rounded body end with several spines. Rare. Freshwater, epibenthic and semiplanktonic family Neogosseidae 17
- 16b. No cephalic tentacles; reduced or no scales; groups of very long and motile spines on the trunk; truncated or rounded body end which may show bristly protuberances or spines. Rare. Freshwater, epibenthic, periphytic, hyperbenthic and semiplanktonic family Dasydytidae 18

- 17a. Truncated body end with two protuberances, each provided with a tuft of long spines; fine spined scales. Epibenthic and semiplanktonic *Neogossea* (Fig. 3g)
- 17b. Rounded body end with a median group of spines and no protuberances; keeled scales. Epibenthic and semiplanktonic *Kijanebalola* (Fig. 3h)
- 18a. A few dorsal spines up to 1/4 of the total body length scattered on the trunk, or just two caudal spines; ventral cilia arranged in two longitudinal bands; pharynx with two bulbs *Anacanthoderma* (Fig. 4a)
- 18b. Long, lateral spines arranged in groups or in longitudinal rows; ventral cilia arranged in tufts; pharynx with one or no bulbs 19
- 19a. Simple lateral spines or with one lateral denticle; if present, few large and oval scales on the trunk; pharynx without bulb 20
- 19b. Lateral spines with a bifurcate tip and one lateral denticle, or with a sharp tip and 2-3 lateral denticles; if present, numerous, small and keeled scales; pharynx with one bulb 21
- 20a. Dorsal spines and two pairs of caudal spines; thick trunk and caudal spines with a noticeable lateral denticle; a few very large dorsal scales with a lace-like surface *Ornamentula* (Fig. 4i)
- 20b. No dorsal spines; one pair of caudal spines or none; if very long, the lateral spines are strongly bent at the base and gradually become thinner up to a hair-like distal part; spines with or without lateral denticle; if present, small and weakly keeled scales 22
- 21a. Lateral spines with a sharp tip and 2-3 lateral denticles; no scales; body end with a pair of bristled protuberances *Stylochaeta* (Fig. 4h)
- 21b. Lateral spines with a bifurcate tip and one lateral denticle; scales; body end rounded *Dasydytes* (Figs 4b-c)
- 22a. Caudal spines present or absent; straight, medium length, lateral spines; no ventral saltatorial spines 23
- 22b. Caudal spines absent; very long and strongly bent lateral spines extending over the dorsal side; ventral saltatorial spines *Haltidytes* (Fig. 4d)
- 23a. Caudal spines present *Setopus* (Fig. 4e)
- 23b. Caudal spines absent *Metadasydytes* (Fig. 4f)

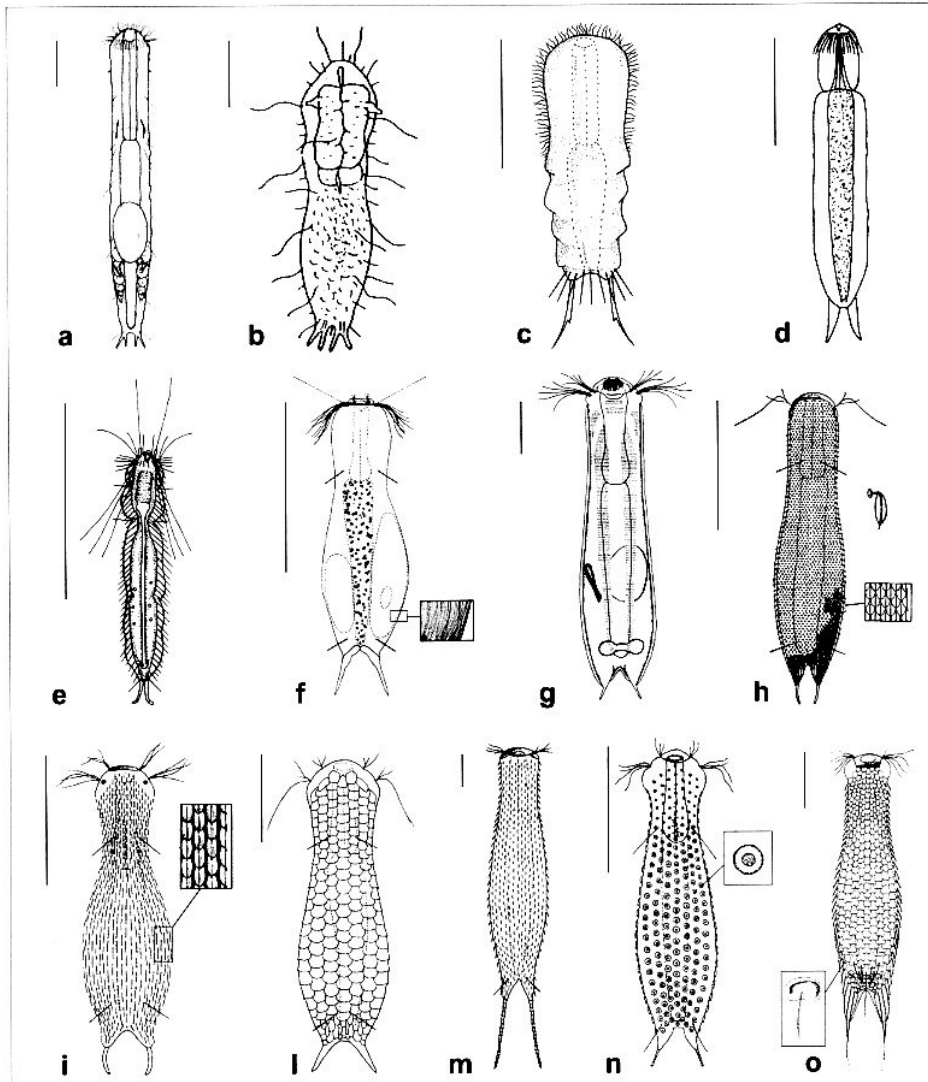


Fig. 2. Morphotypes of some freshwater gastrotrich genera. Macrotrichida, *incertae sedis*: a - *Redudasys*; b - *Marinellina*. Chaetonotida: Dichaeturidae - c, *Dichaetura*; Proichthyidae, d - *Proichthyidium*; e - *Proichthyoides*; Chaetonotidae, f - *Ichthyidium*; g - *Arenotus*; h - *Aspidiophorus*; i - *Heterolepidoderma*; l - *Lepidodermella*; m - *Polymerurus*; n - *Lepidochaetus*. Scale bars, 50 μ m. (a, g, modified from Kisielewski, 1987; b, modified from Ruttner-Kolisko, 1955; c, f, h-n, modified from Balsamo, 1983; d, modified from Cordero, 1918; e, redrawn from Sudzuki, 1971)

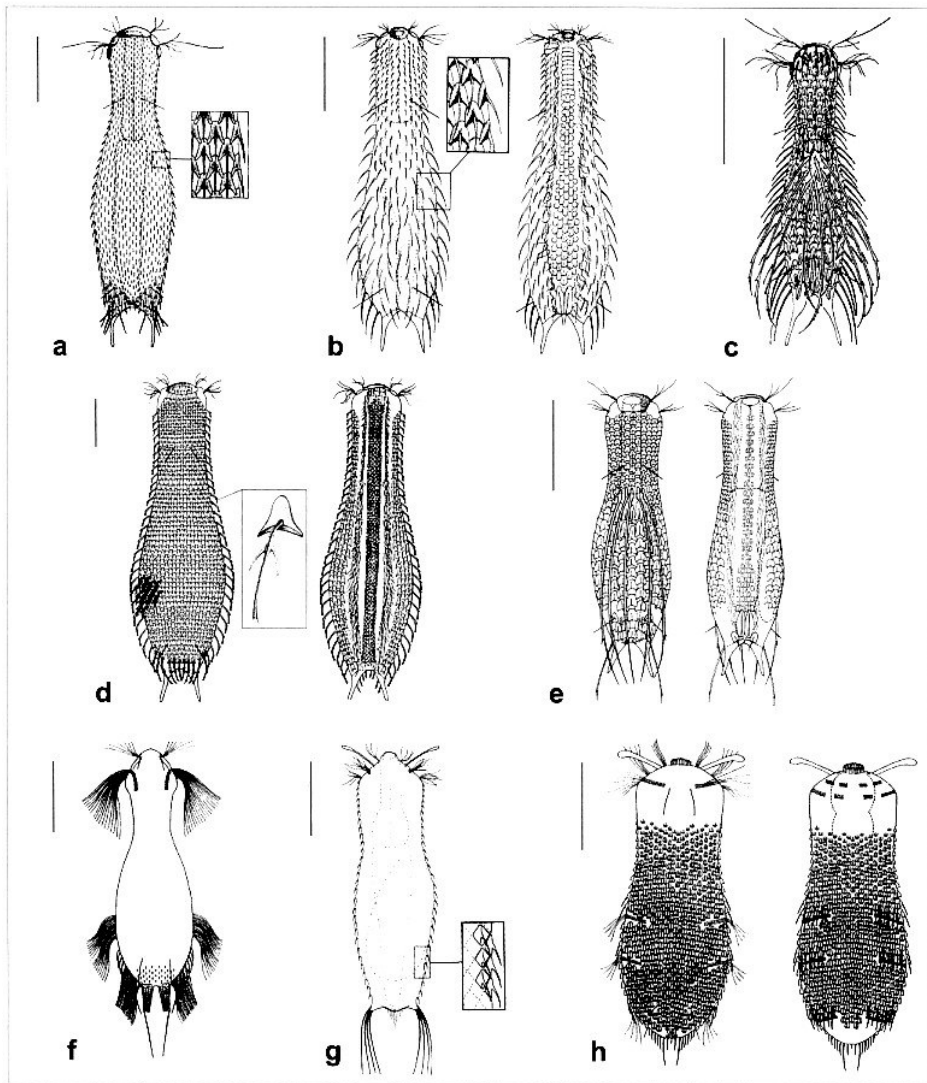


Fig. 3. Morphotypes of some freshwater gastrotrich genera and subgenera. Chaetonotida: Chaetonotidae, a – *Chaetonotus* (*Euchaetonotus*); b – *Chaetonotus* (*Euchaetonotus*); c – *Chaetonotus* (*Hystricochaetonotus*); d – *Chaetonotus* (*Schizochaetonotus*); e – *Chaetonotus* (*Zonochaeta*); f – *Undula*; Neogosseidae, g – *Neogosseia*; h – *Kijanebalola*. Scale bars, 50 μm . (a-e, g, modified from Balsamo, 1983; f, h, modified from Kisielewski, 1990)

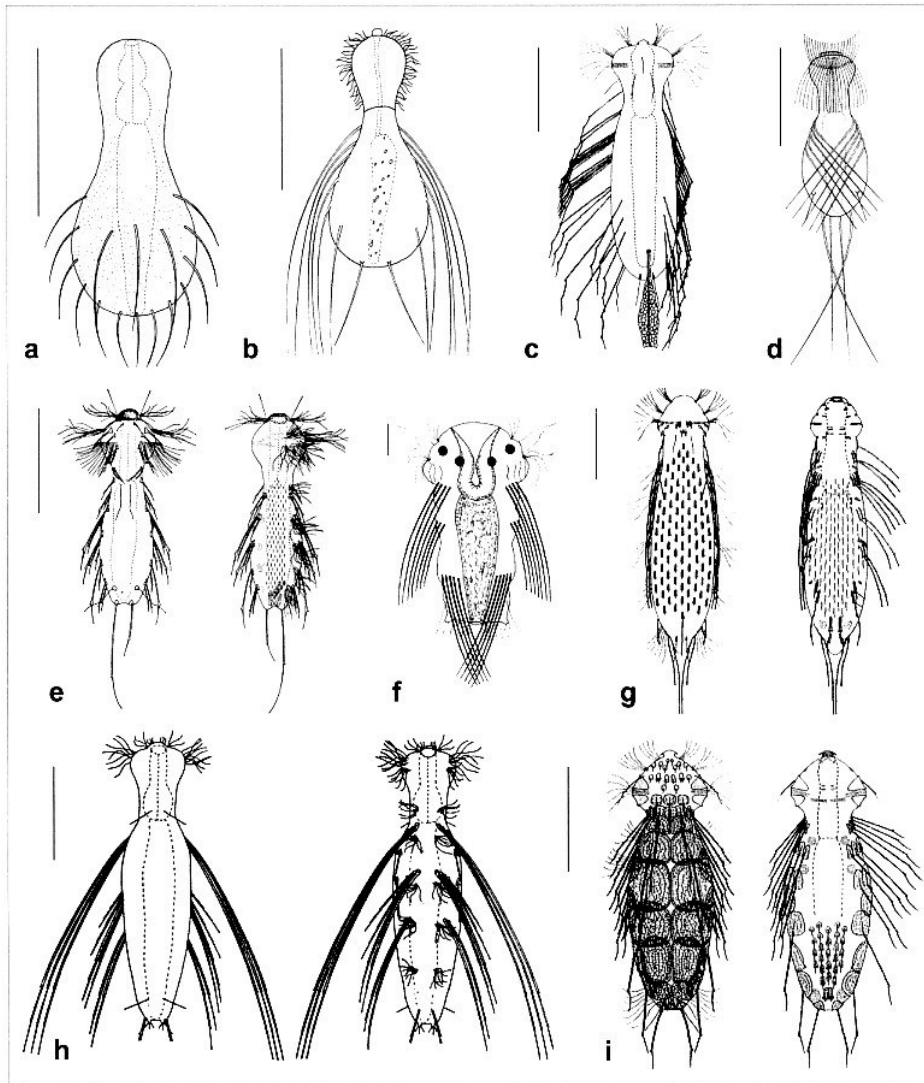


Fig. 4. Morphotypes of some freshwater gastrotrich genera and subgenera. Chaetonotida: Dasydytidae, a – *Anacanthoderma*; b – *Dasydytes* (*Chitonodytes*); c – *Dasydytes* (*Dasydytes*); d – *Haltidytes*; e – *Setopus*; f – *Metadasydytes*; g – *Dasydytes* (*Prodasydytes*); h – *Stylochaeta*; i – *Ornamentula*. Scale bars, 50 μ m. (a, b, d, e, modified from Balsamo, 1983; c, g, i, modified from Kisielewski, 1990; f, modified from Roszczak, 1971)

Characteristics and morphology

There are two freshwater macrodasyid species known to date to fit the general morphology of this order, i.e. a worm-like body shape, a muscular pharynx with a triradiate Y-shaped lumen and two dorsolateral openings (pharyngeal pores), and numerous adhesive tubes along the entire body (Fig. 1a). Macrodasyida are proterandric or simultaneous hermaphrodites, with one or two testes and one or two ovaries lateral to the anterior and the posterior gut, respectively. A pair of sexual accessory organs are usually present, making the reproductive system much more complex than that of chaetonotids (Ruppert, 1991). Adults of *R. fornerisae* show testes and ovaries, but no accessory organs (Kisielewski, 1987), whereas the sexual condition of *Marinellina* is still unknown.

Chaetonotid gastrotrichs differ from the macrodasyids in their tenpin-shaped, transparent body which is divided into three, easily recognizable regions: a distinct head, an ovate trunk and a caudal furca (Fig. 1b,c). The body is very small (60-770 μm) and completely covered with a cuticle usually with scales and spines. An extensive ventral ciliature, in some species reduced to a few tufts, allows gliding locomotion. The rounded head bears clusters of sensory cilia, several cuticular plates with a protective function, and the subapical mouth which is often strengthened by a ring of protrusible, hook-like structures. A thick, muscular pharynx with a triradiate, inverted Y-shaped lumen, very similar to that in the Nematoda, extends up to the trunk region and is surrounded by a large, bilobed brain. The intestine often contains refractile inclusions and opens into the ventral, subterminal anus. A cyrtocytic protonephridium lies at each side of the anterior gut emptying into a ventral pore. There are two lateral and caudal ovaries in the trunk, which appears very enlarged when one or two full-grown oocytes are present. Compared with the size of the adult, the dimensions of the mature oocyte are among the largest in the animal kingdom: the length of the egg can reach more than one third that of the body. In older specimens of several species (mostly Chaetonotidae), a cluster of spermatozoa develops at each side of the intestine, and an unpaired, ventrolateral, horse-shoe organ of unclear function (X-organ) winds ventrally round the terminal portion of the gut (see below). Two long, duo-gland adhesive tubes form the caudal furca, which is reduced or even absent in semiplanktonic species (Ruppert, 1991). Remane (1936), Hyman (1951), Schwank (1990) and Ruppert (1991) provide detailed accounts of the gross and the microscopic anatomy of Gastrotricha, which are summarised in Table 1.

The general morphology of gastrotrichs can be regarded as advantageous to a meiobenthic life style, as all are minute, with a more or less slender, flat and soft body (Giere, 1993). Freshwater gastrotrichs usually glide on the sediment or vegetation surface, occasionally swimming for short distances by ciliary locomotion. However, they can also creep into interstitial narrow spaces using muscular contractions of the body.

The caudal furca may act as an anchor, as secretions from a duo-gland system allow the animal to stick firmly to surfaces and detach soon after (Ruppert, 1991). This ability is especially evident in interstitial and lotic species, which also usually bear smaller cuticular scales and spines than those in epibenthic species. These short spines may work in the same way as annelid chaetae, allowing the animal

Table 1. The anatomy and habitat requirements of gastrotrich families.

Order Macrodasysida The systematic position of *Redudasys fornerisae* (Fig. 2a) and *Marinellina flagellata* (Fig. 2b), both reported only once from interstitial freshwater habitats, is still unclear (cf. Strayer & Hummon, 1991).

Order Chaetonotida

Family Dichaeturidae: no cuticular armature; caudal furca with four adhesive tubes. One genus, two species. Freshwater, interstitial (Fig. 2c)

Family Proichthyidiidae: no cuticular armature; caudal furca with two adhesive tubes. Two genera, two species. Freshwater, hyperbenthic, semiplanktonic (Fig. 2d,e).

Family Chaetonotidae: cuticular scales and spines generally present and greatly differing in morphology among genera and species; caudal furca with two adhesive tubes. Ten genera are found in inland waters, five of which, *Aspidiophorus*, *Chaetonotus*, *Heterolepidoderma*, *Ichthydium* and *Lepidodermella*, also include marine species. In freshwater environments, 265 periphytic, epibenthic and interstitial species have been reported (Figs 2f-n, 3a-f).

Family Neogosseidae: cuticular armature; no caudal furca; a couple of knob-like, cephalic tentacles. Two genera and eight species. Freshwater, epibenthic and semiplanktonic (Figs 3g,h).

Family Dasydytidae: cuticular armature which may be secondarily reduced; groups of very long and motile spines; caudal furca reduced or absent. Eight genera and 31 species. Freshwater, epibenthic, periphytic, hyperbenthic and semipelagic (Fig. 4a-h).

to burrow into the sediment. In contrast, the spines of various lengths and morphologies usually present in the epibenthic gastrotrichs, appear to have only a protective role. The very long and motile spines typical of the semiplanktonic species, which are actively raised after disturbance or during pauses in swimming, probably have a dual function of protection and support.

Collection and specimen preparation

Most studies have been qualitative compilations of gastrotrich species (e.g., Schwank, 1990), and it is only during the last two decades that quantitative studies have been carried out (e.g. Kisielewski & Kisielewska, 1986; Hummon, 1987; Nesteruk, 1991, 1996a,b).

Sampling techniques in freshwater habitats are generally similar to those used in marine systems. Qualitative sampling of sediment involves using a shovel, a jar or a corer, while quantitative work mostly uses a small corer (2-5 cm in diameter), such as a syringe with a cut-off anterior end. Nesteruk (1991) devised a special apparatus for studying the vertical distribution of lacustrine species. Periphytic and semiplanktonic species are collected by sampling clumps of vegetation mixed with sediment and by repeatedly filtering the water through a 30 µm mesh plankton net. Replicated small samples are more representative of the community of a site than a single large sample, because the distribution of gastrotrichs, as for most meiofaunal taxa, is patchy (Higgins & Thiel, 1988; Giere, 1993).

The sample should be processed directly to extract living animals, which for most uses are more suitable than fixed specimens. Vegetation is repeatedly rinsed and squeezed, and the supernatant is filtered through a 30 µm mesh sieve. Either

stirring the sediment into a suspension and decanting the water through a fine mesh net, or centrifugation using a density gradient, are effective methods for the qualitative extraction of gastrotrichs. However, these techniques cannot be used for quantitative studies, as these animals are too small to be retained efficiently, even in very fine mesh sieves (Hummon, 1981). Additional checks of the sample some time after collection are recommended, since as a result of resting eggs, species initially absent may be found later (Fregni, 1998).

Prior treatment of the sample with a narcotic agent in order to detach the animals from sediment particles is effective. This can be done by repeated washings of small amounts of substrate (2-3 cm²) in a 4% aqueous solution of MgCl₂ (Higgins & Thiel, 1988). Staining the sample with a vital stain such as neutral red in a very dilute aqueous solution (1:10 000) may be useful to recognize living specimens. Treatment with a 1% aqueous solution of MgCl₂ for 10 minutes is recommended if the sample must be immediately preserved. Preservation may be carried out in 10% borax-buffered formalin with rose bengal (1%) to facilitate sorting. The loss of specimens that adhere to sediment particles can only be avoided by careful scanning of the sediment material and manual extraction with a pipette under a stereomicroscope.

Due to the great difficulty in extracting all the animals from the sediment, and especially from organic matter and mud, the efficiency of the procedure followed in quantitative studies must be verified so as not to underestimate the number of specimens (Hummon, 1981; Nesteruk, 1987, 1993).

Gastrotrichs should ideally be studied when freshly collected, as the shape and general morphology of their soft bodies are badly distorted by fixatives. Narcosis may be performed by means of a few drops of an aqueous solution of MgCl₂ (4%) or bupivacaine (0.5%) slowly added to the water containing animals. Once relaxed, specimens can be directly mounted in the same medium on a slide for observation. Permanent mounts can be prepared in 10% formalin or in a mixture of formalin-glycerol (3:1) and sealed with glyceel or nail polish. However, permanent mounts do not allow a complete taxonomic study, as many diagnostic features deteriorate over time.

For taxonomic analysis, the use of a light microscope equipped with DIC optics is essential. Cuticular details may require SEM survey, for which specimens are prepared by critical point drying or the hexamethyldisilazane technique (Luporini & Tongiorgi, 1972; Hochberg & Litvaitis, 2000b). Micrographs and videotapes should be used for intra-specific morphological comparisons of specimens from different localities (Todaro *et al.*, 1995).

Biology and life history

Chaetonotids are eutelic (i.e. the body cell number remains unchanged from juveniles to adults) and show direct development, a relatively short life cycle and parthenogenetic reproduction. Three life stages follow after hatching: a pre-reproductive phase, when somatic growth occurs; a reproductive phase, during which the animal successively lays several, parthenogenic eggs; and a post-reproductive phase, in which several species produce spermatozoa so becoming hermaphrodite.

The functionality of these spermatozoa is still open to question (Hummon, 1984a; Levy, 1984; Balsamo & Todaro, 1988).

At 20° C, the lifespan of chaetonotids usually ranges from 15-23 days (Hummon, 1986; Balsamo & Todaro, 1988). At hatching, a chaetonotid is about two thirds the length of the adult and reaches adulthood 2-5 days later depending on the temperature. At this time, the first egg is laid by rupture of the body wall. Four eggs are usually produced over a period of 5-10 days, each developing in 1-2 days by apomictic parthenogenesis (Hummon, 1984b). The final egg may be a resting egg, which is morphologically distinguishable from the others by its thick envelope, dark colour and slightly larger size (Levy, 1984). The resting eggs can survive in unfavourable conditions, allowing maintenance of the population over seasons and species dispersal over long distances. These eggs are produced in higher number in response to environmental stress, but the factors which influence the rate of their production and cause their hatching are not known (Levy, 1984).

The post-reproductive phase of numerous chaetonotids is characterized by the development of one or two clusters of spermatozoa and the appearance of the X-organ (Hummon, 1984a). Spermatozoa are few and differ in morphology depending on the species, often being aflagellate (Kisielewska, 1981; Balsamo & Todaro, 1988). A third kind of egg, subject to meiotic events, has been reported in *Lepidodermella squamata* (Chaetonotidae) during this phase (Hummon, 1984c).

Sperm transfer has never been observed, although an internal cross-fertilization is presumably carried out, in which the X-organ may play an important role. More detailed studies are necessary to explain the real importance of this peculiar sexual phase which in combining parthenogenic and hermaphroditic phases in the same generation seems to be unique in the animal kingdom (Levy, 1984; Hummon, 1986). Such a life history might allow fast growth of the population through parthenogenesis, and also introduce genetic variation through cross-fertilization (Balsamo, 1992).

Ecological role and requirements

Gastrotrichs are part of the microphagous, detritivorous, benthic community, with bacteria representing their primary food source (Bennett, 1979). However, they feed also on unicellular algae, protozoans, fungi, particulate organic matter, and occasionally very small invertebrates. Like nematodes, gastrotrichs ingest food by means of the powerful sucking action of the muscular pharynx. The chemotactile ability of marine macrodasyids to discriminate among different strains of natural bacteria (Gray & Johnson, 1970) is likely to occur in freshwater species.

Due to their minute size, gastrotrichs may constitute a link between the microbial-loop and the higher trophic levels of freshwater ecosystems. They feed on particles of a size not efficiently grazed by larger invertebrates and, in turn, they serve as prey for a number of other organisms, including heliozoans, amoebae, cnidarians and tanypodine midges (Strayer & Hummon, 1991).

The contribution of gastrotrichs to the functioning of freshwater ecosystems is little known, and studies to date have produced conflicting results. In a study of Mirror Lake, New Hampshire (USA), Strayer (1985) estimated gastrotrich pro-

duction at about $100 \text{ g (dw)m}^{-2} \text{ y}^{-1}$, a value representing less than 1% of the total production of the zoobenthic community. In contrast, Nesteruk (1996a) found densities and biomass up to 20 times higher in three Polish lentic water bodies. Gastrotrichs, together with nematodes and rotifers, are one of the most abundant freshwater meiobenthic components. (e.g. $158 \text{ ind}/10 \text{ cm}^2$ equal to 3.9% of total meiofauna in Hummon, 1987; 9.8% of total meiofauna in Schmid-Araya, 1997). Given their high rate of population turnover and selective trophic behaviour, a significant influence of gastrotrichs on ecosystem dynamics can be hypothesized (Palmer *et al.*, 1997).

With the exception of Nesteruk (1986), who demonstrated a frequent decrease in density of some populations during the winter season, factors controlling natural population dynamics have not yet been examined thoroughly. Field and laboratory studies suggest that the physical and chemical characteristics of water and pollutants of anthropogenic origin can strongly affect gastrotrich populations (Hummon, 1974; Hummon *et al.*, 1978; Hummon & Hummon, 1979). Freshwater gastrotrichs appear very tolerant to a variety of abiotic environmental factors, such as the particle size of the sediment, water temperature and pH, but sensitive to variations in water regime. Drought and freezing periods affect not only the abundance but also the structure of community, since the ability to maintain populations, presumably from resting eggs, varies among species (Kisielewski, 1981).

The spatial and temporal distribution of gastrotrichs, which are found predominantly in lentic rather than in lotic waters, is often patchy and likely depends on the presence of particular organic matter and bio-film as food sources. The occurrence and abundance of most freshwater species which are epibenthic, hyperbenthic and periphytic are clearly influenced by the degree of eutrophication of the water body, the neighbouring gastrotrich assemblages, the water regime and the presence of aquatic vegetation (Kisielewski, 1981). Usually, the more eutrophic the water body, the richer and more diverse the gastrotrich fauna, often including species secondarily adapted to a semiplanktonic lifestyle (Kisielewski, 1981, 1991; Nesteruk, 1996a,b). Densities ranging from 9.2 to $63.9 \text{ ind}/\text{cm}^3$ have been reported for water bodies with a medium to high trophic degree, whereas in oligotrophic waters, density values range from 1.6 to $5.8 \text{ ind}/\text{cm}^3$ (Kisielewski & Kisielewska, 1986; Tretjakova, 1991; Nesteruk, 1993).

As reported for other meiobenthic taxa, the vertical distribution of freshwater gastrotrichs is presumably affected by oxygen, water flow, predation, grain size and the detritus content of the sediment (Palmer, 1990; Danielopol *et al.*, 1997). While in muddy substrates gastrotrichs are preferentially epibenthic or hyperbenthic, in sandy bottoms interstitial species prevail (Balsamo & Fregni, 1995) and are most abundant in the upper five centimetres, even if they can reach a depth of 30-40 cm (Schmid-Araya, 1997). Gastrotrichs move by crawling, sliding or creeping on sand grains, and should be regarded as not capable of burrowing into compact sediments. In contrast with this view, Nesteruk (1991) reported an abundant gastrotrich fauna down to 10-17 cm in the silty sediment of three Polish lakes of different trophic status. However, since the same study reported gastrotrichs with a semiplanktonic life-style (i.e. Dasydytidae) deep in the sediment, these findings should be considered with caution.

In lotic gravel sediments, gastrotrich abundance is related to a variety of inter-

acting parameters, such as sediment depth, flow and water temperature, and decreases with increasing discharge. The highest gastrotrich densities have been reported in deeper lotic sediments, possibly due to heterogeneous grain sizes facilitating oxygen penetration into interstitial habitats (Schmid-Araya, 1997).

The dynamic interaction between the different ecosystem compartments in freshwater sediments (Ward *et al.*, 1998) probably influences gastrotrichs in the same way as it does other meiobenthic taxa (see Chapter 9). Sediments derived from crystalline primary rocks (i.e. quartz) with an open pore system are traps for detritus, while terrigenous sand tends to become clogged with fine silt, reducing permeability and making colonization difficult.

Hence, lotic and lentic sandy sediments are richer in species and individuals if the silt fraction is slight, meaning that medium to coarse substrata are colonized preferentially. The morphological and lithological features of the substratum, as well as its geographical location, appear to be of secondary importance, in agreement with the findings on the ecological preferences of interstitial gastrotrichs inhabiting marine sediments (Todaro *et al.*, 1995). Interstitial freshwater species are still poorly documented as is their biology. However, there is growing evidence that most meiobenthic species can move between the epibenthos, periphyton and plankton, suggesting that they are not exclusive to the interstitial habitat but ubiquitous (Kisielewski, 1991; Balsamo & Fregni, 1995; Fregni *et al.*, 1998).

Resting stages, parthenogenetic reproduction and relatively short life cycles are the key features enabling gastrotrichs to survive in ecologically distinct habitats where they are diverse and abundant. Moreover, in lotic environments, at least, gastrotrich species show a notable resistance and resilience to many kinds of disturbances (Palmer *et al.*, 1992, 1997). Their ability to transfer passively among different water bodies by means of resting eggs, or between different habitats in the same water body through drift in the water column, may account for their wide distribution and their important role among the fauna of 'recovering' benthic ecosystems.

Biogeography/global distribution patterns

Gastrotrichs are a regular component of the freshwater meiobenthic community world-wide, and many species are assumed to be cosmopolitan. The wide geographical range reported for a number of species is explained mainly by the passive dispersal of resting stages, which allow for species dispersal over long distances. However, information regarding the geographical distribution of single species is patchy, as most studies have focused on only a few regions and sampling strategies are not comparable. Further problems arise from difficulties in species identification, due to intraspecific morphological variability and taxonomic instability. Based on current knowledge, it seems that most genera have a cosmopolitan distribution, with the exception of the questioned *Fluxiderma*, or of the taxa recorded only once or twice: *Marinellina* and *Dichaetura* in Europe; *Arenotus*, *Ornamentula*, *Proichthyidium*, *Redudasys* and *Undula* in South America; and *Proichthydioides* in Japan. The apparent localized distribution of these genera may

be in part due to limited investigation of similar biotopes in different regions of the world.

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