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Gastrotricha

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Introduction

Gastrotrichs (Figure 1) are small invertebrates that live on sediments, among vegetation, and sometimes in the pelagic zone of standing and running waters around the world. They are among the smallest of invertebrates – most species are less than 0.2 mm long. They are among the most widespread and abundant of freshwater animals, with population densities often 100 000–1 000 000 m^{-2}, but are often neglected because of their small size. Their ecology and distribution is poorly known, many species remain to be discovered, and their roles in freshwater ecosystems have scarcely been investigated.

Anatomy and Physiology

Gastrotrichs are small colorless animals (Figure 1); the species of inland waters are 0.05–0.8 mm long when fully grown, but most are 0.1–0.2 mm. The chaetonotids, which are prevalent in inland waters, are shaped like a bowling pin, with a more or less distinct head (Figure 2), and the macrodasyids are strap shaped (Figure 3). In many species, the body is covered with scales, which often bear spines. The long lateral spines of *Haltidytes* are movable and are used in locomotion. The posterior end of most inland-water gastrotrichs is formed into a furca (fork) that contains adhesive tubules, which allows the animal to attach itself to the substratum. The ventral side of the animal bears long rows or patches of cilia, which the animal uses to propel itself with a gliding motion.

Gastrotrichs are small and transparent enough that internal organs are readily visible in living animals (Figure 4). The digestive system begins with a typically subterminal mouth, sometimes surrounded by a ring of bristles. Behind the mouth is a muscular pharynx, similar to that of nematodes, which is capable of a powerful pumping action, and a long gut ending at the anus.

Developing eggs often are visible on either side of the gut. There are no oviducts, so ripe eggs are released through a break in the body wall. Older animals may contain sperm sacs and developing sexual eggs lateral to the gut. The unpaired X-organ, whose function may be reproductive, lies behind the developing eggs, near the anus.

The bilobed brain lies astride of the pharynx. Inland-water gastrotrichs do not have eyes, but the head bears tufts of sensory bristles. Gastrotrichs probably can sense light, smells, and touch. There are protonephridia in the anterior midbody, but no special circulatory or respiratory systems.

Life History

The life history of freshwater gastrotrichs is remarkable and only partially understood (Figure 5). Gastrotrichs hatch from the egg at a large size – about two-thirds of adult body length. When hatched, they already contain developing parthenogenetic eggs. These eggs develop rapidly, and may be laid within a day of the mother's hatching. It appears that gastrotrichs may lay a series of four parthenogenetic eggs within the first few days of their lives. Parthenogenetic eggs usually are tachyblastic, developing and hatching rapidly after being laid. Less commonly, the last parthenogenetic egg may be an opsiblastic egg, a resting egg that has a thick shell and is resistant to freezing and desiccation.

Remarkably, after the animal lays its last parthenogenetic egg, it develops into a hermaphrodite, which produces sperm and meiotic sexual eggs. Sperm transfer and fertilization have not yet been observed; because the sperm are few (32–64) and nonmotile, it seems likely that some special mechanism of sperm transfer must exist. The entire life span is only a few days to a few weeks.

The gastrotrich life cycle allows for considerable ecological flexibility. The parthenogenetic phase can produce very rapid population growth under favorable conditions – growth rates of 10–50% day^{-1} have been reported from laboratory cultures. The tough resting eggs can carry a population through unfavorable times, and the sexual phase introduces genetic recombination.

Diet

Gastrotrichs feed by browsing on biofilms of bacteria, algae, fungi, and dead organic matter. There have been no detailed studies of gastrotrich diets in nature, but bacteria and possibly bacterial exopolysaccharides probably are the most important food of most species. No one has described whether the feeding behavior or diet of the few planktonic gastrotrichs might be distinctive.

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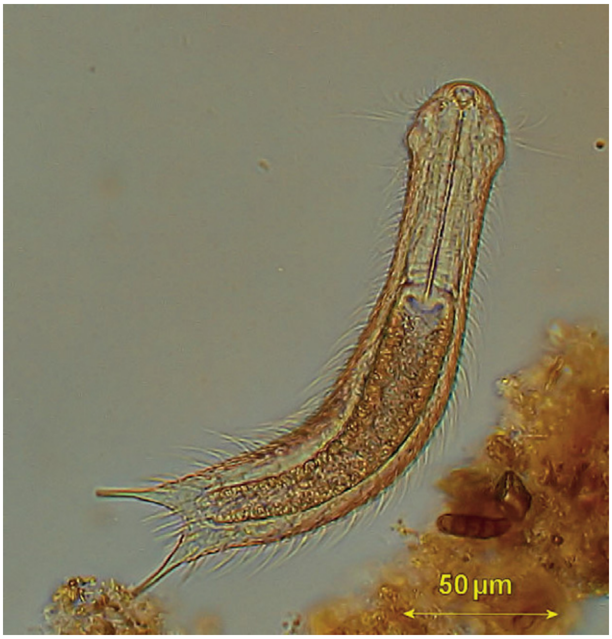

Figure 1 Photograph of *Chaetonotus*, a common inland-water gastrotrich. Courtesy of Graham Matthews (http://www.gpmatthews.nildram.co.uk/microscopes/pondlife_worms.html).

Distribution and Abundance

Gastrotrichs are abundant in most kinds of inland-water habitats. The few careful attempts to quantify population density have reported densities of 50 000–1 200 000 gastrotrichs m^{-2}, which, because of their tiny body size, represents a biomass of <0.1 g dry mass m^{-2}. Many bodies of inland water support 10–50 species of gastrotrichs. *Chaetonotus* and other members of the Chaetonotidae often are dominant genera in inland waters, in terms of species richness and density. Dasydytids often are common in weedy waters, and dasydytids and neogosseids seem to be more common and species rich in the tropics.

Gastrotrichs are found in all climatic zones of the world, from Antarctica to tropical lakes. Many genera of inland-water gastrotrichs are widely distributed across most continents. Exceptions include the rare genera *Redudasys*, *Arenotus*, *Undula*, and *Ornamentula* (known only from Brazil), *Dichaetura* and *Marinellina* (Europe), *Proichthydium* (Argentina), and *Proichthyioides* (Japan). It is not clear at this point if these apparently restricted distributions are real, or simply are artifacts of inadequate collecting. Quite a few gastrotrich species have been reported to have multicontinental distributions, but such reports should be treated cautiously until more critical studies are made of the taxonomy and limits of gastrotrich species. The ranges of individual species are poorly understood, and there is no information at all about the conservation status, endangerment, or extinction of any inland-water gastrotrich species.

Most gastrotrichs live on vegetation or at the sediment–water interface. In muddy lake and pond sediments, most gastrotrichs are found within 1 cm of the sediment–water interface, but it seems likely that gastrotrichs may live in deeper layers of coarse-grained stream sediments. A few species, particularly neogosseids, are part of the plankton of tropical ponds and lakes. Gastrotrichs are especially abundant in habitats that are rich in organic matter, such as eutrophic lakes, organically rich sediments, beds of vegetation, and bogs, and it has been suggested that gastrotrich density is positively correlated with lake productivity.

Although few animals can tolerate anoxic environments, gastrotrichs often are abundant in anoxic lake sediments. The physiological basis for their tolerance of anoxia is not understood. Gastrotrichs are sensitive to salinity, so inland brackish waters probably support a distinctive gastrotrich fauna. I am not aware of any studies of the gastrotrichs of brackish inland waters, however. Other factors that probably influence the distribution and abundance of individual gastrotrich species include water temperature, the grain size and stability of sediments, populations of bacteria (which serve as food), competitors and predators, and the concentrations of anthropogenic contaminants.

Only a few studies have followed gastrotrich populations through the year. It appears that populations may be lowest during the winter.

Ecological Roles

Little is known about the roles that gastrotrichs play in inland-water food webs and ecosystems. In view of their high densities (often >100 000 m^{-2}) and their high rates of population growth (10–50% day^{-1}, in culture), it is conceivable that gastrotrichs may be abundant enough in some places to affect the composition of bacterial communities or contribute significantly to benthic productivity. They are eaten by various invertebrates, but it is not known whether they often are an important part of the diet of any predator.

Evolutionary Relationships

The evolutionary relationships between gastrotrichs and other invertebrate phyla have long been controversial and remain unresolved despite the recent application of molecular techniques. Gastrotrichs traditionally were allied with rotifers, nematodes, kinorhynchs, priapulids, and nematomorphs in a

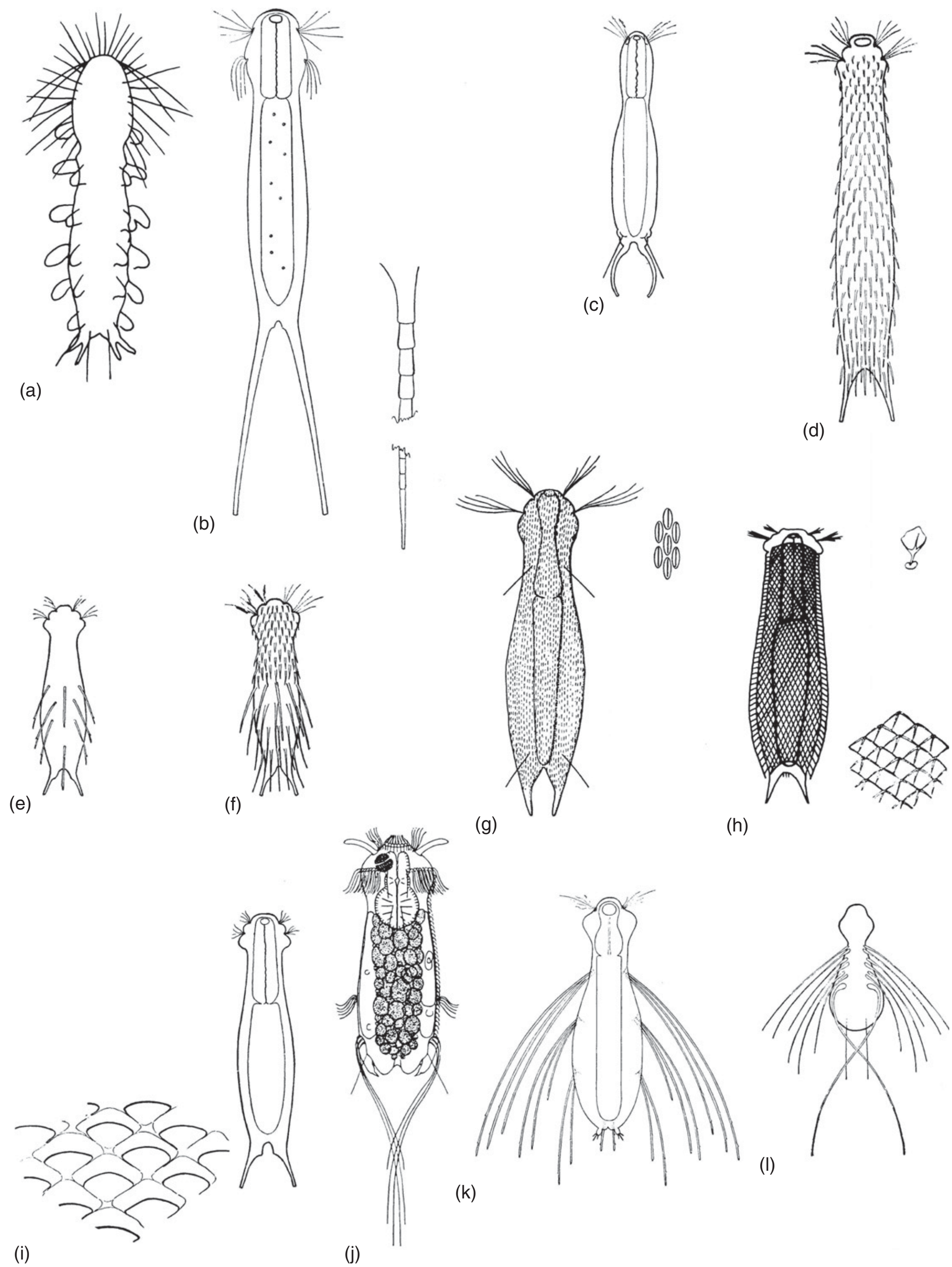

Figure 2 Some inland-water chaetonotid gastrotrichs. (a) *Dichaetura*; (b) *Polymerurus*, showing detail of ringed furca; (c) *Ichthydium*; (d–f) *Chaetonotus*, showing examples of different kinds of spines; (g) *Heterolepidoderma*, with detail of scales; (h) *Aspidiophorus*, with detail of coat of scales and single stalked scale; (i) *Lepidodermella*, with detail of scales; (j) *Neogossea*; (k) *Stylochaeta*; (l) *Dasydytes*. From Strayer and Hummon (1991), after various sources.

loosely defined group called the Aschelminthes. While rejecting the idea of the aschelminthes, various recent phylogenetic analyses have placed the gastrotrichs with the rotifers, micrognathozoans, and cycliophorans, with the nematodes, arthropods, and tardigrades, or with the flatworms, rotifers, acanthocephalans, and gnathostomulids, so the origin and relationships of the gastrotrichs are still far from clear.

Classification of the different groups of gastrotrichs likewise is in a state of flux. The phylum contains two

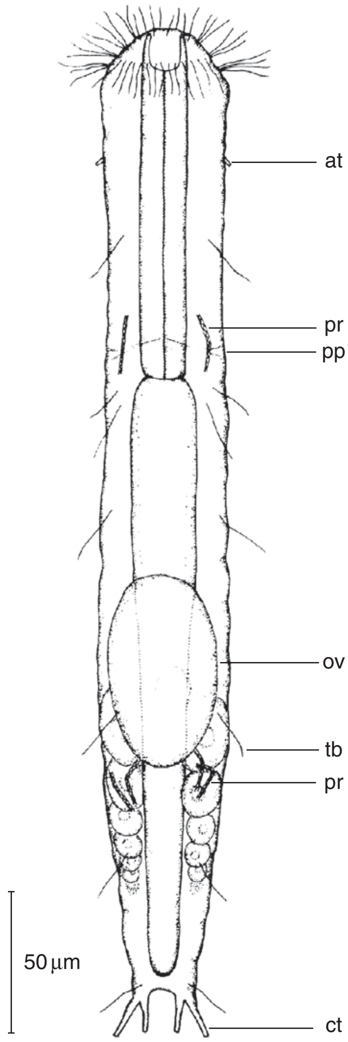

Figure 3 A freshwater macrodasyid gastrotrich, *Redudasys fornerise*, from Brazil; at, anterior adhesive tubules; ct, caudal adhesive tubules; ov, ovum (egg); pp, pharyngeal pore; pr, flame bulbs of protonephridia; tb, tactile bristle. From Kisielewski, J. (1987). Two new interesting genera of Gastrotricha (Macrodasyida and Chaetonotida) from the Brazilian freshwater psammon. *Hydrobiologia* 153: 23–30. With kind permission of Springer Science and Business Media.

generally well-defined orders: the Macrodasyida and the Chaetonotida (Table 1). The macrodasyids are almost entirely marine, so far known from inland waters by just one species from Austria and another from Brazil (Figure 3). Some recent molecular analyses suggest that the macrodasyids do not form a natural evolutionary unit and may need to be reclassified. In any case, the evolutionary connections between the two poorly known freshwater macrodasyids and the remainder of the class are obscure. It is almost certain that additional macrodasyids will be discovered in inland waters, which may elucidate the origins and evolutionary relationships of these animals.

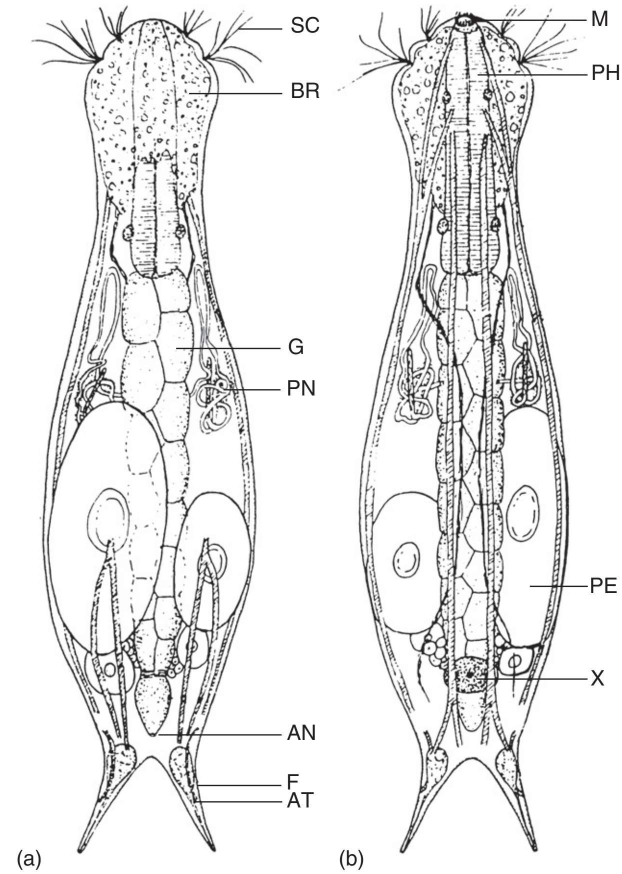

Figure 4 Diagram of gastrotrich anatomy, in (a) dorsal and (b) ventral views; AT, adhesive tubes; AN, anus; BR, brain; F, furca; G, gut; M, mouth; PH, pharynx; PE, parthenogenetic egg; PN, protonephridium; SC, sensory cilia; X, X-organ. From Strayer and Hummon (1991), after Voigt (1958).

The Chaetonotida contains ~300 described species from inland waters, but many more species certainly remain to be discovered and described. Table 1 shows the current classification of the inland-water gastrotrichs. Very little is known about the evolutionary relationships among families and genera of the Chaetonotida. Morphological analyses suggest that most members of the Chaetonotidae are more primitive than the Dasydytidae and Neogosseidae, but that the Chaetonotidae might not constitute a natural evolutionary group. Further, some of the chaetonotid genera that are currently recognized (e.g., *Chaetonotus*, *Ichthydium*) are almost surely not natural evolutionary units and will need to be redefined.

Collection and Identification

Qualitative samples of gastrotrichs may be collected simply by washing bits of vegetation or sediment and

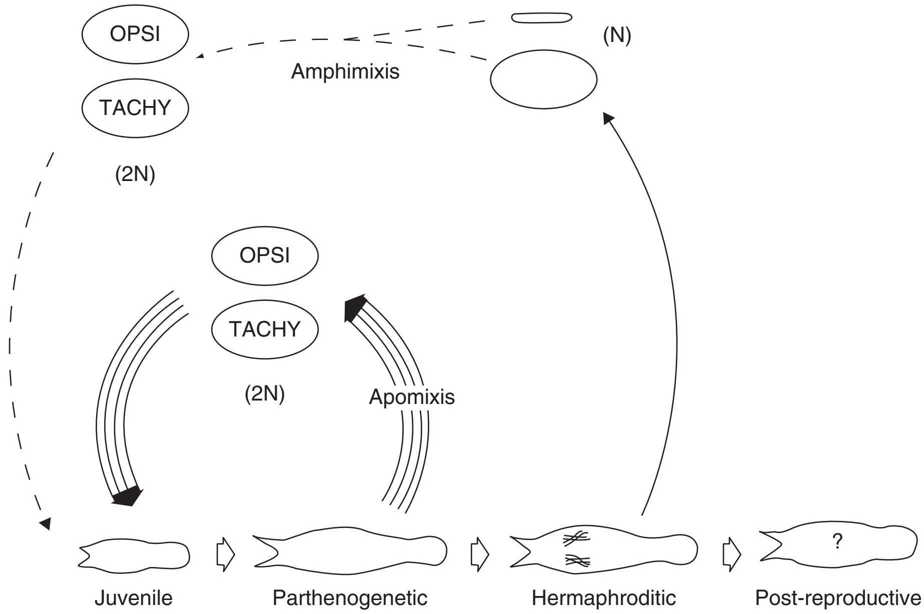

Figure 5 Schematic diagram of the proposed generalized life cycle for freshwater chaetonotid gastrotrichs, based predominately on study of *Lepidodermella squamata*. Dashed lines show hypothetical events which have not yet been demonstrated. From Strayer and Hummon (1991), from Levy (1984), after ideas presented by Levy and Weiss (1980). OPSI, opsiblastic egg; TACHY, tachyblastic egg.

Table 1 Current classification of the inland-water gastrotrichs

Phylum Gastrotricha
Order Macrodasyida
Genera *Marinellina*, *Redudasys*[a]
Order Chaetonotida
Family Chaetonotidae
Genera *Arenotus*, *Aspidiophorus*, *Chaetonotus*, *Fluxiderma*, *Heterolepidoderma*, *Ichthydium*, *Lepidochaetus*, *Lepidodermella*, *Polymerurus*, *Rhomballichthys*, *Undula*
Family Dasydytidae
Genera *Anacanthoderma*, *Chitonodytes*, *Dasydytes*, *Haltidytes*, *Ornamentula*, *Setopus*, *Stylochaeta*
Family Dichaeturidae
Genus *Dichaetura*
Familt Neogosseidae
Genera *Kjanebalola*, *Neogossea*
Family Proichthydidae
Genera *Proichthydium*, *Proichthydioides*

[a]The familial placement of the freshwater macrodasyids is uncertain.

examining the residue under a microscope at 25–50 power. Quantitative samples may be taken using small-diameter cores. Whatever the method of collection, care should be taken not to wash the sample through too coarse a sieve; even sieves as fine as 37 μm are too coarse to retain most gastrotrichs. It is much easier to pick and identify living gastrotrichs than dead ones. If the sample must be preserved before examination, it may be useful to narcotize the animals with 1% $MgCl_2$ for 10 min before fixation. It is possible to slow down living animals for close examination by gently squeezing them under a cover slip (by removing a little of the water with a tissue) or narcotizing them with 1.8% neosynephrine. Osmium tetroxide is the best fixative for serious taxonomic work, but it is dangerous to handle and should be used carefully.

Keys for the identification of freshwater gastrotrichs were presented by Schwank (1990), Strayer and Hummon (2001), and Balsamo and Todaro (2002); it often is fairly easy to identify gastrotrichs to genus. However, because many species descriptions are incomplete and most species of inland-water gastrotrichs probably still have not been formally described by scientists, it is very difficult to identify gastrotrichs to the species level.

Further Reading

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Relevant Website

Todaro MA (2006) Gastrotricha world portal. http://www.gastrotricha.unimore.it/.