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Phylogeny of Gastrotricha: a Morphology-Based Framework of Gastrotrich Relationships

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Abstract. Currently, the phylum Gastrotricha is divided into the orders Macrotrichida and Chaetonotida, with the structure of the myoepithelial pharynx being an important distinguishing feature. Macrotrichida currently has six recognized families, and Chaetonotida comprises seven families. However, within-group relationships are poorly understood. To arrive at a better understanding of gastrotrich systematics and phylogeny, we performed the first cladistic analysis of nearly all known gastrotrich genera using 71 morphological characters. Results suggest that the Gastrotricha is a monophyletic group (supported by 82% of bootstrap replications) with its most primitive taxa distributed among the families Dactylopodolidae and Neodasyidae. Monophyly of Macrotrichida and Chaetonotida was supported by 90% and 52% bootstrap replications, respectively. Within the Macrotrichida, the families Dactylopodolidae, Turbanellidae, Macrotrichidae, and Thaumastodermatidae all formed monophyletic clades. The families Planodasyidae and Lepidodasyidae were paraphyletic. Among the Chaetonotida, the marine family Xenotrichulidae was monophyletic, supported by 51% of bootstrap replications. A second clade containing all freshwater families was supported by 62% bootstrap values. However, Chaetonotidae were paraphyletic. Using this analysis as a framework, we now can explore possible patterns of evolution within it, and arrive at a consensus of the gastrotrich ground pattern. Moreover, in future molecular studies of metazoan phylogeny, we will be able to select gastrotrich species that are more appropriate representatives of the phylum.

Introduction

Gastrotrichs figure prominently in metazoan phylogeny because they share a suite of complex morphological char-

acteristics with several other members of the Bilateria, including the Gnathostomulida and the Nematoda. But their microscopic size, their cryptic interstitial habitat, and the lack of fossil record have exacerbated the usual barriers to phylogenetic analysis. As a consequence, gastrotrichs are one of the least understood groups of aquatic invertebrate animals. Furthermore, the relationship of Gastrotricha to other extant metazoans is uncertain; results from recent molecular and morphological studies are in conflict (Winnepeinnckx *et al.*, 1995; Littlewood *et al.*, 1996; and Wallace *et al.*, 1996). The currently accepted classification of the phylum Gastrotricha is based on morphological features (Hummon, 1982; Ruppert, 1988) and has two monophyletic orders, the Macrotrichida and Chaetonotida. Both orders are defined primarily by the structure of the myoepithelial pharynx (Ruppert, 1991), yet several other characteristics are important in the systematic classification of genera (Hummon, 1982; Ruppert, 1988; Ruppert, 1991) (Fig. 1).

Accepted morphological homologies supporting gastrotrich monophyly include the presence of unique, cuticle-covered duo-gland adhesive organs (Tyler and Rieger, 1980), a multilayered epicuticle (Rieger and Rieger, 1977), and cuticle-covered locomotory and sensory cilia (Rieger and Rieger, 1977). Other features often used to categorize gastrotrichs—cross-striated muscles (Travis, 1983), monociliated epidermis (Rieger, 1976), triradiate myoepithelial pharynx (Schmidt-Rhaesa *et al.*, 1998), and bilayered nature of the cuticle (Schmidt-Rhaesa *et al.*, 1998)—are plesiomorphies and, therefore, of limited systematic value. Of particular significance is the presence of a monociliated epidermis; this condition is considered a primitive trait among Metazoa (Rieger, 1976). A monociliated epidermis is found in several gastrotrich taxa (Rieger, 1976), including the Dactylopodolidae and Neodasyidae, arguing further for their basal positions within their respective orders. That the

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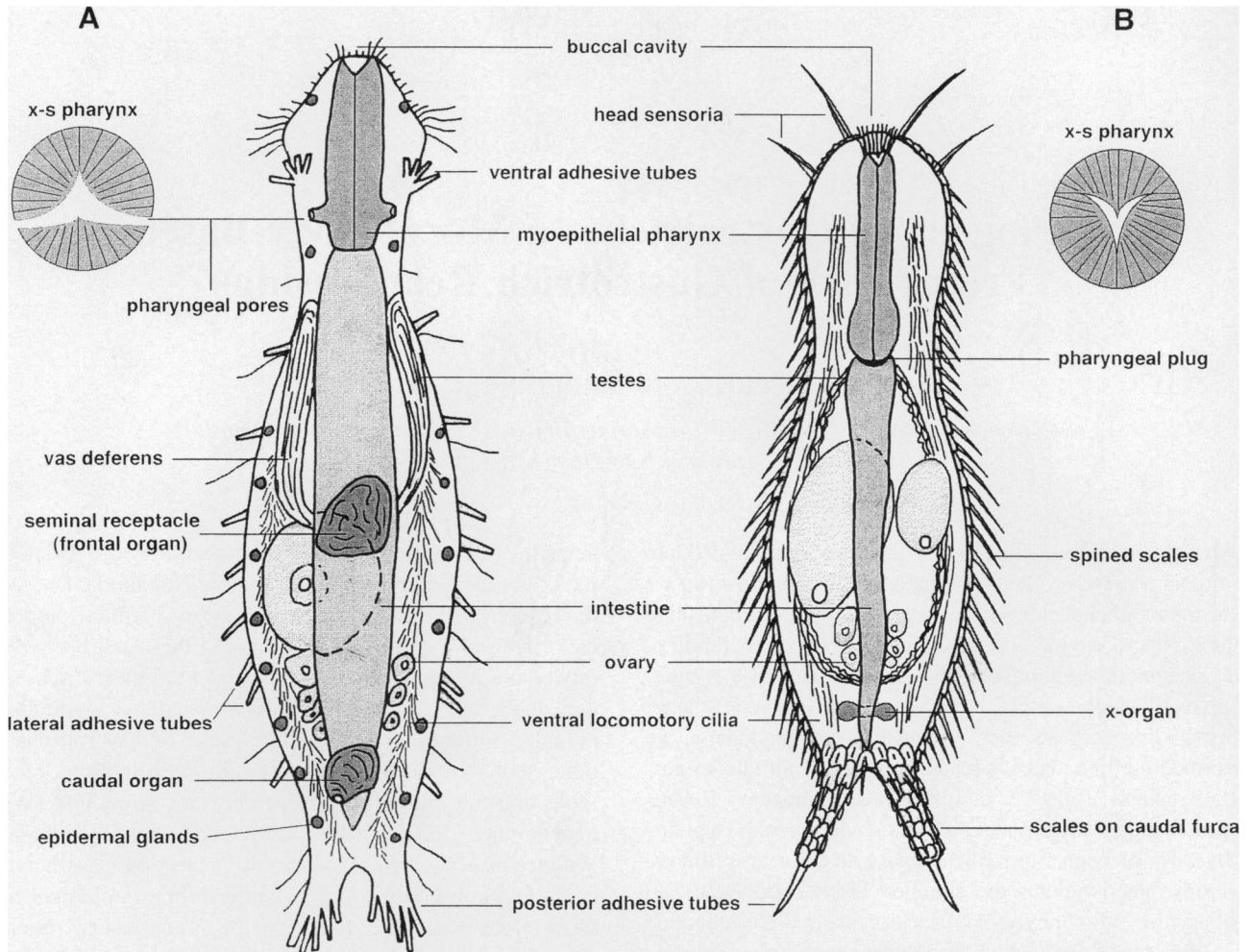


Figure 1. Schematic representation of (A) a macrodasyidan and (B) a chaetonotidan gastrotrich, showing characters separating the two orders. Cross-sections through pharynges show orientation of lumen and, in the macrodasyidan, the pharyngeal pores.

order Chaetonotida may be paraphyletic with respect to the phylum Nematoda, as suggested previously (Ruppert, 1982), is indicated by similarities in cuticular and pharyngeal ultrastructure (upright Y-shaped lumen, pharyngeal-intestinal valve), and pharyngeal innervation. Because of the complete absence of locomotory cilia in Nematoda, in conjunction with several other morphological characters, we agree with Lorenzen (1985) that the Nematoda is, at best, a sister taxon to the Gastrotricha.

Materials and Methods

We have analyzed relationships of nearly all known gastrotrich genera and evaluated them using parsimony analysis (PAUP 4.0*; Swofford, 1999). Eighty-one characters were used in the analysis, all unordered and unweighted (Table 1). For maximum parsimony, default settings included ACCTRAN, and multistate taxa were treated as

uncertainties. Bootstrap options included 1000 replicates of 81 characters. Full heuristic searches were performed with starting trees obtained by stepwise random addition (10 replicates with two trees held at each step). Tree bisection-reconnection (TBR) branch swapping was performed with the MULTREES option to save all minimum-length trees. Two genera, *Marinellina* and *Undula*, were excluded from the analysis due to a lack of information. The Gnathostomulida and Nematoda were used as outgroups. The data matrix is available upon request from the first author.

Results

Our analysis resulted in a monophyletic Gastrotricha (82% bootstrap values). Within the phylum, Chaetonotida (supported by 52% of bootstrap replications) and Macrodasyida (90% of bootstrap replications) formed two monophyletic clades (Fig. 2). Although the Macrodasyida is a

Table 1

Characters and character states used in parsimony analysis of Gastrotricha (a = absent, p = present)

Adhesive Tubes

1. Cuticularized adhesive organs (tubes) (0 = a, 1 = p)
2. Lateral adhesive tubes (0 = a, 1 = p)
3. Lateral adhesive organs indistinguishable, present as minute papillae (0 = a, 1 = p)
4. Ventrally placed anterior adhesive tubes (0 = a, 1 = p)
5. Anterior adhesive tubes in arc-like orientation (0 = a, 1 = p)
6. Anterior adhesive tubes on a mobile elevated base (0 = a, 1 = p)
7. Anterior adhesive tubes arranged together—as hands or clumps (0 = a, 1 = p)
8. Posterior adhesive tubes (0 = a, 1 = p)
9. Rounded caudal end bearing numerous adhesive tubes (0 = a, 1 = p)
10. Caudal end with tail-like extension bearing adhesive tubes (0 = a, 1 = p)
11. Caudal end with elongate peduncle bearing adhesive tubes (0 = a, 1 = p)
12. Caudal end is biramous/forked (0 = a, 1 = p)
13. Caudal end with only 2 adhesive tubules (0 = a, 1 = p)
14. Proximal/distal separation of caudal adhesive tubules on elongate peduncle (0 = a, 1 = p)
15. Median caudal cone (0 = a, 1 = p)
16. Caudal furca reduced to bilateral protuberances without adhesive tubes (0 = otherwise, 1 = p)
17. Ventrally placed extraordinary adhesive tubes as Seitenfüsschen (0 = a, 1 = p)
18. Seitenfüsschen as paired “brocha” tubules (0 = a, 1 = p)
19. Seitenfüsschen as single “cirrata” tubules (0 = a, 1 = p)

Alimentary System

20. Condition of buccal capsule (0 = simple opening, 1 = extended/folded/etc.)
21. Wide flaring buccal region (0 = a, 1 = p)
22. Shape of myoepithelial pharyngeal lumen (0 = a, 1 = Y-shape, 2 = upside-down Y-shape)
23. Pharyngeal clefts (0 = a, 1 = p)
24. Myoepithelial pharynx with cilia (0 = a, 1 = p)
25. Microvilli penetrate pharynx exocuticle (0 = a, 1 = p)
26. Pharyngeal foldings/plug (0 = a, 1 = p)
27. Pharyngeal intrusions “teeth” (0 = a, 1 = p)
28. Small pharyngeal pores (0 = a, 1 = p)
29. Ciliated gut epithelium (0 = a, 1 = p)
30. Distinct head enclosing most of the pharynx (0 = a, 1 = p)

Body Wall

31. Y-cells derived from longitudinal muscle block (0 = a, 1 = p)
32. Muscle striation pattern (0 = X-Striated, 1 = Oblique)
33. Y-cell with myofilaments (0 = a, 1 = p)
34. Epidermal glands with band-like contents (0 = a, 1 = p)
35. Circular muscles (0 = p, 1 = a)
36. Circular muscles absent from lateral body regions (0 = p, 1 = a)
37. Dorsal epidermal glands (0 = absent, 1 = present)
38. Body shape (0 = elongate, 1 = ten-pin)

Ciliation

39. Epidermal ciliation (0 = monociliation, 1 = multiciliation, 2 = no ciliation)
40. One pair of short “cirri” (0 = a, 1 = p)
41. Ventral cilia and head sensoria modified as cirri (0 = a, 1 = p)
42. Construction of ventral and head cirri (0 = a, 1 = constructed as a singular unit, 2 = each cilium with own cuticle)
43. *Stylochaeta*-type ciliation (0 = a, 1 = p)
44. Ventral locomotory cilia restricted to head region as a distinct patch (0 = a, 1 = p)
45. Ventral locomotory cilia present in 2 longitudinal rows (0 = a, 1 = p)
46. Longitudinal rows of locomotory cilia abbreviated at mid-body region (0 = otherwise, 1 = p)
47. Cilia covered with cuticle (0 = a, 1 = p)

Cuticle

48. Scales constructed from basal cuticular layer—form solid endocuticular thickenings (0 = a, 1 = p)
49. Cuticular hooks/ancre (triancre, tetrancre, pentancre) (0 = a, 1 = p)
50. Spines sculpted from surface zone of basal cuticular layer (not originating from flat scales) (0 = a, 1 = p)
51. Keeled scales derived from surface-zone of basal cuticular layer (0 = a, 1 = p)
52. Ventrolateral hydrofoil scales derived from surface-zone of basal cuticular layer (0 = a, 1 = p)

Table 1 (Continued)

-
53. Surface zone (of basal layer) spines present in groups (0 = a, 1 = p)
 54. Surface-zone (of basal layer) scales (0 = a, 1 = p)
 55. Surface-zone (of basal layer) scales lacking stalk and endplate (0 = a, 1 = p)
 56. Surface-zone (of basal layer) scales in ventral interciliary field (0 = a, 1 = p)
 57. Surface-zone (of basal layer) scales in ventral interciliary field reduced to terminal field (0 = a, 1 = p)
 58. Elongate scale-covered furca (0 = a, 1 = p)
 59. Head plates (0 = a, 1 = p)

Nervous System/Sense Organs

60. At least one pair of "soft, palp-like organs" on head (0 = a, 1 = p)
 61. Club-shaped tentacles on head (0 = a, 1 = p)
 62. Posterior nerve cords leaving circumpharyngeal ganglion (0 = multiple, 1 = 2 total)
 63. Cephalic chemoreceptors present as piston pits, pestles, cones or palps (0 = a, 1 = p)
 64. Single pair of posterior head cones (0 = a, 1 = p)
 65. Number of longitudinal tracts of pharyngeal nerves (0 = >3 nerves, 1 = 3 nerves)

Reproductive System

66. Paired ova mature in anterior to posterior direction (0 = a, 1 = p)
 67. Sperm ducts join caudal organ (0 = a, 1 = p)
 68. Seminal receptacle (frontal organ) (0 = a, 1 = p)
 69. Caudal organ (penis) (0 = a, 1 = p)
 70. Complex frontal and caudal organs without tissue connection (0 = connection present, 1 = connection absent, 2 = not applicable)
 71. Rosette organ (0 = a, 1 = p)
 72. Paired testis (0 = otherwise, 1 = p)
 73. Reduced left testis—single right testis only (0 = otherwise, 1 = p)
 74. Reflexed vas deferens (0 = a, 1 = p)
 75. Lumen of caudal and frontal organs continuous (0 = a, 1 = p)
 76. Parthenogenesis (0 = a, 1 = p)
 77. U-shaped gonad with caudal anastomosis (0 = a, 1 = p)
 78. Vas deferentia (0 = elongate, 1 = reduced/absent)
 79. Testes present as bilateral packets in post-parthenogenetic phase (0 = testes otherwise, 1 = p, 2 = no testes)
 80. X-organ (0 = a, 1 = p)
 81. Condition of vas deferentia (0 = a, 1 = separate, paired or unpaired, 2 = paired and fused)
-

highly heterogeneous group defined primarily by pharyngeal structure (Ruppert, 1991), the presence of groups of adhesive tubules (Hummon, 1982; Ruppert, 1988), and curious reproductive organs (Ruppert and Shaw, 1977; Ruppert, 1978), our analysis confirmed several monophyletic families within the order (Fig. 2). In fact, characters of the latter two organ systems substantiate monophyly of the two ecologically most diverse families, the Turbanellidae and Thaumastodermatidae (Fig. 2). These two families occur in nearly all marine environments at all depths, inhabit a wide array of sand types, and are probably among the most ubiquitous and successful groups of interstitial animals. As noted previously (Ruppert, 1988), the Lepidodasyidae is an unnatural taxon difficult to define on current morphological criteria. Our analysis found a paraphyletic Lepidodasyidae with some genera clustering with other families, although with low bootstrap values (Fig. 2). The monophyletic Dactylopodolidae (95% bootstrap values) is affirmed as the most primitive macrodasyidan family, with retention of several plesiomorphic traits including epidermal monociliation, alimentary canal ciliation, cross-striated muscles, and

separate multiple nerve cords in some genera (Fig. 2). Additional research on this family, in particular the relatively unknown *Dendrodasyis* and *Dendropodola*, should further elucidate the ground pattern for the Gastrotricha.

Bootstrap values advocating a monophyletic Chaetonotida are relatively strong (52%), and values for the monophyly of the suborder Paucitubulatina are even more robust (93%) (Fig. 2). All chaetonotidans are largely defined by the configuration of the pharyngeal lumen (upright Y-shaped) and the absence of pharyngeal pores. But often, body-shape ("ten-pin") and the absence of anterior or lateral adhesive tubules are the most easily seen diagnostic characters. The monogeneric Multitubulatina, however, contains an anomalous vermiform *Neodasyis* that shares traits with both Macrodasyida and Paucitubulatina. However, unlike all other members of the Chaetonotida, *Neodasyis* is highly elongate and in possession of some potentially plesiomorphic characteristics: hermaphroditic gonads, complex reproductive organs, monociliated epidermis, smooth cuticle, and numerous adhesive tubules (Ruppert, 1991). Furthermore, the adhesive organ of *Neodasyis* lacks a releaser gland (Tyler *et*

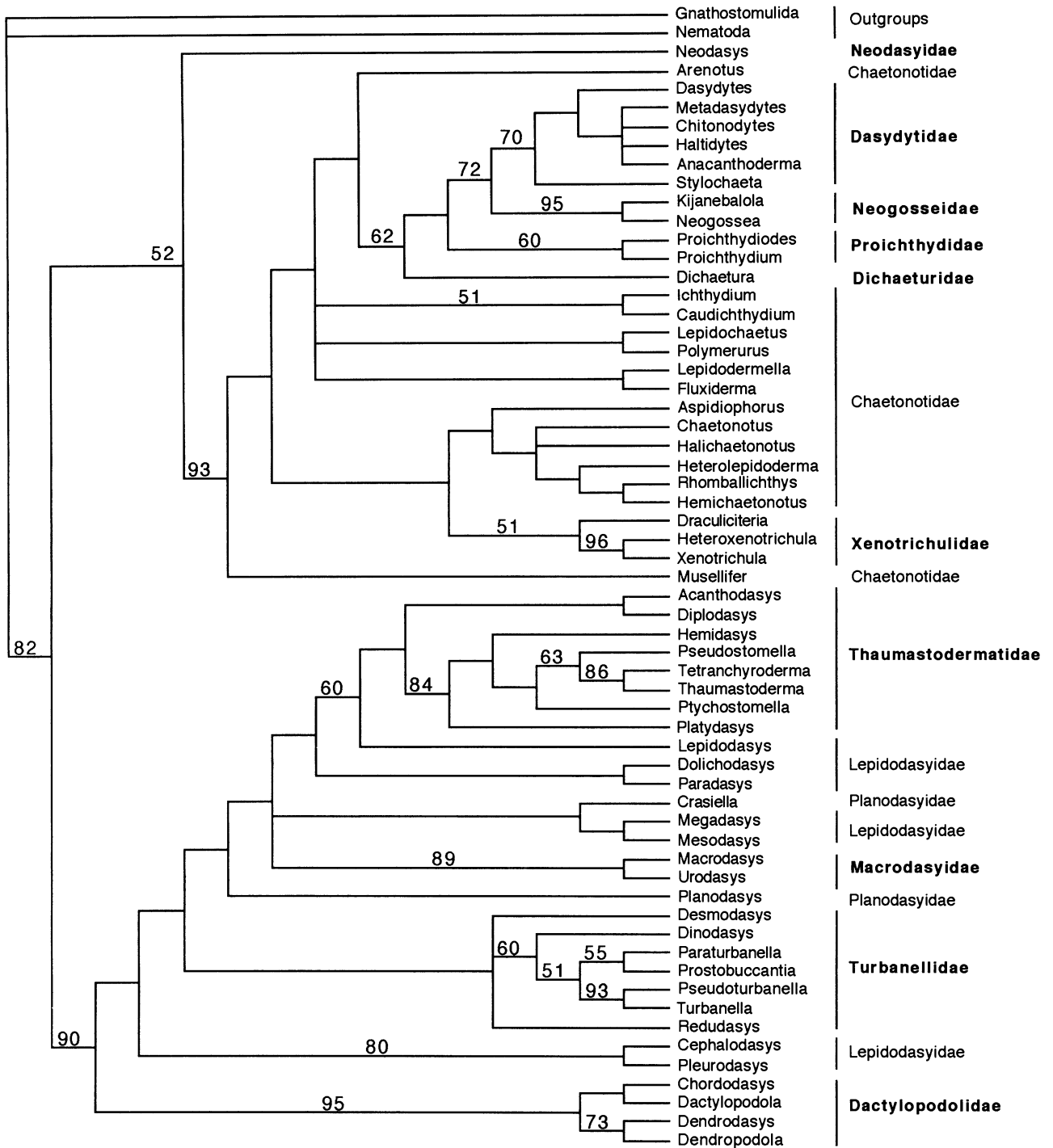


Figure 2. Consensus tree (50% Majority-Rule) of 59 gastrotrich genera. Tree length = 175 steps; CI = 0.503, RC = 0.450. Numbers at nodes represent percentages of 1000 bootstrap replications. Families indicated by bold type are monophyletic.

al., 1980). The presence of only one gland type in the adhesive organ is interpreted as a plesiomorphy when viewed in combination with the retention of other primitive traits (Tyler *et al.*, 1980). Still, the presence of duogland adhesive organs in all Gastrotricha has not been confirmed, and it remains to be seen whether the presence of only a

single gland is actually the “primitive” condition or is secondarily derived.

Within the Paucitubulatina, the largest and structurally most diverse family—the Chaetonotidae—appears to be paraphyletic (Fig. 2). This highly speciose taxon (>250 spp.) is extremely heterogeneous with respect to cuticular

armature, habitat type, and reproductive anatomy. The family is presumed to have evolved in the freshwater benthos, radiating into the marine environment secondarily (Kisielewski, 1990). Yet, the existence of a very basal marine genus, *Musellifer*, might also argue for a marine origin. Resolution of this vastly diverse taxon will undoubtedly improve with greater attention to its reproductive anatomy (presence of hermaphroditic organs is unknown for many genera; the homology of the X-organ is in question) and the complex microstructure of both scales and spines.

Still, several important monophyletic groupings were confirmed within the Chaetonotida, including the entirely freshwater Dasydytidae, Neogosseidae, and Proichthyidae (Fig. 2). Our analysis thus confirmed a clade of freshwater families with 62% of bootstraps. In addition, the marine family Xenotrichulidae and the subfamily Xenotrichulinae were also monophyletic (Fig. 2).

Discussion

The current analysis goes beyond classification; it is aimed at an elucidation of phylogenetic trends. In particular, trends in nervous-system structure in the Gastrotricha are revealed within the tree topology of the Macrotrichida. Basal genera often have multiple, separate nerve cords (4 in *Dactylopodola*), whereas more derived genera show partial fusion of nerve cords (4 fuse into 2 in *Turbanella*) or presumably complete fusion (2 in Thaumastodermatidae). The functional significance of this transition series is unknown; moreover, the trend is more ambiguous than supposed because other "intermediate" forms like *Cephalodasys maximus* show fusion ("schmelzen") of multiple (12) nerve cords, followed by subsequent bifurcation (Wiedermann, 1995). Other trends are also evident. For example, changes in reproductive biology (from hermaphroditic to parthenogenetic) seem to have occurred in chaetonotidan transitions from marine to freshwater biotopes.

This cladistic analysis also provides evidence that many characters used to define gastrotrichs in morphology-based phylogenies of extant Metazoa often are apomorphic for the phylum and, therefore, inappropriate. For example, Wallace *et al.* (1996) used the characters parthenogenesis, syncytial epidermis, and hypodermic impregnation in their analysis. The first two characters are known only in some chaetonotidans, and the third is unconfirmed except for the family Macrotrichidae and is unknown in basal taxa such as Dactylopodolidae. Backeljau *et al.* (1993) incorrectly used eutely (found only in some chaetonotidans) and radial cleavage (gastrotrichs have aberrant bilateral cleavage) as characters defining gastrotrichs as a whole in their analysis. Finally, Zrzavy *et al.* (1998) used the character pseudo-coelomate in their analysis, although all gastrotrichs are acoelomate.

Our cladistic analysis also provides a good test for molecular phylogenetic studies. Several earlier molecular studies have focused on derived taxa (*Chaetonotus* sp., *Lepidodermella squamata*) to resolve phylum-level relationships (Winnepenninckx *et al.*, 1995; Littlewood *et al.*, 1998; Zrzavy *et al.*, 1998; Ruiz-Trillo *et al.*, 1999). Such taxa are particularly easy to culture, but their utility as representative models is questionable. *Lepidodermella squamata* is especially controversial because it inhabits fresh water and is parthenogenetic—characteristics that are uncommon among chaetonotidans and virtually absent in macrotrichidans. The use of such derived forms should be avoided until the systematics of the Chaetonotida is better resolved.

Additionally, molecular systematics place the Gastrotricha in a variety of positions within the metazoan tree: as a sister group to either the Acanthocephala (Carranza *et al.*, 1997), the Gnathostomulida (Littlewood *et al.*, 1998), the Nematomorpha (Carranza *et al.*, 1997), or the Platyhelminthes (Winnepenninckx *et al.*, 1995). Other studies place the Gastrotricha basal to most of the Bilateria (Carranza *et al.*, 1997), or to the Lophotrochozoa (Ruiz-Trillo *et al.*, 1999) or the Spiralia (Littlewood *et al.*, 1998). We, however, contend that the position of the Gastrotricha remains questionable until more primitive gastrotrich species are used, namely *Neodasys* or species of the Dactylopodolidae. These additions to the molecular data set would be a good test of tree strength and confirmation of their branching point from the remaining phyla.

A comprehensive and congruent classification of the phylum Gastrotricha is essential if its origin and phylogenetic significance are to be fully appreciated. The currently accepted classification is in dire need of revision, especially concerning the order Chaetonotida and the family Lepidodasyidae. At the same time, though, previous work on the systematics of the phylum has successfully navigated the treacheries of convergence and parallelism and displayed good phylogenetic congruence (Remane, 1933; Hummon, 1982; Ruppert, 1988). Yet, despite the rather small size of the phylum, the species are highly variable in particular characters (*e.g.*, adhesive tubes, ciliary patterns, cuticular sculpture, reproductive anatomy), and recognition of plesiomorphy is often difficult.

Our study presents an evolutionary hypothesis for all Gastrotricha. Within this morphological framework, we now can address specific questions of relationships within and among individual gastrotrich taxa. For example, characters of the nervous system (*i.e.*, number of nerve cords, fusion, distribution of neurotransmitters) can now be evaluated in light of the presumed primitiveness of the Dactylopodolidae. This framework also allows for a more careful selection of gastrotrich species representing the phylum as a whole in future global molecular studies.

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