Spring 1985

THE OXYTRICHINA JANKOWSKI, 1980: MORPHOLOGY, MORPHOGENESIS, AND SYSTEMATICS (SPORADOTRICHINA, CILIPHORA, CYST)

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THE OXYTRICHINA JANKOWSKI, 1980: MORPHOLOGY, MORPHOGENESIS, AND SYSTEMATICS (SPORADOTRICHINA, CILIPHORA, CYST)

Abstract
The hypotrich suborder Oxytrichina Jankowski, 1980 is a poorly characterised, systematically ambiguous taxon. A lack of ultrastructural and developmental information on a variety of oxytrichine species resulted in the establishment of multiple and disparate systematic categorizations for these species. I chose 8 species for morphologic and developmental studies: Oxytricha fallax, Oxytricha quadruinucleata, Oxytricha similis, Stylonychia pustulata, Tachysoma sp., Gonostomum affine, Pleurotricha lanceolata, and Paraurostyla sp. I used light microscopy and SEM for the study of trophozoites and dividing cells, and TEM and SEM in my investigations of cysts. The major unifying developmental characteristic of the suborder is the production of longitudinal F-V-T streaks during division and reorganization. Encysting organisms resorb all kinetosomes and produce desiccation resistant cysts with 4 or 5 layered walls. Interspecific morphologic and developmental differences including presence of absence of multiple right mariginal cirral rows and ventral longitudinal rows suggest recognition at at least 3 oxytrichine families: Oxytrichidae, Amphisiellidae, and Gonostomidae (n.fam.). I consider the family Amphisiellidae ancestral to the other 2 families. It is clear from previously published information that the families Keronidae and Kahliellidae share a common ancestry with the aforementioned 3 families and may be con-subordinal. A traditional view of interfamilial evolutionary relationships holds that the kahliellids, with multiple longitudinal rows of cirri, are primitive and perhaps ancestral to the rest of the suborder. I propose an alternative evolutionary scenario based upon a novel concept of somatic origin of the frontal ciliature. An ancestral hypotrich similar to Epiclintes with extensive ventral somatic ciliature and vanishingly scant frontal ciliature may have given rise to families with frontal ciliature increasing at the expense of somatic ciliature. In this second scenario, recognition of the frontal, and therefore relatively non-primitive origin of the ventral longitudinal rows of cirri necessitates disqualification of the kahliellids as ancestral to the amphisiellids, oxytrichids, and gonostomids.

Keywords
Biology, Zoology

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THE OXYTRICHINA JANKOWSKI, 1980:
MORPHOLOGY, MORPHOGENESIS, AND SYSTEMATICS

BY

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A DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy
in
Zoology

May, 1985
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April 26, 1985
Date
TO MY FAMILY
ACKNOWLEDGEMENTS

Thanks are due to numerous individuals who have helped cobble the winding path to the completion of this dissertation. Dr. Arthur C. Borror, my advisor, is foremost among them. His exhaustive knowledge of ciliates, his ability to stimulate rather than spoon feed, and especially his patience were always at my disposal. I made liberal use of them all.

I thank also the rest of my committee for the careful readings of my dissertation and the many thoughtful comments pertaining thereto. Special thanks are due to Drs. Larry Harris and Charles Walker whose assistance and services were always available and whose minds were always ripe for picking. Additionally, much of my research would not have been possible without equipment made available by Dr. Walker.

I thank my friend, Eileen Wong, for her untiring assistance in the typing, copying, and collating of this dissertation, often in the face of impeding deadlines. Many others, especially Patty Burke, Frank Smith, and Barry Wicklow, were always available for technical assistance or, most importantly, comradery. Thanks to all.

Finally, my most heartfelt gratitude goes to my wife, Nicole, who provided the illustrations for this dissertation, and to my children, Adam and Veronica. It was the boundless confidence, encouragement, and love of my family which, in the end, brought me to the successful completion of my graduate studies.
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ABSTRACT

THE OXYTRICHIINA JANKOWSKI, 1980:
MORPHOLOGY, MORPHOGENESIS, AND SYSTEMATICS

by

Donald E. Culberson
University of New Hampshire, May, 1985

The hypotrich suborder Oxytrichina Jankowski, 1980 is a poorly characterised, systematically ambiguous taxon. A lack of ultrastructural and developmental information on a variety of oxytrichine species resulted in the establishment of multiple and disparate systematic categorizations for these species. I chose 8 species for morphologic and developmental studies: Oxytricha fallax, Oxytricha quadri-nucleata, Oxytricha similis, Stylyochia pustulata, Tachysoma sp., Gonostomum affine, Pleurotricha lanceolata, and Paraurostyla sp. I used light microscopy and SEM for the study of trophozoites and dividing cells, and TEM and SEM in my investigations of cysts. The major unifying developmental characteristic of the suborder is the production of longitudinal F-V-T streaks during division and reorganization. Encysting organisms resorb all kinetosomes and produce desiccation resistant cysts with 4 or 5 layered walls. Interspecific morphologic and developmental differences including presence or absence of multiple right marginal cirral rows and ventral longitudinal rows suggest recognition of at least 3 oxytrichine families: Oxytrichidae, Amphisiellidae, and Gonostomidae (n.fam.). I consider the family Amphisiellidae ancestral to the other
2 families. It is clear from previously published information that the families Keronidae and Kahliellidae share a common ancestry with the aforementioned 3 families and may be con-subordinal. A traditional view of interfamilial evolutionary relationships holds that the kahliellids, with multiple longitudinal rows of cirri, are primitive and perhaps ancestral to the rest of the superorder. I propose an alternative evolutionary scenario based upon a novel concept of somatic origin of the frontal ciliature. An ancestral hypotrich similar to Epiclinetes with extensive ventral somatic ciliature and vanishingly scant frontal ciliature may have given rise to families with frontal ciliature increasing at the expense of somatic ciliature. In this second scenario, recognition of the frontal, and therefore relatively non-primitive origin of the ventral longitudinal rows of cirri necessitates disqualification of the kahliellids as ancestral to the amphisiellids, oxytrichids, and gonostomids.
INTRODUCTION

The protozoa are widely recognized as a loose assemblage of single-celled eukaryotic organisms (Levine et al., 1980). Use of the taxon "Phylum Protozoa" has diminished because of the apparently diverse, polyphyletic origin of this group of over 65,000 known species. The Committee on Systematics and Evolution of the Society of Protozoologists (Levine et al., 1980) decided that the protozoa represent 7 of the phyla of the kingdom Protista: the Sarcomastigophora, Labyrinthomorpha, Apicomplexa, Microspora, Acetospora, Myxozoa, and Ciliophora.

Each of the aforementioned phyla has undergone repeated taxonomic revision resulting in the modern classification scheme. The Ciliophora are no exception. The history of ciliophoran taxonomy is beyond the scope of this dissertation, but was reviewed by Corliss (1979). Of more immediate interest is our present understanding of ciliophoran systematic interrelationships and, particularly, resulting effects of further contributions to ciliophoran biology.

Ciliates are currently categorized into 3 classes: Kinetofragminophorea, Oligohymenophorea, and Polyhymenophorea. The latter class is generally accepted as the most recent or highly evolved of the 3 and is composed of 4 orders: Heterotrichida, Odontostomatida, Oligotrichida, and Hypotrichida. The Hypotrichida, in turn, are considered the most advanced of Polyhymenophorean ciliates. Table 1, an abridged version of Protistan classification derived from
Levine et al. (1980) and Corliss (1979), illustrates the taxonomic position of organisms considered in this dissertation.

The hypotrichs were likewise subjected to intense scrutiny with variable results. A review of the wide array of data obtained thereby may serve as an introduction to the order Hypotrichida in general and provide a conceptual framework for the presentation and interpretation of my own research in particular. Specifically, this review will include a brief description of current hypotrich taxonomy and consideration of the state of knowledge of pertinent morphology, morphogenesis, and cystic phenomena.

Recently there has been an explosion in both our understanding of hypotrich biology and also concomitant attempts to reflect this knowledge in updated classification schemes. Ideally, such systematic hierarchies should reflect the biological interrelationships of their constituent species and change, therefore, in conjunction with changing understanding of those interrelationships.

For approximately 200 years hypotrich taxonomy was relatively static with about 3 families (excluding some now placed in other groups) typically being recognized. These 3 families were the Oxytrichidae, Euplotidae, and Aspidiscidae, all of which were described by Ehrenberg (1838). The first of these, Oxytrichidae, was essentially a catch all for forms not readily fitting into the other two, more restricted families. Borror (1972) and Corliss (1979) provide more detailed reviews of early hypotrich taxonomy.

The size and remarkable diversity of the family Oxytrichidae led Fauré-Fremiet (1961) to attempt the construction of a more modern system of hypotrich classification which reflected the current
understanding of hypotrich biology. His division of the order into 2 suborders, the Stichotrichina (4 families) and the Sporadotrichina (4 families) was based largely upon interphase morphology but accounted for and dealt with the disparity of forms observed in the old family Oxytrichidae. Briefly, the Stichotrichina consisted of those forms (all of which were previously included in the Oxytrichina) which exhibited ventral longitudinal rows of relatively uniform, undifferentiated cirri. The Sporadotrichina contained hypotrichs without such cirral rows and whose ventral ciliature developed from a series of about 6 kinetosomal streaks during cell division. In addition to the Euplotidae, Aspidiscidae, and Gastrocirrhidae (closely related to the Euplotids and Aspidiscids), the Sporadotrichina contained the family Oxytrichidae reduced by the numerous forms removed to the Stichotrichina.

Fauré-Fremiet's (1961) classification has since been modified by various authors (Table 2). Borror (1972) challenged the original bisubordinal division on the basis of diversity within each suborder and occurrence of characters common to both. Corliss (1979) accepted the bi-subordinal classification but suggested that the erection of a third, intermediate suborder composed mostly of oxytrichid genera might alleviate some of the problems recognized by Borror (1972). Borror and Evans (1979) carried these considerations to a similar conclusion by suggesting the utility of subdivision to "several" suborders including separation of the Oxytrichidae and Euplotidae. The two latter proposals for further splitting of the order were based upon the assumption that considerable new comparative information (particularly of a morphogenetic nature) would be required to support such a move
since traditional reliance on interphase morphology proved at least partially misleading. Hill (1980a) provided some of this information and supported subordinal recognition of the more "advanced" sporadotrichine hypotrichs, the family Euplotidae and related families. Jankowski (1980) divided the order into 6 suborders: the Urostylina, Holostichina, Oxytrichina, Euplotina, Gastrocirrhina, and Aspidiscina. His revision, which encompassed major changes at all taxonomic levels, was not supported by any new evidence. Indeed, many of the changes Jankowski proposed were contrary to already published information. Wicklow (1981) and Borror and Wicklow (1982, 1983) demonstrated the logical subordinal inseparability of several families in Jankowski's suborders Urostylina (Urostyliidae, Keronopsidae) and Holostichina (Holostichidae, Bakuellidae, Pseudourostylidae) and suggested inclusion of these families in a single suborder, the Urostylina, on the basis of new as well as already published ontogenetic information. Wicklow (1981) also pointed to the polyphyletic origin of many of the other families that Jankowski assigned to the Urostylina (Psilotrichidae, Kiirrichidae, Strongyliidae, Atractidae, Spirofilopsidae, Hypotrichidiidae, Spiretellidae, and Chaetospiridae). These latter families may deserve additional comparative information to confidently place them in other suborders.

Morphology, development, and phylogeny in 3 of Jankowski's other 4 suborders, the Euplotina, Gastrocirrhina, and Aspidiscina, were discussed at length by Hill (1980a), whose opinion was that the 3 groups were somewhat distinct from one another, but this distinction did not deserve elevation to subordinal status. In the absence of contradictory information, it is reasonable to accept Hill's
classification since it was based on an in depth morphological and
ontogenetic study of the group.

The primary subject of this dissertation is an evaluation of
relationships within the remaining Jankowskian suborder, the
Oxytrichina. Revisions (Borror, 1972; Tuffrau, 1979; Jankowski, 1967,
1978, 1979, 1980) and suggested revisions (Borror and Evans, 1979;
Corliss, 1979) are at odds with one another, demonstrating the need for
new comparative information on members of this suborder.

Hemberger (1982) supplied morphogenetic information on a number of
species in the Oxytrichina and erected a new family, the
Amphisiellidae. His efforts resulted in an important advance in our
understanding of the Oxytrichina even though they were limited almost
entirely to soil dwelling forms and thus tended to overlook
evolutionary lines into other habitats. In addition, recently
published information on various genera previously placed in the
Stichotrichina reveals similarity to other non-Stichotrichine groups,
particularly the Oxytrichina (Culberson, 1982; Martin et al., 1981;
Fleury and Fyrd-Versavel, 1982; Hemberger and Wilbert, 1982).

On the basis of interphase cell morphology, the "traditional"
criterion for membership in a taxon of hypotrichs, at least 3 major
groups may exist within the Oxytrichina. These are:

A. Forms with single left and right marginal rows of cirri and
   fairly stable numbers and placement of fronto-ventral cirri,
   not in rows (Oxytricha, Stylonychia, Tachysoma, and
   Gonostomum, Fig. 1).

B. Forms with multiple right marginal rows of cirri (Pleurotricha,
   Fig. 2a).
C. Forms with varying numbers of longitudinal rows of cirri and often reduced numbers of fronto-ventral cirri (Paraurostyla and Amphisiella, Figs. 2b, c).
OXYTRICHINE MORPHOLOGY AND MORPHOGENESIS

Definitions of ciliary terminology for interphase trophozoite as well as transitory structures of dividing cells exist and will form the basis for my designations (Borror, 1972, 1979; Borror and Evans, 1979; Jerka-Dziadosz, 1980, 1981a,b, 1982). Although Jerka-Dziadosz (1981b) objects, Borror's (1979) designations of the 3 major divisions of ciliate: buccal, frontal, and somatic, provide useful categories upon which to base more detailed descriptions of hypotrich ciliate. Because Paraurostyla hymenophora (Fig. 3) possesses all ciliary features found in oxytrichine hypotrichs, it illustrates the locations and general appearance of important ciliary groups in the following description of oxytrichine morphology.

Trophozoite Morphology and Ultrastructure

Buccal Ciliature

The most striking feature of the buccal ciliate is the adoral zone of membranelles (AZM), located to the left (from the organism's point of view) of the oral cavity and extends antero-dorsally to a point at the far anterior right of the cell. The two other major features of the buccal ciliate are the endoral (EM) and paroral membranes (PM). The EM and PM are separated by a cortical ridge, the right buccal overture (RBO). The EM extends from beneath the RBO into the oral cavity and typically originates from a single longitudinal row of kinetosomes. The PM lies on the ventral surface of the cell just to the right of the RBO and oral cavity and originates from a longitudinal array of 1-6 oblique rows of kinetosomes. Spatial relationships of
these structures are clearly demonstrated for and *O. similis* (Fig. 7c) *Paraurostyla* sp. (Fig. 18c).

**Frontal Ciliature**

The frontal ciliature or fronto-ventral-transverse (F-V-T) system comprises a ventrally dispersed group of locomotory cirri which share a common developmental origin. For simplicity, this system may be considered as several subgroups, including frontal, post-buccal (often referred to as ventral), transverse (sometimes called anal), longitudinal, and (in some non-oxytrichine hypotrichs) midventral cirri.

Frontal cirri (FC) are situated on the anterior ventral surface to the right of the PM and are variable in number. The post buccal cirri (PBC) lie in the ventral region of the cell posterior to the AZM. Frontal and post-buccal cirri both function in forward directed locomotion, and are often termed simply frono-ventral cirri. The left-most anterior frontal cirrus is functionally and morphologically similar to the other frontal cirri, but is enigmatic in being related developmentally to the buccal ciliature, specifically the PM. Hence, it is termed the paroral cirrus. Borror (1979), noting its origin, included the buccal cirrus in his listing of frontal ciliature, but Borror and Wicklow (1982) emphasized its origin and listed it with the buccal ciliature.

Transverse cirri (TC) are located near the posterior end of the ventral surface of the cell. They range in number from 2 (Fig. 12) to many and are even completely absent in some of the seemingly more primitive, non-oxytrichine hypotrichs. Together with the frontal and post-buccal cirri they comprise the total frontal ciliature in those
oxytrichine hypotrichs I designated as belonging to groups A (the typical Oxytricha-like forms) and B (the Pleurotricha-like forms).

In addition to the 3 ciliary groups discussed above, Paraurostyla possesses a group of 2 or more (sometimes as many as 7 in Paraurostyla weissei (Jerka-Dziadosz and Frankel, 1969)) longitudinal rows (LR) of cirri which extend from the anterior region of the ventral cell surface to positions just anterior to the transverse cirri. These rows share the function of forward directed locomotion with the fronto-ventral cirri.

Midventral cirri comprise a special fifth group of frontal ciliature which is diagnostic of the suborder Urostyлина (Wicklow, 1981; Borror and Wicklow, 1982). These cirri are not encountered in the Oxytrichina and exhibit a unique developmental pattern (Borror, 1979; Wicklow, 1981; Borror and Wicklow, 1982). They are included in this review because one of the species considered here, Gonostomum affine, previously was included among the urostyline hypotrichs, but, as shown, does not possess midventral cirri.

Somatic Ciliature

A third major type of ciliature, somatic, occupies the latero-ventral and dorsal surfaces of the hypotrich cell. In oxytrichines, somatic ciliature includes marginal and caudal cirri and dorsal bristles or cilia. Marginal cirri are locomotory; dorsal bristles are probably sensory (Corliss, 1979; Görtz, 1982); and caudal cirri are of uncertain variable function.

Marginal cirri occur on both left and right latero-ventral surfaces of the cell. The number of rows is inter- (and sometimes intra-) specifically variable on both sides of the cell. Right
marginal rows (RMR) of cirri extend from the right end of the anterior portion or collar of the AZM to the right posterior region of the cell, while left marginal rows (LMR) extend from the area of the posterior end of the AZM and buccal cavity to the left posterior region of the cell. Oxytrichine hypotrichs usually possess 1 row of each, but those in group B, represented by Pleurotricha, possess an additional row of right marginal cirri.

Dorsal cilia occur in rows (DK) on the dorsal surface of hypotrichs. Numbers of rows range from 3 to 6 in the Oxytrichina. Typically, each bristle surmounts a dyad of kinetosomes lying in a pit on the dorsal surface. Typically only the most anterior of the pair of kinetosomes is ciliated; the other member of the dyad (absent in some species of Stylonychia) is usually topped by a short "stub". Dorsal bristles are non-motile and are thought to be sensory in function.

Caudal cirri are poorly understood features of the postero-dorsal surface of hypotrichs. They may be stiff as in Stylonychia mytilus or flexible as in O. fallax. Since they are developmentally associated with the rows of dorsal bristles they may share a sensory function. Alternatively, since they are at the posterior end of the cell and may orient laterally at times, they may be involved in steering. Species considered in this study possess either 2 (T. saltans) or 3 caudal cirri.

Division and Reorganization Morphogenesis

Buccal Ciliature

While many hypotrichs resorb and reform part of the AZM during cell division (Borror, 1979), members of the Oxytrichina typically do
Cortical reorganization in non-dividing cells does involve the resorption of posterior or "lapel" membranelles, but the proters of dividing pairs retain the parental AZM. The PM and EM are at least partially resorbed but reform in situ.

The earliest cortical sign of beginning cell division is the appearance of an anarchic field of kinetosomes on the left ventral, post-buccal surface (Fig. 5a). These kinetosomes proliferate into a triangular oral primordium (OP) that extends from a posterior apex near the left transverse cirrus to just posterior of the AZM. These randomly arranged kinetosomes align into paramembranelles (Puytorac and Grain, 1976) beginning at the most anterior section of the field eventually producing the opisthe AZM. Jerka-Dziadosz (1981b), in her detailed analysis of this process in *P. weissei*, pointed out that similar processes take place in other oxytrichine hypotrichs (Grimes, 1972; Grimes and L'Hernault, 1978; Tuffrau, 1969, 1970).

The PM and EM in both proter and opisthe develop from common primordia (Jerka-Dziadosz and Frankel, 1969; Jerka-Dziadosz, 1981b). In the proter this primordium is derived from the constituent kinetosomes of the parental UM and subsequently reorganizes to form the new UM of the proter. The new UM of a reorganizing cell is also produced in this manner and although the process was observed in numerous hypotrichs it was never subjected to rigorous ultrastructural analysis (Bakowska and Jerka-Dziadosz, 1978; Borror, 1972, 1979; Borror and Evans, 1979; Fleury and Fryd-Versavel, 1981; Grimes, 1972; Grimes and Adler, 1978; Grimes and L'Hernault, 1978, 1979; Jerka-Dziadosz, 1972a,b, 1974, 1981b; Jerka-Dziadosz and Frankel, 1969; Jerka-Dziadosz and Janus, 1972; Walker and Grim, 1973; Wicklow, 1981).
Development of the opisthe UM, on the other hand, received
detailed ultrastructural attention from Jerka-Dziadosz (1981b). The
origin of the "founder" kinetosomes of the opisthe UM field is not
known with certainty. There is some evidence that they may be
contributed by the AZM primordium which, in early stages of
development, produces an anteriorly directed streak of kinetosomes
(Jerka-Dziadosz, 1981b). This streak quickly disappears but may be
involved in the production of the UM field which arises in its place,
separate from the AZM field. Initially kinetosomes in the UM field are
randomly arranged, but in the course of development, acquire a more
orderly appearance. Kinetosomes along the left margin of the UM field
first become aligned in pairs. The EM is produced first by a
separation of the kinetosomal pairs along the left margin of the UM.
This is accompanied by growth of the RBO which increases the distance
between the rows of right and left kinetosomes produced by the
separation of the old row of kinetosomal pairs. The remaining
kinetosomes of the UM field then become aligned into a varying number
(from 1 in *Oxytricha* to as many as 6 in *Paraurostyla*) of longitudinal
rows to form the PM.

**Frontal Ciliature**

The paroral cirrus, or frontal cirrus #1 in some terminologies
(Jerka-Dziadosz, 1981b), arises from the right anterior portion of the
UM primordium as was clearly demonstrated by Grimes and L'Hernault
(1978) and Jerka-Dziadosz (1981b) (see also Figs. 8c and 18 for
examples in this text).

The remainder of the frontal ciliature arises from 2 series of
longitudinal streaks which, in oxytrichine species, typically appear in
anterior and posterior latitudinal zones (Fig. 5). Dedifferentiation of various parental fronto-ventral cirri provides kinetosomes for initial formation of these sets of longitudinal streaks. Ultrastructural details of this dedifferentiation and subsequent streak development are provided by Grimes (1972) and Jerka-Dziadosz (1981a). All cirri in the F-V-T system, with the exception of the buccal cirrus, arise from these streaks. Details of apportionment of parental cirri for streak production and kinetosomes for cirral development vary from species to species. In all species that I studied, however, development of the kinetosomal streaks into procirri (Jerka-Dziadosz, 1981a) and, eventually, into cirri, progresses from anterior to posterior and from left to right (Figs. 5, 18). During cirral development, procirri move toward the positions of the mature cirri. The mechanism of this migration is uncertain but apparently involves microtubular formations in either direct (active) or indirect (serving as "tracks" of migration) roles (Jerka-Dziadosz, 1981a).

**Somatic Ciliature**

The onset of left and right marginal cirral row development is marked by dedifferentiation of parental marginal cirri in 2 latitudinal zones. Component kinetosomes become aligned into anterior and posterior streaks offset somewhat to the right of their respective marginal cirral rows; new kinetosomes are produced, and procirri and mature cirri are formed much as with frontal cirral development (Jerka-Dziadosz, 1981a).

Dorsal bristle row development in the suborder can be viewed as 2 separate but not mutually exclusive processes: dorsal and dorsomarginal. The first, dorsal kinetal development (or 1 of several
slight variations thereof), is observed in all hypotrichs studied to date. In *Gastrostyla steinii*, which has 4 dorsal bristle rows, kinetosomal streaks are produced within the parental rows in 2 latitudinal zones corresponding to the frontal and marginal streaks. The 4 dorsal bristle rows of the proter and opisthe develop from these streaks. Three caudal cirri are produced at the posterior ends of these streaks, 1 each from the 2 right streaks and 1 at a posterior convergence of the 2 left streaks. Similar processes of dorsal bristle row development occur in oxytrichine hypotrichs with more than 4 dorsal kineties, and a second process, dorsomarginal development, accounts for the production of additional right rows. The 3 left rows produce kinetosomal streaks in 2 zones. During elongation the leftmost of these rows breaks to form 2 rows which eventually overlap and come to lie beside each other in the mature cell. Additional right rows of dorsal bristles are produced from streaks of kinetosomes which arise near the right marginal row in both proter and opisthe and extend dorsally and posteriorly. Caudal cirri are typically produced at the ends of rows 1, 2, and 4 (counting from the left). Caudal cirri move to the postero-dorsal area of the cell at the end of division and often come to appear continuous with the 2 marginal rows.

**Cyst Morphology**

Ultrastructural information on the hypotrich cyst is more limited than for interphase and dividing cells. Walker *et al.* (1980) reiterated Corliss and Esser's (1974) observation on the paucity of knowledge of ciliate cystic phenomena in general and hypotrich cyst fine structure in particular. Walker and Maugel (1980) observed that ultrastructural information on cysts of *Oxytricha fallax* (Grimes,
1973a,b,c), Stylonchia mytilus (Walker et al., 1975), Gastrostyla steinii (Walker et al., 1980), and Diophyrys scutum (Walker and Maugel, 1980), allows recognition of at least 2 classes of hypotrich cysts: kinetosome resorbing (KR) and non-kinetosome resorbing (NKR). This classification was based on differences in a number of categories including development, structure, and relative thickness of the cyst wall, extent of resorption, and organization of retained cytoplasmic and cortical organelles, macronuclear fusion, and retention of vegetative cell volume. Gutierrez et al. (1981, 1983) later described the fine structure of the cyst wall of Laurentiella acuminata and demonstrated that it produces a KR cyst. The only NKR cyst-producing species of these 5 is the eutroplane D. scutum. A detailed description of this cyst type can be found in Walker and Maugel (1980). KR cyst production is observed in the remaining 4 oxytrichine species.

The Cyst Wall

KR cysts possess a protective wall comprised of 4, mostly fibrillar, layers (Fig. 20). The outermost of these, the ectocyst, is a thin, loosely packed layer of lamellae. A thicker mesocyst is composed of more tightly packed fibers in alternating layers. This layer alternation produces what is termed a "herringbone" appearance (Walker et al., 1975). The third cyst wall layer, the thin endocyst, is composed of tightly packed, usually electron dense fibers. The innermost, "granular" layer appears coarse and is of intermediate thickness and electron opacity. The chemical compositions of these layers remain unknown.
Hypotrich cysts are usually described as "spherical" and although surface sculpturing is observed and commented upon, no detailed descriptions of specific details or interspecific differences in this sculpturing are made.

Cytoplasm

Loss of water during encystment results in a dramatic increase in cytoplasmic density (Trager, 1963). This desiccation is thought to retard hydrolytic degradation (Walker et al., 1980). Cytoplasmic microtubular structures, including kinetosomes, are absent. Broad bands or clusters of mitochondria occupy the peripheral cytoplasmic region just interior to the cyst wall and at a distance from the central macronucleus and 1 to several adjacent micronuclei. Macronuclear chromatin occurs in larger, often more dense, clusters than in excysted cells, and nucleoli are smaller and less differentiated as well. Micronuclei are similar to those of vegetative cells but may be surrounded by layers of membranes and/or amorphous material. The area between the nucleus and mitochondria is occupied by autolysomes, ribosomes, and apparent starch reserve granules, all of which may be interspersed, in smaller numbers, among the mitochondria.

Cyst Development

Encystment

Ciliate encystment involves 4 separate and distinct processes (Trager, 1963): (1) cyst wall production, (2) nutrient reserve storage, (3) dedifferentiative activities, including resorption of various organelles and modification of cell shape to conform to cyst morphology, and (4) water loss producing increased cytoplasmic density.
Electron microscopy revealed finer details involved in some of these processes, most notably, cyst wall production.

The development of KR cysts involves the production of 4 distinct types of cyst wall precursors, each corresponding to 1 of the 4 cyst wall layers. Ectocyst precursors originate as discs or stacks of discs formed from an amorphous material in deep cytoplasmic vacuoles. These precursors migrate to the cell surface where they are deposited between the cell membranes. Interspecific differences in this process may exist. Walker et al. (1980) found that in *O. steinii* ectocyst precursors are released from the vacuole into the cytoplasm and migrate independently to the cell surface, while in *O. fallax* (Grimes, 1973a) the vacuoles apparently migrate and release the precursors directly between the membranes. Production of the other 3 types of precursor follows ectocyst deposition. Mesocyst precursors, formed from loose fibrous material are larger than endocyst and granular layer precursors. Grimes (1973a) published photographs of endocyst and granular layer precursors, and Walker et al. (1980) showed "probable" granular layer precursors differing, at least in size, from those of Grimes, but neither offered any description of their contents. All appear amorphous or granular. The contents of mesocyst, endocyst, and granular layer precursors are laid down sequentially inside the newly formed ectocyst.

Cytoplasmic and cortical changes during encystment include loss of water and the resultant increase in cytoplasmic density, resorption of all microtubular elements of both kinetosomal and cytoplasmic origin, clustering of mitochondria with tightly packed cristae, and the production of granules resembling those shown by Verni and Rosati.
to be involved in polysaccharide storage. Macronuclei, regardless of number, fuse to form a single, central, dense macronucleus. While microtubular elements are resorbed in the cytoplasm, they are produced in quantity in the macronucleus, possibly aiding in macronuclear fusion (Walker et al., 1980), but disappear prior to the cessation of encystment activity. Micronuclear preparation for encystment involves elaboration of several surrounding layers of amorphous or membranous material (Walker et al., 1980). Micronuclear fusion was never observed during hypotrich encystment, but resorption occurs frequently (Walker et al., 1980).

**Excystment**

Excystment begins with the dispersal of the mitochondrial clusters, presumably in preparation for provision of the soon to be increased energy requirements of the cell. Pairs of kinetosomes are formed de novo deep in the cytoplasm and migrate to the cell surface where they proliferate to form a kinetosomal field. Further development of vegetative ciliary structures (AZM, cirri, etc.) proceeds through elaboration of groups of kinetosomes from this field, migration, further kinetosomal replication, and final ciliary differentiation. Production of specific primordia and their subsequent differentiation to mature ciliary structures corresponds closely to that observed in dividing and reorganizing cells (Grimes, 1973a; Tuffrau and Fryd-Versavel, 1977; Jareno, 1977; Jareno and Tuffrau, 1979; Gutierrez et al., 1981).

Macronuclear division in excystment occurs amitotically and produces the diagnostic number of macronuclei prior to the first post-
cystic cell division. Micronuclear activity involves a complex series of mitotic divisions and resorptions (Grimes, 1973a; Walker, 1976).

In an effort to clarify relationships within the Oxytrichina I investigated the morphology and ultrastructure of both interphase cells and cysts as well as division morphogenesis in representatives of each of the 3 groups listed above. Interphase cell structure and division morphogenesis represent classical approaches to the study of ciliate phylogeny (Borror and Evans, 1979; Corliss, 1979). Cyst structure however, an area of considerable importance to other groups of protozoa (Mehlhorn et al., 1976), has seen limited use as a tool in phylogenetic investigations of ciliates (Corliss and Esser, 1974). With regard to hypotrich cysts, only Grimes (1972, 1973a,b,c), Hashimoto (1962, 1963, 1964), Walker (1976), Walker and Goode (1976), Walker and Maugel (1976, 1980), Walker et al. (1975, 1980), and Gutierrez et al. (1981, 1983) recently published comparative information on a total of 5 species. I intend to combine information from this neglected, but potentially useful, area of hypotrich biology with morphological and developmental data to produce a unified view of inter- and intrasubordinal relationships of the Oxytrichina.
MATERIALS AND METHODS

Collection

The 11 oxytrichine hypotrichs (of 75-80 species listed in the
suborder by Borror, 1972) for comparison are from a variety of sources.

I received Oxytricha fallax Stein 1859 from Dr. D.M. Prescott,
University of Colorado, Boulder, Colorado, U.S.A. who, in turn,
received the line from Dr. T.M. Sonneborn, University of Indiana,
Bloomington, Indiana. I collected a second strain from a moss in the
Wentworth Greenhouses in Rollinsford, New Hampshire, U.S.A. (43°12' N.
Lat., 70°52' W. Long.).

The orange lichen, Xanthuria polycarpa, growing in abundance on
Appledore Island, Isles of Shoals, Maine, U.S.A. (42°59' N. Lat.,
70°37' W. Long.) yielded my strain of Oxytricha quadri-nucleata Drajeaco
and Njiné, 1971.

Oxytricha similis Engelmann, 1862 appeared as a contaminant in a
culture of Stylonychia pustulata kept at the Jackson Estuarine
Laboratory, Durham, New Hampshire (43° 5' N. Lat., 70° 52' W.
Long.).

I received 2 strains of Stylonychia pustulata (Müller, 1786)
Ehrenberg, 1838 from Dr. D.M. Prescott who collected them from
freshwater near Boulder, Colorado (40° 2' N. Lat., 105° 19' W. Long.),
and as a contaminant in a Paramecium culture from the Carolina
Biological Supply Company.
I collected *Histriculus histrio* (Müller, 1786) from Crommet Creek at its intersection with Dame Road in Durham, New Hampshire (43°06' N. Lat., 70°52' W. Long.).

I collected *Tachysoma* sp. from a tidal marsh on Adams Point, Durham, New Hampshire (43°06' N. Lat., 70°52' W. Long.).

My collections of *Gonostomum affinum* (Stein, 1859) Kahl, 1932 arose from the same lichens (*Xanthuria polycarpa*) on Appledore Island, Maine as *O. quadrinucleata*.

Dr. Gary Grimes of Hofstra University, Hempstead, New York, U.S.A. provided a sample of his strain PLB3 of *Pleurotricha lanceolata* (Ehrenberg, 1838).

I also received my strain of *Paraurostyla weissei* (Stein, 1859) from Dr. Grimes.

A small pond on Adam's Point, Durham, New Hampshire produced cultures of *Paraurostyla hymenophora*.

I received 2 strains of *Paraurostyla* sp. from Dr. A.C. Borr, University of New Hampshire, Durham, New Hampshire. Dr. Borr collected the samples from 2 locations: a small pond on Appledore Island, Isles of Shoals, Maine, and a rainwater puddle on the campus of La Universidad National Autonoma de México, México City, México (19°25' N. Lat., 99°07' W. Long.).

**Culture Methods**

I maintained *O. quadrinucleata, O. similis, Paraurostyla hymenophora*, and *G. affinum* in Pringsheim's solution (Chapman-Andreson, 1962) with a split pea to encourage bacterial growth. I stored cultures at 20° C or, where more rapid growth was desired, room temperature. In the case of *O. quadrinucleata* the actual food organism
was an unidentified species of the carteriid flagellate *Polytomella* Aragao, 1910 which occurred in the same lichen from which I recovered the hypotrich. While *Parurostyla hymenophora* has previously been fed the ciliate *Tetrahymena* (Grimes and L'Hernault, 1978), the strain used here was exclusively bactivorous.

I cultured *T. saltans* at room temperature in filtered seawater (35°/oo) with a split pea to encourage bacterial growth.

I maintained *O. fallax*, *S. pustulata*, *H. histrio*, *Parurostyla weissei*, and *Parurostyla sp.* in Pringsheim's solution at 20° C or room temperature. I cultured the ciliate *Tetrahymena pyriformis* in the following manner: I dissolved 10 gm of proteose peptone and 0.2 gm K$_2$HPO in 1 liter of 18 megohm distilled water. I then dispensed the solution in 100 ml volumes to 250 ml Erlenmeyer flasks, stoppered them with foam, autoclaved them at 121° C for 15-20 min and cooled. I inoculated flasks as needed with *T. pyriformis* and wild bacteria and stored them at 20° C. Cultures were ready for use in 2-3 days. I concentrated food organisms by either light centrifugation followed by rinsing in fresh Pringsheim's solution (repeated once) or, where more immaculate cell suspensions were desired, a modification of van Wagendonk and Soldo's (1970) density layering migration technique. In the latter, I poured approximately 50 ml of "log phase* Tetrahymena culture into a 50 ml volumetric flask and let it stand 30-60 min to allow the ciliates to migrate upward. I then gently layered approximately 1 ml Pringsheim's solution onto the culture medium. After 30 min I could remove a dense suspension and feed it directly to the hypotrichs.
I also cultured *Pleurotricha lanceolata* with *Tetrahymena* as a food organism, but due to the apparently extreme toxicity of proteose peptone for this hypotrich, it was necessary to use another method for growing the *Tetrahymena*. I prepared a Cerophyl (Cerophyl Corporation, Kansas City, Missouri) infusion by the Sonneborn (1970) method. I boiled 2.5 gm dehydrated cereal leaves for 5 min in 1 liter of 18 megohm distilled water with 0.7 gm Na$_2$HPO$_4$, filtered the resulting solution, transferred it in 100 ml volumes to 250 ml Erlenmeyer flasks, stoppered them with foam, and autoclaved them at 121° C for 15 to 20 min. When the medium was cool I added *Tetrahymena* and stored the culture at 20° C. When adequate numbers of *Tetrahymena* were present (subjective observation), I mixed the culture 1:1 with a clean suspension of *Pleurotricha lanceolata* in Pringsheim's solution.

I maintained all cultures in a primarily trophic condition by periodic replacement of 50% or more of the culture medium with either fresh Pringsheim's solution or filtered sea water.

**Induction of Excystment and Encystment**

In 10 of the 11 species considered (*T. saltans* apparently does not form cysts) I induced excystment as follows: I added fresh Pringsheim's solution to encysted cells (in both original lichen collections and established cultures). To this I added a split pea and 2-3 1" pieces of dried Timothy hay stalk. Excystment typically occurred within 1-3 days. I found that by drying cysts of *O. quadrinucleata* and *O. affine* (lichen dwellers which would be subject to periodic drying in nature) prior to induction of excystment, I obtained higher percentages of excystment than I observed for undried cysts. In other forms, I noted no observable difference. I often added
Tetrahymena with the other materials to O. fallax, S. pustulata, and Paraurostyla sp. cultures. While this had no apparent effect on percentage or rate of excystment, dense cultures were produced more rapidly, presumably due to the immediately available food organism to the newly excysted hypotrichs.

I initiated production of cysts for subsequent study or culture storage in the species which were fed Tetrahymena by withholding food. Encystment occurred within 1-3 days of the last feeding. Cultures of O. quadrinucleata and the bactivorous hypotrichs were not renewed with fresh culture medium. The decrease in available food resulted in encystment, although this technique usually took longer, with 5-7 days typically being required to produce large numbers of cysts. Complete encystment of these cultures often took as long as 4 weeks.

**Light Microscopy**

I performed all light microscopy and photomicrography with a dissecting stereomicroscope or a compound microscope with attached automatic camera.

Observation of living cells for determination of cortical stiffness and behavior preceded preparation of permanent slides or for electron microscopy. I concentrated cells by light centrifugation or manually via a micropipette. I prepared permanent slides by 2 methods. One was a modification (Borror and Evans, 1979) of Borror's (1969) Nigrosin-Mercuric Chloride-Formalin method using Champy's fluid as a fixative (15 min.) followed by adherence to albuminized slides and cortical staining. I accomplished the adherence and staining in 1 step with a 1:1 mixture of t-butanol and 0.5% (w/v) aqueous nigrosin. I
found that addition of 1-3 drops of glacial acetic acid to 2 ml of the adherence-stain mixture often improved the stain, particularly for hypotrichs over 100 um in length.

The other staining procedure was a modification of the Bodian Protargol technique (Deroux and Tuffrau, 1967; Grimes, 1972; Jerka-Dziadosz and Frankel, 1969; Tuffrau, 1967; Hill, 1980a). After concentration, I used a modification of Perenyi's fixative (1% chromic acid w/v, 3 ml; 10% nitric acid v/v, 8 ml; 95% ethanol v/v, 0.5 ml; distilled water, 3 ml; t-butanol, 5.5 ml) to fix and adhere cells to albuminized cover slips. The time of fixation was 3 min. I then passed cover slips with attached cells through the following series of solutions:

1. Formol alcohol (85% ethanol v/v, 9 parts; 20 min commercial formalin, 1 part)
2. 95% Isopropanol 5 min
3. 100% Isopropanol (2x) 5 min each
4. 100% Methanol 10 min
5. Collodion (2.8 ml commercial solution dip (2-3 sec) in 7.2 ml methanol)
6. 95%, 70%, 50%, 30%, 15% Isopropanol 5 min each
7. Distilled water (2x) 5 min each
8. 0.5% potassium permanganate w/v 10 min
9. Distilled water (2x) 5 min each
10. 5% Oxalic Acid w/v 10 min
11. Distilled water (2x) 5 min each
12. 0.2% Protargol w/v at 70° 20 min (prepared during step 5)
13. Distilled water 5 min
14. 1% Hydroquinone, 5% NaSO₃ w/v until collodion turns dark
15. Distilled water (2x) 5 min each
16. 2% Oxalic acid w/v 10 min
17. Distilled water (2x) 5 min each
18. 5% Sodium Thiosulfate w/v 10 min
19. Distilled water (2x) 5 min each
20. 15%, 30%, 50%, 70%, 95% Isopropanol 5 min each
21. 100% Isopropanol (2x) 5 min each
22. 100% Methanol 10 min
23. 1:1 100% Ethanol:Xylene 10 min
24. Xylene 10 min
25. Mount

This technique yielded excellent results with marine hypotrichs including *T. saltans*, but was usually unsuccessful for freshwater and lichen dwelling forms. An exception was a set of slides of *G. affine* which, immediately following preparation, were of marginal quality (too dark, poor differentiation of ciliary structure), but over a period of 2 years eventually yielded an excellent stain.

**Electron Microscopy**

I fixed cells to be prepared for electron microscopy in a 1:1 mixture of 2.0% osmium tetroxide (w/v) and 4% glutaraldehyde (v/v), both in Sorensen's buffer. Fixation time for trophic cells was 15 min while 1 hr was required for adequate fixation of cysts.

Following fixation, I dehydrated cells to be prepared for SEM (15 min each in 15%, 30%, 50%, 85%, 95%, 100% ethanol). I then dried the
cells with a SAMDRI carbon dioxide critical point drying apparatus, coated them with a 3.0 \( \times \) 10\(^{-8} \) m layer of gold palladium (60:40), and viewed them with an AMR 1000 scanning electron microscope (at 20 kV).

I embedded fixed cysts for TEM by one of two methods. In the first, I dehydrated the cells as for SEM and passed them stepwise through mixtures (v/v) of 1:3, 1:1, 3:1 Spurr Low Viscosity Embedding Medium (Polysciences, Inc.):100% ethanol (1 hr each solution). I followed this with 6 hr in 100% embedding media and polymerization at 70° C for at least 16 hr.

The second method of preparation for TEM was a modification of Robbins and Jentzsch's (1967) method for rapid embedding of cell monolayers and suspensions. I passed fixed cysts through the following mixtures: 20% ethanol, 60% ethanol with Spurr's medium replacing water as the solvent, 30% ethanol in Spurr's medium (15 min each solution). I then placed the cells in 100% embedding medium for 1 hr or longer, passed them through a second change of embedding medium and polymerized them at 70° C for at least 16 hr. This has the advantage of rapidity over the first method and avoids the use of high concentrations of ethanol which could extract lipids from the cells. Continuity of medium across the cyst wall was also improved which enhanced sectioning qualities.

Following embedding, I cut individual cells from the block of hardened medium and glued them to blank stubs prepared in BEEM capsules from the same medium. I sectioned the cysts on a Reichert OMU-3 ultramicrotome and viewed them with a JEOL 100s transmission electron microscope (at 80 kV). No fewer than 4 60-90 nM sections from each of 5 or more cysts were studied.
RESULTS

The naming and numbering of hypotrich ciliary organelles is an imperfect art because of interspecific and even intraspecific variability. Nevertheless, specific groups of ciliary organelles are distinguishable. In this section I use the designations and abbreviations listed in the Introduction (see especially pp. 7-14 and Figs. 1 and 3). The kinetosomal streaks which produce the UM are considered separately from those which produce the F-V-T cirri and are designated EM and PM streaks respectively. Kinetosomal streaks which produce F-V-T cirri and any longitudinal cirral rows are numbered from left to right (I-N). Cirri produced within each streak are numbered from anterior to posterior (1-n).

Bases for identification of species come from a variety of sources. Publications by Kahl (1932), Borror (1972), and Corliss (1979) are especially useful in hypotrich identification. It is usually necessary, however, to refer to specific publications concerning individual species for certain identification. Such references are noted in the sections dealing with the respective hypotrich species.

Trophozoite Morphology and Morphogenesis

Group A: Oxytricha and Similar Genera

Oxytricha fallax. O. fallax (Fig. 4) is probably the best known member of the Oxytrichina. It was described by various authors (Grimes, 1972; Grimes and Adler, 1976; Hashimoto, 1961, 1962, 1963), and my observations are in general agreement with their
descriptions. Specimens from 2 populations (Boulder, Colorado and Rollinsford, New Hampshire) exhibited the measurements listed in Tables 3 and 4. Average width (measured at the widest point) was approximately 1/2 the cell length in both populations. The 2 macronuclei are both associated with 1, or, infrequently, 2 micronuclei. Cells are flexible. *O. fallax* is encountered in diverse freshwater or terrestrial habitats.

The adoral zone of membranelles ranges in total length (measured in fixed, stained specimens from the anterior end of the cell to the posterior end of the buccal cavity) from approximately 35-50% of the total body length. The endoral and paroral membranes extend from the posterior end of the AZM anteriorly about 2/3 the length of the AZM.

F-V-T cirri tend to be conservative in number. Typically there are 8 frontal, 5 postbuccal, and 5 transverse cirri. Although Grimes (1972) interpreted the posteriormost postbuccal cirrus as a transverse due to its proximity to other transverse cirri, it was clearly separate from the 5 transverse cirri in both of my populations, and therefore counted with the postbuccals. Developmental information also supports its inclusion in the latter group. I observed some variation in frontal and postbuccal cirrall number in the Boulder strain.

Without exception, both strains exhibited single left and right marginal rows of cirri. The right marginal row extends from a point at the right anterior margin of the cell to the posterior end. The left marginal row extends from a point lateral to the posterior end of the AZM to the posterior end of the AZM to the posterior end of the cell and typically contains fewer cirri than the right marginal row. The marginal rows appear almost continuous posteriorly in both populations.
Dorsal ciliation in *O. fallax* consists of 6 rows of dorsal bristles and 3 flexible caudal cirri. No exceptions appeared in either population.

Cortical changes associated with cell division in *O. fallax* (Fig. 5) begin with the elaboration of kinetosomes in close proximity to the left transverse cirrus. These proliferate anteriorly to a typical, triangular, postbuccal, anarchic field of kinetosomes, the opisthe oral primordium. AZM development in the opisthe results from the proliferation and migration of kinetosomes in this field to form orderly arrays of membranelles (Fig. 5b). The parental AZM is retained as the AZM of the proter with little or no differentiation.

The undulating membrane of the opisthe arises in close association with the opisthe oral primordium and develops from a narrow, elongate primordium several kinetosomes wide to 2 streaks from which the paroral and endoral membranes are formed. In the proter the parental UM dedifferentiates and UM primordium develops from its constituent kinetosomes. EM and PM streaks are produced by splitting of the UM primordium as in the opisthe. In both proter and opisthe a single cirrus, the paroral cirrus, is elaborated from the anterior end of the paroral streak.

Dedifferentiation of frontal cirri I2, II2, and III1 provides kinetosomes from which the 5 frontal cirral streaks are produced (Fig. 5c). These streaks proliferate and develop into the F-V-T system of the proter. Opisthe F-V-T cirri are produced in a similar fashion following the dedifferentiation of postbuccal cirri III2 and IV1. Although Grimes (1972) was uncertain about the contribution of postbuccal cirrus IV2, it did not appear to dedifferentiate in either
of my populations and thus may be assumed not to have contributed
kinetosomes to the development of opisthe F-V-T cirral streaks. In
addition, frontal cirri II, III, IIII, and V1 and V2 postbuccal cirri
IV3 and V3, and the transverse cirri apparently do not contribute
kinetosomes to the developmental process and are resorbed shortly after
the conclusion of cell division.

Development of F-V-T cirral streaks follows a specific pattern in
O. fallax (Fig. 5) and other members of this group (those resembling O.
fallax. As already stated, the paroral cirrus develops from the
anterior end of the PM streak. Frontal cirri I1 and I2 and transverse
cirrus I3 develop from the leftmost of the 5 frontal streaks (streak
I). Streak II produces frontals II1 and II2 and transverse II3.
Streaks III and IV migrate posteriorly (Fig. 5e) with respect to the
other frontal streaks and are involved primarily in the production of
postbuccal and transverse cirri. Streak III produces frontal III1,
postbuccal III2, and transverse III3, while streak IV yields postbuccal
VI1, VI2, and VI3 and transverse VI4. Streak V produces frontals V1
and V2, postbuccal V3, and transverse V4. Grimes (1972) demonstrated
that some variation in this scheme may occur naturally, particularly in
regard to production of extra cirral primordia which may or may not be
resorbed prior to the end of division. This variability allows for the
infrequent occurrence of extra F-V-T cirri in the mature cell.
Nevertheless, specific cirri do normally develop from specific streaks
in a fashion which is highly conserved in Oxytricha-like genera.

Marginal cirral streaks are produced in both proter and opisthe by
dedifferentiation and proliferation of kinetosomes within the parental
marginal rows (Figs. 5c-e). Development of dorsal ciliature (Fig. 5f)
occurs as described in the introduction: the 3 leftmost rows (1, 2, and 3) produce streaks of kinetosomes through dedifferentiation of parental dorsal bristles. Streak 1 splits to produce 2 separate streaks (3 and 4). The 2 rightmost streaks (5 and 6) are produced in close proximity to the right marginal row and proliferate posteriorly to produce dorsal bristle rows 5 and 6. Caudal cirri are produced at the posterior ends of dorsal streaks 1, 2, and 4.

*Oxytricha quadrinucleata.* Members of Kahl's (1932) subgenus *Steinia*, of which *O. quadrinucleata* is a member, are distinguished by a hypertrophied paroral membrane. PM cilia increase in length and number anteriorly and the membrane forms a distinctively hooked anterior border to the buccal cavity (Fig. 6a). No EM is visible in either Nigrosin stained cells or those prepared for SEM. Cells are flexible. Possession of 4 macronuclei is diagnostic of the species. There are usually 2, sometimes 3, micronuclei usually associated with macronuclei 1 and 3 (counting from anterior to posterior). Otherwise the species closely resembles *O. fallax*. Measurements are given in Table 5.

Frontal, postbuccal, and transverse cirri are highly conservative in number (8, 5, 5 respectively), as are numbers of left and right marginal rows (1 and 1). Possession of 3 flexible caudal cirri is the rule, although 1 cell was found which had only one. Another cell had a 4th caudal cirrus in a somewhat more dorsal than usual position. This cirrus may have been a relict of the previous generation. The 6 dorsal kineties are aligned in a fashion similar to that encountered in *O. fallax* (Fig. 6b).

Division in *O. quadrinucleata* (Fig. 6c-f) proceeds almost precisely as in *O. fallax*. The opisthe oral primordial field forms
(Fig. 6c) in a similar manner (albeit not in proximity to the transverse cirri); the F-V-T cirral streaks develop from the dedifferentiation of the same parental cirri (frontals 6, 7, and 8 in the proter, and postbuccals 1 and 2 in the opisthe). Postbuccal cirrus 3 (Fig. 6d, e) is clearly not involved in the dedifferentiative activity leading to the development of opisthe F-V-T streaks. Further F-V-T cirral development occurs as in O. fallax in all details, including differentiation of specific streaks to the same specific cirri. Marginal, dorsal, and caudal ciliature are formed as in O. fallax as well.

The endoral membrane, not visible in non-dividing cells, is produced at least fleetingly during division, and can be seen in both nigrosin stained cells and with SEM (Fig. 6f). Whether this membrane is resorbed or merely obscured after division is not known.

Oxytricha similis. O. similis (Fig. 7) is a small (< 100 μm, \( \bar{x} = 88 \) μm), flexible, elongate (2-3x as long as wide) hypotrich from freshwater. Measurements are given in Table 6. There are 2 macronuclei and 2, or occasionally 4, micronuclei.

The AZM ranges from about 1/3 to 1/2 of total body length and is bordered on the right by a raised RBO crested by a short PM (Fig. 7c). A correspondingly short EM is located deep in the buccal cavity. Membranellar cilia (Fig. 7c, MC) are short and inconspicuous.

All cells observed had 8 frontal, 5 postbuccal, and 5 transverse cirri, in addition to single left and right marginal cirral rows. Dorsal ciliature (Fig. 7b) is similar to that in O. fallax. The 3 flexible caudal cirri are sometimes, but not always, noticeably longer than the marginal cirri.
Morphogenetic activity during division (Fig. 7d) results in elaboration of 5 somewhat diagonally situated frontal streaks. Development of these streaks to F-V-T cirri occurs as in O. fallax as does development of all somatic ciliature.

*Stylonychia pustulata.* *S. pustulata* is a medium-sized hypotrich ranging in length from 101 μm - 121 μm. Its more or less parallel sides distinguish it from the other common member of the genus, *S. mytilus*. Both are freshwater forms with stiff cortices and stiff caudal cirri. Fixed and mounted specimens from my population had an average L:W ratio of 1.78. This figure is somewhat lower than might be expected due to tendency toward lateral bulging under coverslip pressure. The BCL:L ratio averaged .52. My specimens invariably possessed 2 macronuclei. There are typically 2 micronuclei, 1 associated with each macronucleus, although 4 micronuclei were encountered in 1 specimen. Measurements are given in Table 7.

The oral area of *S. pustulata*, as indicated by the BCL:L ratio (see above) is high. The AZM itself is in no way hypertrophied or flared laterally as is often the case in *S. mytilus*, but extends to approximately the middle of the cell. The UM occupies approximately 2/3 of the distance from its origin at the apex of the buccal cavity to the anterior end of the cell.

F-V-T cirri are conservative in number with 8 frontal, 5 postbuccal, and 5 transverse cirri being the norm although cells with 9 (or in 1 case 10) frontal cirri were encountered. Typical placement of these cirri is depicted in Figures 8a and 8b.

*S. pustulata* has single rows of left and right marginal cirri. The right row typically contains more cirri (26-37) than the left (22-
Both rows extend almost to the posterior end of the cell. There are 6 rows of dorsal bristles and 3 stiff caudal cirri, shorter than those of *S. mytilus*.

Cortical events associated with morphogenetic activity reported by Sapra and Dass (1970) and Grimes (1972) were verified in this study. Development, including streak formation and deployment as well as eventual placement of ciliature on both dorsal and ventral surfaces, is similar to that encountered in *O. fallax* (Figs. 8b-d).

*Tachysoma* sp. (Figs. 9a, 10a) is a salt marsh dwelling hypotrich ranging in length from 29–40 µm (\( \bar{x} = 34 \mu m \)). The buccal cavity and AZM occupy approximately 1/3 of the length. The L:W ratio is low (\( \bar{x} = 1.8 \)). The cortex is flexible. There are usually 2 macronuclei, although 4 are not uncommon (Fig. 10a) and 1 cell with 8 was encountered. Micronuclei are dorsal to the macronuclei, thus they are difficult to count in protargol stained specimens but 2 seemed to be typical. Measurements are given in Table 8.

The AZM courses around the anterior end of the cell, around the anterior left side, and continues to curve sharply inward to a point near the midline of the body. This is in contrast to most of the other species discussed in this paper and is especially noticeable in living specimens, giving them a somewhat cephalized appearance. The bases of PM and EM are well separated from the apex of the AZM and buccal cavity but extend forward almost to the anterior terminus of the cell.

The 8 frontal and 5 (occasionally 6) postbuccal cirri are arranged much as in *Oxytricha* or *Stylonychia*. A lone cirrus in the postbuccal region near the left margin of the cell (Fig. 9) proves
morphogenetically to be 1 of the transverse cirri, the other 4 of which are situated more typically.

There are single rows of left and right marginal cirri which end posteriorly well ahead of the posterior end of the cell.

There are 3 dorsal rows of long cilia. Their arrangement can be confusing, however, due to the wide spacing and low numbers of cilia (3-5) in a row and because portions of some parental rows are apparently retained after cell division. The frequent result is a cell with about 12-16 seemingly scattered long, delicate dorsal cilia.

There are 2 caudal cirri.

Dedifferentiation of the isolated transverse cirrus 1 is the first indication of beginning division. Kinetosomes from this cirrus apparently provide the initial basis for the opisthe oral primordium (Figs. 10a, b). The UM streak arises adjacent to the developing opisthe AZM. In the proter the parental AZM is retained and the UM dedifferentiates (Figs. 10b, c) and redifferentiates in situ as is typical in the Oxytrichina.

T. sp. produces frontal ciliary primordia in a manner once thought to be unique among the Oxytrichina (Culberson, 1979). Hemberger (1982) showed that the process is common, at least in certain soil dwelling hypotrichs. A single latitudinal zone of 5 frontal streaks is produced initially in the anterior 1/3 of the ventral surface of the cell (Figs. 10b-d). Frontal cirri II2, II2, III1, and V2, as well as postbuccal cirri III2, IV1 and IV3 apparently participate in the formation of these streaks by dedifferentiation and contribution of kinetosomes. As these streaks develop, they first assume a diagonal arrangement (Fig. 10d), which soon changes to the longitudinal pattern typical of the
Oxytrichina. As the streaks attain longitudinal orientation, they begin to divide latitudinally (Fig. 10e), beginning with streak 1, the right streak, and proceeding toward the left side of the cell. After the proter and opisthe fields are separate, development proceeds as in O. fallax (Figs. 10f-h) with a single exception. Transverse cirrus I3 moves into a right lateral, postbuccal position where it ceases its migration, not accompanying the other transverse cirri to the posterior portion of the ventral surface.

Right marginal cirri develop in a pattern similar to that set by the frontal ciliature. A single latitudinal streak is formed initially (Fig. 10e) and later separates, in coordination with the left to right separation of the frontal streaks, into proter and opisthe right marginal streaks. Proter and opisthe left marginal streaks arise separately as is typical for the Oxytrichina.

The 3 rows of dorsal cilia develop from separate "in row" production of kinetosomal streaks in both proter and opisthe. The 2 caudal cilia both develop at the end of the left dorsal streak (Fig. 10e).

Gonostomum affine. Shape, reflected by L/W ratio, is highly variable in fixed, mounted specimens of G. affine. This conclusion is supported by observation of living cells in culture. Cells studied ranged in length from 35 μm - 61 μm (\(\bar{x} = 51.3\) μm) and L/W ratios varied from 2.1-4.3 (\(\bar{x} = 3.1\)). BCL/L ratios (\(\bar{x} = .5\)) tended to vary (.41-.66) inversely with cell length, longer cells having lower BCL/L ratios, a reflection of relatively consistent BCL/L length (\(\bar{x} = 25.5\) μm). The cortex is relatively flexible. There are 2 macro- and 2 micronuclei. Measurements are given in Table 9.
The AZM of *G. affine* differs in several aspects from the "typical" oxytrichine AZM. There is a distinct "collar" portion (Figs. 11a, 12a, b) with noticeably enlarged membranelles. The "lapel" portion of the AZM curves only slightly around the anterior left 1/3-1/2 of the cell and, in SEM micrographs (Fig. 12a), seems to end laterally. Photomicrographs (Fig. 12b) reveal that at this point the AZM courses sharply inward and passes beneath the ventral surface to a point near the interior midline of the cell.

The paroral membrane of *G. affine* is also atypical. Interphase cells from my population possess only a short row of 9-11 separated long cilia (Figs. 12b,d). Foissner (1982) and Hemberger (1982) both described this unusual PM, but mistook it for an endoral membrane. SEM micrographs (and careful light microscopic observation) reveal that it lies atop (ventral to) the right buccal overture (Figs. 12a,d). This confusion is caused by the fact that the endoral membrane, normally a single row of cilia, appears in protargol preparations (Fig. 12b) as the more substantial of the 2 membranes. In addition, it lies so deep inside the buccal cavity that it is positioned to the right of (but dorsal to) the PM. Thus, the 2 membranes are easily confused in protargol impregnated specimens viewed without regard to relative depths of structures under observation.

Specimens from my population almost invariably had 11 frontal cirri, including the buccal cirrus. The arrangement of those cirri is unusual (Figs. 12a,b) and had led various authors (Tuffrau, 1979; 1979) to place it among the Urostylina. A group of 5 or 6 cirri arranged in a "zig-zag" pattern are reminiscent of the midventral cirri found in the suborder Urostylina. Hemberger's (1982) investigations indicate
greater variation in numbers of frontal cirri allowing for increased superficial urostyline similarity. There are 2 small postbuccal cirri situated just anterior to 2 slightly enlarged transverse cirri. There are single left and right marginal rows of cirri.

Dorsally there are 3 rows of cilia. The left and middle rows are usually separated by a broad expanse of cortex which may contain relict parental dorsal cilia (Fig. 12c). There are 3 flexible caudal cirri (Fig. 12c).

In 1982, I reported on morphogenetic information obtained primarily from reorganizing cells. A few cells fixed and stained early in the division process show that an opisthe AZM field forms in the usual location and, in common with Tachysoma sp., a single latitudinal zone of F-V-T streak proliferation is initially produced. Hemberger (1982) showed that this then splits to form proter and opisthe F-V-T fields. Reorganizing cells demonstrate the 5 longitudinal frontal streaks and the UM streak typical of the Oxytrichina (Figs. 12e,f). Development proceed from this point much as in O. fallax with all kinetosomes in streaks 3 and 4 migrating posteriorly to become the more posteriorly placed frontal cirri, and posterior portions of streaks 4 and 5 producing the posterior group of 2 transverse cirri and 2 postbuccal cirri (Fig. 13).

Marginal cirri are produced following the elaboration of streaks of kinetosomes within the parental rows. Dorsal rows of cilia are produced by "in row" proliferation of kinetosomes with each streak producing a caudal cirrus at its posterior end.

Group B: Forms With Multiple Right Marginal Rows of Cirri

Pleurotricha lanceolata. The genus Pleurotricha is characterized
by an Oxytricha-like arrangement of F-V-T cirri and possession of 2 or more right marginal cirral rows. The population of Pleurotricha lanceolata (Figs. 14, 15) I studied varied from 112 μm-143 μm (X = 126 μm) in length and 51.7-70.4 μm (X = 64.5 μm) in width. The cortex is flexible and there are 2 micro- and 2 macronuclei. Measurements are given in Table 10.

The AZM is similar to that found in other typical oxytrichine hypotrichs, although Pleurotricha tends to have more membranelles (X = 47) than others I studied. The posterior end of the paroral membrane arises anterior to the posterior end of the AZM and buccal apex. At its anterior end the PM curves inward in a fashion reminiscent of, but of considerably lower magnitude than, that seen in O. quadrinucleata and other members of Kahl's (1932) subgenus Steinia. The endoral membrane lies within the buccal cavity and does not extend as far anteriorly as the PM.

Placement of F-V-T cirri is similar to that observed in O. fallax with the exception that transverse cirri 1, 2, and 3 are more anterior (Fig. 14) than in Oxytricha.

There are 2 rows of right and 1 row of left marginal cirri which are essentially confluent posteriorly. There are 6 rows of dorsal bristles and 3 caudal cirri (Fig. 14b).

Morphogenesis of F-V-T cirri (Figs. 15b, 16) is similar to that seen in O. fallax. Five longitudinal streaks are produced separately in the proter and the opisthe. Cirral development in each streak reflects the pattern in O. fallax.

Development of left marginal cirri occurs as in Oxytricha, but the 2 right marginal rows are produced in an atypical, although not unique,
fashion for taxa with multiple rows of cirri. The inner of the 2 rows
does not participate in the developmental process and thus may be
considered vegetative.

Cirri in the outer row dedifferentiate in 2 zones (proter and
opisthe), but form 2 streaks of kinetosomes in each zone rather than
adhering to the usual 1 row-1 streak relationship. Thus, the outer row
may be considered the germinative right marginal row. The 2 streaks
develop into the right marginal rows of the mature cell.

Development of dorsal bristle rows and caudal cirri is identical
to development of the same in Oxytricha.

Group C: Forms With Ventral Longitudinal Rows of Cirri

Paraurostyla sp. The genus Paraurostyla consists of several
species, with varying numbers and placement of apparently typical
oxytrichine F-V-T cirri, and from 2 to many longitudinal rows of cirri
and single left and right marginal rows. Paraurostyla sp. is similar
to Paraurostyla hymenophora in its possession of 2 of these ventral
longitudinal rows of cirri (Fig. 17a). It differs, however, in
possession of a greater number of frontal cirri (7-11 as opposed to 6,
typically, in Paraurostyla hymenophora) and 6 macronuclei (2 in
Paraurostyla hymenophora). In addition, the longitudinal rows of the 2
species are produced by slightly different morphogenetic processes.

Paraurostyla sp. is a freshwater hypotrich. One of my strains was
isolated from an Appledore Island, Maine pond fouled by gull droppings,
and the other was recovered from a puddle in a parking lot in Mexico
City, Mexico. In culture, both strains were able to withstand
bacterial buildup that more fastidious organisms could not tolerate.
Both strains averaged approximately 134 μm in length and lengths,
widths, and buccal cavity lengths, as well as L/W and BCL/L ratios were comparable. The ciliate is about twice as long as wide and the BCL occupies approximately 40-45% of the total body length. The cortex is supple and there are invariably 6 macronuclei and 2-4 micronuclei. Measurements are given in Tables 11 and 12.

The adoral zone of membranelles contains 36-49 membranelles and is accompanied by very long membranelar cilia (Figs. 18c, mc). The paroral and endoral membranes extend forward from a point just anterior to the AZM buccal cavity apex about 3/4 of the distance to the anterior end of the cell. The anterior end of the PM appears to curve somewhat toward the left side of the cell.

Up to 11 frontal cirri occupy the area between the PM and the longitudinal rows. The 3 most anterior of these (1 of which is the buccal cirrus) are noticeably enlarged (Figs. 18a, b). Number and placement of the other frontal cirri varies from cell to cell. Postbuccal cirri vary in number from 0 (Fig. 18b) to 4. There are typically 4 or 5 transverse cirri, although I saw 1 cell with only 2 (Fig. 18b).

The 2 longitudinal rows extend from a point just ahead of the transverse cirri anteriorly to about the middle of the cell where they begin to curve to the right (Fig. 18a, b) around the AZM and frontal cirri. The anterior terminus of the left longitudinal row is slightly posterior to the enlarged frontal cirrus and the right row ends laterally and adjacent to them. A short row of cirri frequently occurs between the right longitudinal row and the right marginal row of cirri. These are developmental relicts of the parental right longitudinal row, as will be demonstrated below.
The single left and right marginal rows of cirri are almost confluent posteriorly. They extend on the left to about the middle of the AZM "lapel" (Figs. 17a, 18a,b) and on the right to the right end of the AZM "collar". Dorsal bristles occur in 6 rows (4 long and 2 short; Figs. 17b, 18d), and there are 3 caudal cirri.

Cortical morphogenesis in division begins with proliferation of a typical, anarchic field of kinetosomes in the area adjacent to the left transverse cirrus (Figs. 18e). The opisthe PM and EM primordi arises as a small, triangular group of kinetosomes anterior and to the right of the developing oral primordium (Fig. 18e). The parental AZM is retained intact. PM and EM dedifferentiate and redifferentiate in situ. A single paroral cirrus is produced at the anterior end of the PM streak in both proter and opisthe.

Five longitudinal frontal streaks of kinetosomes are produced separately in the proter and opisthe. Three arise in conjunction with dedifferentiation of frontal cirri in the proter and postbuccals in the opisthe (Figs. 18i-k). Streak 1 gives rise to as many as 6 or 7 frontal cirri and may produce a postbuccal cirrus and/or a transverse cirrus, and, occasionally, a postbuccal cirrus. Streak 3 yields up to 3 postbuccal cirri and a transverse cirrus. The other 2 frontal streaks are derived from kinetosomes produced in dedifferentiation of the left longitudinal row, and produce the longitudinal rows of the mature cell and 1 transverse cirrus apiece. The right longitudinal row remains morphogenetically inactive and often is resorbed incompletely following division, accounting for the relict cirri encountered occasionally in the posterior portion of the cell between the right marginal and right longitudinal rows of cirri.
Right and left marginal rows of cirri, the 6 rows of bristles and the 3 caudal cirri develop as do their counterparts in *O. fallax*.

**Cyst Ultrastructure**

SEM observation of mature resting cysts of 6 oxytrichine hypotrichs, in addition to the few hypotrich cyst descriptions in the literature, reveal 3 basic types of cortical sculpturing (Fig. 19):

a. Scallops or depressions lying in linear or concentric ring patterns. Examples: *O. fallax* (Fig. 19a), *Paraurostyla sp.* (Fig. 19c).

b. Spines or papillae in linear or concentric ring patterns. Examples: *O. quadriqu措施ata* (Fig. 19b), *S. pustulata* (Fig. 19d), and *Pleurotricha lanceolata* (Fig. 19f).

c. Irregular or rough surfaces with small, isolated papillae. Example: *G. affixe* (Fig. 19e).

All are essentially spherical.

**Cysts with Scalloped Surfaces**

The extent of scalloping in cysts with non-papillate surfaces is variable, appearing almost smooth at the light microscope level. At the SEM level sculpturing can vary, in both *O. fallax* and *Paraurostyla sp.* from depressions as shallow as shown in Fig. 19a to as deep as shown in Fig. 19c.

*Oxytricha fallax* cysts (Fig. 19a) averaged 49 µm (range, 39-56 µm) in diameter, more than twice that reported by Grimes (1973a) (18-20 µm) even though trophic cells in both studies were of similar size. There are about 80-90 scallops or depressed areas on the surface of the cyst although their enumeration is difficult due to the relative
irregularity of the surface. Grimes (1973) described internal cyst ultrastructure and I did not repeat his work.

**Paraurostyla sp.** Cysts of *Paraurostyla sp.* (Fig. 19c) have an average diameter of 51 μm (47-55 μm) and possess about 76-78 surface depressions. In cross section (Fig. 20d), the cyst wall is seen to vary in thickness from about 2.5 μm in the depressed areas to about 4.5 μm along the ridges. There are 4 cyst wall layers: (1) a thin ectocyst (Ec), (2) a thick, lamellar mesocyst (M), (3) a thin, dark staining endocyst (En), and (4) an inner, "granular layer" (G). These layers resemble those reported for other oxytrichine hypotrichs (Grimes, 1972; Walker et al., 1975, 1980; and Gutierrez et al., 1983). The ectocyst is about 0.2-0.5 μm thick and appears to be composed of loosely packed lamellar material. This reflects its probable development from the "disk-like" ectocyst precursors reported by other authors. The mesocyst varies from 1.5-4 μm. It appears fibrous and is much more tightly packed than the ectocyst. Dark staining inclusions such as those in Fig. 20d are common. The dense, fibrous endocyst is relatively uniform in cross section, about 0.15 μm thick. The granular layer varies in thickness from 0.05-1.0 μm and is composed of an amorphous or granular substance. It also commonly contains small darkly stained inclusions.

Internal morphology is similar to that reported for *O. fallax* (Grimes, 1973a). There is a central macronucleus accompanied by 1 or more micronuclei. Clusters of mitochondria (Fig. 20d) are located just inside the granular layer. Numerous vacuoles evident in Fig. 20 are probably sites of glycogen or paraglycogen storage and appear similar to those reported by Verni and Rosati (1980). Starch-like granules,
similar to those reported by Walker et al. (1980) are also present, though not numerous.

Cysts with Spines or Papillae

*Oxytricha quadrinucleata.* The surfaces of *O. quadrinucleata* cysts exhibit distinct sculpturing varying from the relatively short papillae (Fig. 19b) to the longer spines similar to those in *S. pustulata* (Fig. 19d) or *Pleurotricha lanceolata* (Fig. 19f). These spines range in length from about 3.5 μm to 7 μm and number about 140. Cyst diameter, measured at the bases of the spines, averages about 46 μm. The cross sectional appearance is similar to cysts of *O. fallax* or *Paraurostyla* sp. In areas between the spines, the ectocyst is about 0.1 μm thick. The spines are hollow elaborations of the lamellar components of the ectocyst. The mesocyst is about 1.7-2.8 μm thick, with the thickest areas being situated as "bases" for the spines. The endocyst is of relatively uniform thickness, about 0.04 μm. The inner surface of the granular layer is grooved (Fig. 20b) resulting in a variable thickness of 0.08-0.34 μm.

*O. quadrinucleata* cysts have a central macronucleus, 1 or more micronuclei, and clusters of mitochondria just inside the cyst wall. Nutrient reserve storage bodies are of the 2 types (glycogen or paraglycogen and "starch-like") seen in *Paraurostyla* sp. Autophagic vacuoles similar to those found in *O. fallax* (Grimes, 1973) and, occasionally, *Gastrostyla steinii* (Walker et al., 1980) are present.

*Pleurotricha lanceolata.* *Pleurotricha lanceolata* cysts (Fig. 19e) average 57 μm in diameter. The 160 or so spines arising from the surface vary in length from 4.1 μm to 9.9 μm. As in *O. quadrinucleata*, the spines represent spaces between layers of the ectocyst (Fig. 20c).
The cyst wall is less than 1 μm thick (approximately 0.7 μm) in cross section. The ectocyst is about 0.1 μm thick. The mesocyst is thinner (0.3-0.6 μm) than in some other hypotrichs. The endocyst is also thin (0.02 μm) and the granular layer varies in thickness from areas where it is apparently absent (0 μm) to about 0.1 μm.

Nuclei, mitochondria, and other cytoplasmic inclusions are similar to those seen in previously reported cysts of other species.

**Stylonchia pustulata.** The cyst of *S. pustulata* (Fig. 19f) is similar in external appearance to that of *Pleurotricha lanceolata*, but smaller (about 35 μm in diameter). Spines are 4.4 μm to 7.4 μm long and number approximately 180. The cyst wall is thin (about 0.35 μm) compared to other cysts that resorb kinetosomes. Stages in cyst wall development are shown in Fig. 21. The ectocyst is produced during cirral dedifferentiation (Fig. 21a,b) and eventually comprises an inner, dense portion, and an outer, loosely packed portion (Fig. 21c), about 0.1 μm thick. The fibrillar mesocyst attains an eventual thickness of approximately 0.2 μm. A mesocyst precursor is shown in Fig. 21c depositing its contents during the final stages of mesocyst production. Endocyst precursors (EnP) are present and in position to begin production of a thin endocyst (about 0.01 μm). Nearby are smaller granular layer (GLP) precursors that eventually produce an approximately 0.05 μm thick granular layer. Although the cyst wall is thin, *S. pustulata* cysts are not noticeably less desiccation resistant than those with thicker walls. This is possibly a function of the unique, dense inner layer of the ectocyst which may complement the other layers in water retention.
Cysts with Small Isolated Papillae

*Gonostomum affine*. *G. affine* cysts (Fig. 19e, 22a) are unique among known hypotrich cysts. Externally they resemble *O. fallax* and *Paraurostyloa* sp. cysts, although there is no apparent order to the scalloping in *G. affine* cysts and they additionally possess 8-10 low, isolated bumps or papillae (Fig. 22a, arrows). Cyst diameter averages 32.8 μm (range, 26-39 μm). Cross sections of the cyst (Fig. 22b-d) reveal 3 distinct cyst walls, each composed of 1 or more layers. The inner wall surrounds the dense cytoplasm of the protoplast. Remarkably, the other walls also apparently enclose bits of cytoplasm, some containing degenerate but identifiable organelles (e.g. mitochondria, Fig. 22d). Surface papillae are revealed as pores situated at junctions of the middle and outer cyst walls and closed with tiny caps (Fig. 22c). The outer wall (0.3 μm thick) and the papillary caps are lamellar and similar in appearance to ectocysts of other hypotrich cysts. Degenerate mitochondria are apparent just inside this wall. Bodies similar to contents of ectocyst precursors (as depicted by Grimes, 1973 and Walker et al., 1980), but not membrane bound, are also present here. The cytoplasm is of a density similar to that of trophic cells. An anastomosing network of lamellar ectocyst-like membranes partitions bits of cytoplasm and connects with both outer and middle cyst walls. The middle wall is about 0.7 μm thick and has 3 apparent layers: (1) an outer ectocyst similar to that of *S. pustulata* with outer, loose and inner, dense sublayers (both about 0.16 μm thick), (2) a 0.2 μm mesocyst-like layer, and (3) an inner, approximately 0.15 μm thick endocyst-like layer. This cyst wall also encloses compartments of cytoplasm similar to trophozoite cytoplasm in
density. The inner cyst wall repeats the pattern of the middle wall. The outer layer is divided into a thin (0.02 μm) dense outer sublayer and a more loosely packed, 0.2 μm inner sublayer. A 0.16 μm mesocyst layer and a dense, 0.03 μm endocyst-like layer enclose cytoplasm of typical cyst density. Fixation of organelles in this cytoplasm was poor, probably due to low penetrability of the 3 cyst walls. Oblong bodies around the outer area of this cytoplasm may be mitochondria. In live cysts observed under phase contrast, a centrally located macronucleus is apparent.

**Cyst-Trophozoite Morphology Interrelationships**

Walker et al. (1980) devised a cyst classification based on such characteristics as relationships of cyst volume to trophozoite volume, and cyst wall thickness to cyst radius. Both functions can be expressed as decimal fractions. Formulae used for calculating the volume of the cyst and trophozoite are:

(a) volume of a sphere

\[ v = \frac{4}{3} \pi r^3 \]

where \( r = \) cyst radius

(b) volume of 1/2 of a prolate spheroid

\[ v = \frac{1}{2}(\frac{4}{3} \pi ab^2) \]

where \( a = \) 1/2 trophozoite cell length

\( b = \) 1/2 trophozoite cell width

The results of applying these formulae to species included in this study, as well as comparison of cyst wall thickness and cyst radii, are given in Table 13.
DISCUSSION

Morphogenetic parameters may serve as useful, although not absolute criteria for evaluating ciliate phylogenetic relationships (Borror, 1972, 1979; Borror and Evans, 1978a; Borror and Wicklow, 1982, 1983; Corliss, 1968, 1973, 1979; Culberson, 1979, 1982; Fleury and Fryd-Versavel, 1981, 1982; Hemberger, 1982; Hemberger and Wilbert, 1982; Hill, 1978a,b, 1979a,b,c, 1980a,b, 1981; Jerka-Dziadosz, 1963, 1964, 1965a,b, 1972a,b, 1974, 1980, 1981a,b, 1982; Wicklow, 1978, 1979a,b, 1980, 1981, 1982a,b). In recent years taxonomic efforts conducted in the absence of adequate information on cortical development have resulted in superficial groupings of hypotrich taxa (Jankowski, 1979; Tuffrau, 1979). The observation that certain groups of morphologically similar species are often morphogenetically similar lends subjective support to the concept of the systematic/taxonomic utility of morphogenetic information. Such support is, however, based on the a priori assumption that morphologically similar species are actually closely related and should be viewed as suspect in the absence of additional supportive, corroborative information.

Structural and Developmental Conservation

Lynn (1976a) formulated the "structural conservatism hypothesis" for which he provided considerable ultrastructural support using colpodid ciliates (Lynn, 1976b,c, 1977, 1978, 1979a, 1980). Extension of this work to other ciliate taxa led to implicit (Lynn, 1981) and explicit (Lynn, 1979b) proposals for major, higher level revisions of the Phylum Ciliophora. Briefly, the structural conservatism hypothesis
states that, in general, conservation of a given structure through time is related to its level of biological organization. Thus, the less complex the structure, the more strongly it is conserved. The principle of "stratified stability" (Bronowski, 1970) reflects Lynn's proposal in its truistic observation that the integrity of each level of biological (in this case structural) complexity depends upon the stability of the next lower level.

In what might be termed the "developmental conservatism hypothesis", Wicklow (1982b) extrapolated from Lynn's proposal on static structure to a concept of the evolutionary conservatism of dynamic phenomena. Here, levels of developmental complexity can be "viewed as a series of sequential events: each succeeding step is based on satisfactory completion of a preceding event". Thus, the degree of complexity of a developmental event or process is inversely related to the conservation of that event through time. Just as Lynn's hypothesis relates interspecific differences in structures of low biological organization (e.g. the somatic kinetid) to most ancient common ancestry, the developmental conservatism hypothesis suggests the same for "primary" developmental events (e.g. organellar or organellar complex development).

A question arises from the preceding considerations: if differences in primary structure or development reflect ancient divergence of 2 taxa, should similarities in increasingly complex structure or later "stages" of developmental processes be viewed as indicative of more recent divergence and, thus, a closer phylogenetic relationship? The question cannot be answered emphatically. If examination of established conservative structural or developmental
characters reveals probable ancient common ancestry, it is reasonable to proceed to the next level of conservatism: consideration of characters believed to be increasingly less conservative. Care must be taken, however, when "skipping steps". Sharing of highly conservative and minimally conservative characters does not prove recent divergence and close relatedness. Examination of moderately conservative characters may reveal a chronologically intermediate divergence, in which case the minimally conservative characters are shared as a result of convergence or parallelism. Likewise, highly conservative characters may reveal nothing about recent evolution.

Ancient ancestry is reflected at higher levels of appropriate classification schemes (Corliss, 1979). Highly conservative characters such as kinetid structure (Lynn, 1976b; Small and Lynn, in press) and membrane particle patterns (Bardele, 1980) may be useful for classification at the class or subclass level (Lynn, 1981). Such developmental phenomena as patterns of kinetosome replication might be similarly instructive. Conversely, lower level classification should reflect observations of increasingly less conservative characters. Lengths and numbers of rows of cirri, for example, may serve as suitable indices for classification to genus or species. A developmental equivalent might involve patterns of late cirral migration during cell division. Thus, it is possible to erect tentative taxonomic hierarchies for systematically important characters based on those characters' relative conservatism (Table 14).

One final consideration is in order for potential users of the above mentioned hierarchies. To my knowledge, no single characteristic is absolute for relatedness at any taxonomic level. Cladistic analysis
(Lipscomb and Riordan, 1982) of characters of varying degrees of biological organization in a wide assortment of Protists revealed "a significant amount of reversals, convergencies, and parallelisms" even in ultrastructural characters. Classification schemes based solely on relative structural conservatism are therefore suspect. Similar analysis of morphogenetic features has not been conducted, but it is reasonable to predict that almost any taxonomic system not based on a "constellation of characters" (Corliss, 1979) would be superficial at best and would almost certainly fail to reflect the most important evolutionary trends in many groups.

Concepts of Morphogenetic Patterning

Ciliary Classes and Their Possible Origins

Borror (1979) proposed the recognition of 3 topographically and developmentally distinct types of hypotrich ciliation: buccal, frontal, and somatic. These terms have already been defined and were used as the basis for presentation of much information in the "Results" section of this dissertation. Frontal ciliation was assumed to be "positionally and developmentally closer to buccal ciliation than to somatic ciliation". An extension of this line of reasoning is that the frontal ciliation, apparently unique to the hypotrichs, might have arisen through a progressive increase in the number of streaks adjacent to the buccal cavity. The orderly appearance of the varying numbers of streaks seems to support such an idea. The first 2 streaks are considered buccal streaks and give rise to the endoral and paroral membranes respectively. Frontal streaks I-n, then, would produce varying numbers of assorted F-V-T cirri, which is, in fact, the case. The apparent relationship was further supported in that at least 1 of
the F-V-T cirri, the paroral cirrus, arises at the anterior end of the paroral streak. The somatic ciliature appeared to have a spatially distinct origin and somatic developmental processes (streaks of kinetosomes arising within parental rows of cilia or cirri) seemed somewhat different as well.

Unfortunately, Jerka-Dziadosz's (1980, 1981a,b, 1982) extensive developmental and ultrastructural studies of *Paraurostyla weissei* failed to support Borror's (1979) proposition. The developing paroral and endoral membranes are significantly different in both formation and orientation from the developing ciliary streaks. Additionally, developing F-V-T, marginal and dorsal ciliary streaks are virtually identical. This apparent relationship between frontal and somatic ciliature may allow further insight into the evolution of oxytrichine ciliary groups.

We can postulate the existence of an ancestral "pre-hypotrich" with ventrally located somatic rows of cirri and no frontal cirri. Dorsal bristle rows would be produced by typical somatic "in row" proliferation of kinetosomes. Although no known extant hypotrich fits this description precisely, there are numerous non-urostyline hypotrichs with varying numbers of ventrally located longitudinal rows of cirri which develop via "in row" proliferation. Perhaps the most extreme of these is *Epiclintes* which is dominated ventrally by somatic ciliature (Wicklow, 1979b). Developmentally, frontal ciliature is limited to a single streak which forms only in the opisthe and produces a short row of 5 frontal cirri. The corresponding cirri in the proter develop as somatic cirri as do all other ventral rows in both proter and opisthe. The posterior streaks arise from an area Wicklow termed
the "caudal" primordium. This primordium yields many streaks arising from or within a single, isolated field of kinetosomes and in this is not unlike the "ventral primordia" (Wicklow, 1981) of \textit{Pseudourostrostyle}. Both types may be interpreted as modified somatic ciliature in isolated lines of hypotrichs. The numerous transverse cirri of \textit{Epiclinites} form singly at the ends of each streak (including the single opisthe frontal streak).

Other hypotrichs have progressively less somatically originated ciliature and more of frontal origin. \textit{Wallackia} sp. (personal observation) has varying numbers of longitudinal rows and produces its scant frontal ciliature (4-5 cirri) from 2 streaks. \textit{Cladotricha koltzowii} (Borror and Evans, 1979) is developmentally similar to \textit{Wallackia}.

\textit{Paraurostyla weissei} has several longitudinal rows and produces its F-V-T ciliature from 3 frontal streaks (Jerka-Dziadosz, 1980, 1981a,b, 1982). \textit{Paraurostyla hymenophora} has 2 longitudinal rows produced via "in row" proliferation (Grimes and L'Hernault, 1978) and, in common with \textit{Paraurostyla weissei}, produces 3 frontal streaks. The method of longitudinal streak production in \textit{Paraurostyla} sp., demonstrated earlier, reveals a possible mechanism for a leftward shift of kinetosomal streaks from somatic to frontal development. The right longitudinal row is vegetative and contributes nothing to kinetosomal streak production. The left row, on the other hand, dedifferentiates to produce 2 kinetosomal streaks which develop into the left and right longitudinal rows. The loss of developmental significance by the right longitudinal row removes a major impediment to evolutionary loss of the entire row. The phenomenon of evolutionary oligomerization recognized
by Poljanski and Raikov (1976) as a mechanism of recent ciliate evolution supports the likelihood of such a loss. Furthermore, objective support lies in the observation of a similar process occurring in the right longitudinal row of Paraurostyla weissel. I suggest the possibility of an ancestral form with an additional right marginal row. The onus of developmental activity shifted from this row to the next row to the left and the apparent trend toward oligomerization resulted in the eventual loss of the right longitudinal row. Continuation of this scenario in a line of hypotrichs initially producing 3 frontal streaks could eventually result in forms with a single longitudinal row and 4 or 5 frontal streaks such as Amphisiella (Wicklow, 1982; Hemberger, 1982) or Trachelochaeta, Gastrostyla, or Paragastrostyla (Hemberger, 1982). Finally, loss of the longitudinal row would produce a very Oxytricha-like ciliate.

Character Status of Morphogenetic Patterns

Fronto-buccal-field. Regardless of its evolutionary origin, the frontal ciliature is an important taxonomic/systematic character. Borror (1979) introduced the concept of the fronto-buccal-field as a morphologic character and demonstrated the systematic incompatability of various hypotrichs previously assigned to the Holostichidae and Urostylidae. The fronto-buccal-field pattern shared by these families and several others (Borror and Wicklow, 1983; Wicklow, 1981) is a longitudinal series of about 12 oblique streaks of kinetosomes. These streaks give rise to a "typical" urostyline ventral ciliature exhibiting a longitudinally oriented "zig-zag" pattern of mid-ventral cirri. Species in which this pattern extends a shorter than average distance toward the posterior end of the cell, possess a fronto-
buccal-field of proportionately fewer oblique streaks (Hemberger, 1982).

The fronto-buccal-field pattern observed in members of the suborder Oxytrichina differs dramatically from the above described urostyline pattern. The oxytrichine pattern may be described as a more or less latitudinally oriented series of 2 or more longitudinal streaks of kinetosomes. The upper limit is usually 5-6 streaks although the difference between frontal and longitudinal streaks may be unclear in forms with numerous longitudinal rows of cirri. Thus, if the "in row" streaks of *Paraurostyla weissei*, which develop in a serial pattern with the leftmost frontal streaks and give rise posteriorly to transverse cirri, are considered frontal streaks, *sensu lato*, the total number of frontal streaks may be as high as 8 or so.

**United fronto-buccal field.** For years, only the members of Jankowski's (1980) Euplotina and Wicklow's (1982b) Discoccephalinina were believed to possess a single, united fronto-buccal-field during early stages of cell division. Possession of such a field by *Tachysoma* sp. (Culberson, 1979) was believed to be an anomalous occurrence not indicative of any close relationship with the euplotines or discocephalines. Hemberger's (1982) revelation of the widespread occurrence of this character in soil dwelling oxytrichines demonstrates that the single front-buccal-field may serve as a morphogenetic character diagnostic of some non-euplotine groups as well. Cautious use of such a character is in order though. Observation of earliest possible frontal proliferation of kinetosomes is required to make a decision as to single fronto-buccal-field origins. The assumption was that the double field was the standard in the Oxytrichina. It now
seems likely that forms once believed to initially possess separate protot and opisthe fields may in fact begin frontal cortical development with only 1. An alternative possibility, however, also arises, that the occurrence of a single field in oxytrichines is merely a specialized adaptation to the constraints of the soil habitat. I believe that full understanding of the phenomenon will require considerable further investigation of genera with species from a variety of habitats as well as re-evaluation, by all hypotrich biologists, of previously studied and stored permanent specimens. It is clear that possession of a united fronto-buccal-field by members of the Oxytrichina is a common, non-anomalous occurrence.

**Oral primordial kinetosome derivatives.** Since early patterns of ciliary field development may be used as indices for determination of early common ancestry in the Hypotrichida, it is logical to propose that initial primordial deployment of kinetosomes would represent a similarly useful tool. A strong trend in the Oxytrichina is the apparent parakinetal association of transverse cirrus 1 with the earliest beginnings of opisthe oral primordial development. It is only a trend, however, and not a rule since at least 3 other early oral primordial developmental origins exist. In 2 of these cases (also more or less parakinetal) the oral primordium originates in association with either a ventral longitudinal row of cirri as in *Amphisiella marioni* (Wicklow, 1982) or from dedifferentiation of 1 or more isolated post buccal cirri as in *Tachysoma* (Culberson, 1974; Hemberger, 1982). The 4th oral primordium origin, apokinetal or "de novo" was reported in a few species of *Oxytricha* as well as *Cladotricha koltzowii* (Borror and Evans, 1979) and possibly *Pseudouroleptus* (Hemberger, 1982). Often
evidence of early association with a transverse cirrus is lost as the oral primordium extends anteriorly. In some cases, the reports of de novo origin may simply be the result of observation after an early parakinetal origin. Hemberger's (1982) description of early stomatogenesis in Oxytricha similis includes de novo proliferation of kinetosomes, while I observed the typical transverse cirrus associated parakinetal origin in my own population.

Although certain possible "lines" of hypotrich evolution seem to exhibit specific "trends" of early opisthe oral primordial development, each of the above varied origins can be found in most of the apparent groupings within the Oxytrichina. Thus, earliest stomatogenic patterns should not be considered conservative characters and, in many cases, may represent nothing more than recent ancestral adaptations toward oral primordial association with "nearest neighbor" parental ciliary structures or none at all.

**Interphase Characters**

Foissner (1982) suggested that low coefficients of variation (0.0-2.80) for certain morphological characters indicates high value for species diagnosis. This is certainly true, although where interspecies variation for a given character is also relatively low (as for the bi-macronucleate condition encountered in most of the Oxytrichina), the utility of the character for species differentiation decreases dramatically.

**Oral structures.** Hypotrich oral structures (the AZM, paroral and endoral membranes) have a fairly standardized general morphology. Modifications in size and shape occur but the basic construction is essentially the same throughout the order. Ultrastructural differences
occur, such as intertaxic variations in paroral membrane kinety numbers, but the macromorphologic results are similar.

My own studies, as well as Foissner's (1982) reveal moderate intraspecies variation (C.V. < 12) as a rule for numbers of adoral membranelles. This is probably related to the size of the buccal cavity (also only moderately variable in my populations) such that increasingly larger buccal cavities are bordered by increasingly higher numbers of membranelles.

Paroral and endoral membranes are typically present although endoral structures may be of variable occurrence. I found no evidence of an EM in interphase cells of Oxytricha quadrinucleata. Dragesco and Njiné (1971) found not only an endoral membrane in an African population of apparently the same species, but described an additional short, "rectilinear" preoral membrane lying deep in the buccal cavity. Ammerman and Schlegel (1983) found populations of Stylonychia mytilus apparently lacking an endoral membrane.

Paroral membranes exhibit varying degrees of hypertrophy and/or leftward curvature. Kahl (1932) considered the genus Steinia Diesing, 1866 (identified by its hypertrophied paroral membrane) a subgenus of Oxytricha. Borror (1972) echoed Kahl's decision because of inadequate descriptions of undulating membrane structure. This shortage was remedied to a certain extent (Foissner, 1982; and others). It now appears that paroral hypertrophy and curvature is certainly of taxonomic importance, but evaluation of its level of generic diagnostic importance should probably await further study. My SEM micrograph of the oral area of O. quadrinucleata is the only ultrastructural presentation and no infraciliary information on the character is
available. Additionally, Kahl’s careful rendering of the oral area of *O. platystoma* seems quite different from that observed in *O. quadrinucleata* (see Fig. 23 for comparison). I believe that detailed ultrastructural study is needed to ascertain the phylogenetic importance of the structure with any certainty.

**F-V-T cirral placement.** Clearly, certain patterns of placement of frontal, ventral, and transverse cirri are fairly stable and diagnostic of various groups of hypotrichs. *Stylonychia, Oxytricha, Tachysoma, Histriculus,* and *Parastylonychia* are similar in this regard and ciliary placement in other genera, *Pleurotricha,* for example, may be interpreted as variations on that theme. Where similar patterns of cirral deployment are coupled with like patterns of cirral development, it is probably safe to assume interrelatedness (see Borror and Wicklow, 1982 for discussion of the converse condition).

**Marginal cirral rows.** The number of marginal cirral rows showed no variation in any of the species I studied. Jeffries and Mellot (1968) and Walker and Grim (1973) observed variation in left marginal row numbers in species of *Pleurotricha* and *Gastrostyla,* respectively, as did Borror and Wicklow (1983) for members of the Urostylina.

*Paraurostyla sp.* often retains a portion of the parental right ventral longitudinal cirral row following cell division and it is likely that organisms with the same type of longitudinal row development, such as *Pseudouroleptus* Hemberger, 1982 might exhibit similar morphological variation. Occurrences of this relict row of cirri could be interpreted in interphase cells as a variation in right marginal row numbers. Thus, use of the character for species identification may not be advisable and should certainly be accompanied
by investigation of the developmental origins of apparent marginal rows.

**Dorsal kineties.** The numbers of dorsal kineties for oxytrichine species are apparently very stable (C.V. = 0.0 for all populations of my own observation). The dorsal kineties may originate through both "in row" and right marginal proliferation in species with 5 or more kineties but only the former in species with 4 or less. For this reason, inter-generic and inter-familial variation in dorsal kinety numbers is usual and may be considered taxonomically significant. In some small forms such as *Tachysoma* sp., the presence of relict dorsal bristles (which probably occur frequently in many species) may confuse attempts to count the rows. In general, however, this can be a useful taxonomic feature if staining procedures and/or microscope facilities are adequate for the revelation of the often tiny dorsal bristles.

**The cyst.** Walker and Maugel's (1980) recognition of the separate natures and systematic significance of kinetosome resorbing and non-kinetosome resorbing cysts in various hypotrich species was the first and only attempt to extract taxonomically useful information from this facet of hypotrich biology. Their observation of profound differences between the cysts of certain euplotine hypotrichs and those of several members of the *Oxytrichina* certainly suggests that useful morphological and/or developmental taxonomic characters might be gleaned from various aspects of cyst biology. They listed 9 characters in 5 general areas for comparison of kinetosome resorbing and non-kinetosome resorbing cysts. Several of these, such as distinctions of cyst wall layer precursors and their sites of cortical fusion, ciliary resorption, food vacuole precursor resorption, mitochondrial clustering and macronuclear
fusion seem reasonable in the light of our present, albeit limited knowledge of cyst production and morphology.

Certainly many kinetosome resorbing cysts have 4 cyst wall layers, the number listed by Walker and Maugel (1980) for *Oxytricha fallax* (see Grimes, 1973), *Gastrostyla steinii* and *Stylonychia mytilus*. My own observations of cysts of *Paraurostyla* sp., *Pleurotricha lanceolata*, and *Oxytricha quadrinucleata*, as well as the report of Gutierrez, et al. (1983) for *Onychomus acuminate* revealed a similar condition. It now appears, however, that the 4 layered cyst wall condition does not represent the extent of cortical lamellar construction in all kinetosome resorbing cysts. Ricci, et al. (1982) reported 5 cyst wall layers in *Oxytricha bifaria*, the inner 3 of which correspond morphologically to the mesocyst, endocyst, and granular layer of the 4 layered cyst wall variety. The outer 2 layers (which Ricci, et al., 1982 named lamellar and fibrogranular) could be interpreted as an evolutionary division of the ectocyst of some ancestral species with a 4 layered cyst wall. These layers are, however, chemically distinct. The inner layer apparently is composed of some polysaccharide and the outer layer is of unknown, but non-polysaccharide composition. *Stylonychia pustulata* (Fig. 21) apparently shares the 5-layered cyst wall condition of *O. bifaria*, but exhibits a considerably thinner wall. The cyst of *Gonostomum affine* (discussed below), with 3 distinct cyst walls, each with varying numbers of layers, is obviously distinct from cysts of any of the above mentioned species.

Walker and Maugel (1980) listed what they considered appropriate values for ratios of cyst volume/vegetative cell volume (CVol/TVol, 0.07-0.15) and cyst wall thickness/cyst ratios (T/R, 0.11+0.02) in
kinetosome resorbing cysts. These designations were premature and failed to approximate inter- or intraspecific variability in either characteristic. Cysts in my own studies had $T/R$ values of 0.02-0.13 and $CVol/TVol$ values ranging from 0.19-1.14, disregarding the bizarre *G. affinis* cysts which would have extended both ranges even further. These values significantly overlap the ratios listed by Walker and Maugel (1980) for non-kinetosome resorbing cysts. Values calculated from several other authors' reports on cysts of various hypotrich species support my observation of high interspecific variability in the $T/R$ and $CVol/TVol$ ratios. A compilation of known or ascertainable $T/R$ and $CVol/TVol$ ratios as well as cyst sculpturing is given in Table 15.

At the present time, cyst sculpturing appears to indicate little of phylogenetic interest. Very similar species (ex. *Oxytricha muscorum* and *O. quadrinucleata*) have cysts that are externally dissimilar and relatively distinct species (ex. *Paraurostyla sp.* and *O. fallax*) have similar cysts.

The cyst of *Gonostomum affinis* presents a difficult problem when considered in relation to other known cyst types. I suggest that its unique structure is the result of adaptation to a very rapidly changeable environment. As a lichen dweller, *G. affinis* must be able to cope with extreme desiccation during dry periods, sudden but brief advent of excess moisture during and after rains, and, potentially, rapid drying. While many species engage in a pre-cystic period of cytoplasmic condensation and water loss, a lichen dweller would benefit from the more rapid production of some, at least partially desiccation resistant, protective wall. It is possible that elaboration of the single layered outer wall of *G. affinis* cysts is just such an adaptation
and that it is followed by a serial progression of condensation and
selective loss of non-essential cytoplasmic inclusions culminating in
the production of a secure inner cyst. Such a scenario suggests an
energy expensive sacrifice of cytoplasm in favor of rapid acquisition
of desiccation resistant coats prior to final encystment. My
observation that the "shelf life" of these cysts is short (only about
2-3 months) seems to support the idea.

It is clear that our current knowledge of cyst ultrastructure is
severely limited. Little is known of intra-specific cyst morphology
variability. The diversity evident in the 15 or so reported cysts
suggests a need for further studies. No investigation of any
urostyline cysts has been conducted even though many members of the
Urostylelina are lichen or soil dwellers and are known to form cysts.
Cysts of only 1 member of the Euplotina, D. scutum, were investigated
ultrastructurally. I believe that studies of the cysts of other lichen
and soil dwelling hypotrichs will be particularly revealing since the
harsh conditions encountered in such habitats suggest selective
pressures directly and dramatically affecting cyst construction and
maintainence. Cysts from species dwelling in permanent ponds and other
similarly more stable environments are expected to adhere more closely
to Walker and Maugel's (1980) "norms". Until more information on a
wider array of species is available, it is, in most cases, difficult to
comment on the phylogenetic implications of cyst structure.

Secondary Oligomerization in Soil and Lichen Hypotrichs

Progressive oligomerization occurs in the suborder Oxytrichina
(Fauré-Fremiet, 1961; Poljansky and Raikov, 1976) from the more
"primitive" forms with multiple rows of cirri to the scattered cirral
placement of the "advanced" forms. This can be considered a primary
trend in the suborder and can be demonstrated in most other groups of
ciliates as well. Secondary oligomerization is observed in soil and
lichen dwelling hypotrichs as well as forms from the marine
interstitial habitat (Wicklow, 1982). The unavoidable result is that
species whose closest phylogenetic affinities are with the primitive
members of a taxon may resemble more closely the representatives of
more advanced groups. This phenomenon points out the need for
developmental and ultrastructural information in phylogenetic
investigations. Supercortical structures (cilia, cirri, membranelles,
etc.) interact with the environment (Corliss, 1979) and are therefore
believed to be less conservative than their infraciliary constituents.

The results of secondary oligomerization are, variously, reduced
ciliature of any or all types, including loss or reduction of frontal,
postbuccal, or transverse cirri, loss or reduction in dorsal kinety
numbers with concomitant reduction in numbers of dorsal bristles. Also
common are reductions in numbers of membranelles in the AZM, reduction
and or crypsis of preoral and oral structures (note especially
Gonostomum affine in this regard). Cell elongation or assumption of a
vermiform condition are also often noted. It is important to take
such factors into consideration if possible in reviewing likely
phylogenetic relationships.

Information now available on hypotrich morphology, morphogenesis,
and, to a smaller extent, cystation phenomena suggest several unifying
characteristics of the Oxytrichina. Paramount among these are the
elaboration of longitudinally oriented kinetosomal streaks during cell
division, ciliary reorganization, and excystment and production of
kinetosome resorbing cysts of 4 or more layers. I propose recognition of 3 families relating directly to the results of research presented in this dissertation: Amphisiellidae Jankowski, 1979, Oxytrichidae Ehrenberg, 1838, and Gonostomidae n.fam. In addition, published data from a variety of sources suggest that at least 2 other families, Kahliliellidae Tuffrau, 1979 and Keronidae Dujardin, 1840, should be considered candidates for inclusion in the Oxytrichina. The following discussion is intended to elucidate the morphologic and morphogenetic limits of the Oxytrichidae, Amphisiellidae, and Gonostomidae. Similar discussion of the Kahliliellidae and Keronidae is beyond the scope of this dissertation, but where possible, will be included in my observations on possible inter- and intrafamilial evolutionary relationships.

**Amphisiellidae Jankowski, 1979**

**Diagnosis.** Hypotrichs with 1 or more undifferentiated longitudinal rows of cirri (reduced in some species) which develop "in row" from the kinetosomal products of linear dedifferentiation of similar parental rows. In addition, single right and left marginal cirral rows are present, frontal cirri are present, post-buccal and transverse cirri are present or absent. F-V-T system develops from 3 or 4 typical oxytrichine longitudinal kinetosomal streaks, although some transverse cirri may arise at the posterior ends of the longitudinal cirral rows. Dorsal bristles are present in 4-6 rows. Caudal cirri are present.

**Genera.** Type - *Amphisiella* Gourret and Roeser, 1888

*Paraurostyla* Borrer, 1972

*Pseudouroleptus* Hemberger, 1982
Members of the family Amphisiellidae historically were distributed throughout the order Hypotrichida. Possession of multiple non-marginal longitudinal rows of cirri is extremely common among hypotrichs. The suborders Urostylina and Discoccephalina both exhibit longitudinal or oblique cirral rows which develop in different ways characteristic of each suborder. In the Oxytrichina, longitudinal rows tend to develop within parental longitudinal rows or from the rightmost of a series of F-V-T kinetosomal streaks, or both. It is often difficult to distinguish between the 2 and several variations of the process exist. As I previously stated, I doubt that the 2 modes of streak development are entirely unrelated, but may represent the more primitive and more modern aspects, respectively, of an evolutionary developmental trend.

In the Amphisiellidae, longitudinal rows of cirri develop from kinetosomal dedifferentiation of some or all parental rows. This results in the formation of kinetosomal streaks which elongate to produce longitudinal cirral rows in the daughter cells. F-V-T cirri are produced from 3-4 "typical" F-V-T kinetosomal streaks. The distinction between these modes of development is often blurred, however, as the result of 2 phenomena: (1) the F-V-T and longitudinal row streaks are usually serially arranged (Fig. 16g.i-k) in a single field of 5 or more kinetosomal streaks and (2) the leftmost
longitudinal streaks frequently produce the rightmost transverse cirri, normally the domain of F-V-T development.

This blending of developmental prerogatives is indicative of what I believe to be an evolutionary trend in the family, leading from forms with multiple longitudinal cirral rows with individual developmental potency (for example: *Parurostyla weissei*) toward forms with fewer rows and a leftward shifting of the developmental onus (i.e. *Pseudouroleptus* spp., *Amphisiella* spp., and *Trachelochaeta* spp).

**Gonostomidae (n. fam.)**

**Diagnosis.** Hypotrichs with variable numbers (11-18) of ventrally situated cirri not in rows. There are no postbucoal cirri with the exception of transverse cirri which are present or absent. Single right and left marginal cirral rows are present. A narrow buccal cavity and reduced paroral ciliation is typical of members of the family. F-V-T cirri develop from 4-6 longitudinal kinetosomal streaks. Dorsal bristles are present in 2-3 kineties. Caudal cirri are present or absent.

**Genera.** Type - *Gonostomum* Sterki, 1878

- *Trachelostyla* Kahl, 1932
- *Perisincirra* Jankowski, 1978

*Gonostomum* and its relatives have typically been classified as urostyline hypotrichs or as members of the oxytrichine family *Oxytrichidae*. Clearly, recent information on its morphogenesis (Culberson, 1982; Hemberger, 1982) demonstrate closer phylogenetic affinity for the latter. I believe, however, that several characteristics, including a probable origin distinct from the
Oxytrichidae, warrant placement in a separate family. I suggest the name Gonostomidae.

Among the distinguishing characteristics of the Gonostomidae are: absence of longitudinal, non-marginal, ventral rows of cirri; absence of postbuccal cirri (except for TVs in some species); TV development from posterior ends of rightmost 1 or 2 frontal kinetosomal streaks only; reduced and/or cryptic oral ciliation. Frontal cirri are arranged in a pattern distinct from that observed in the Oxytrichidae, often resembling the zigzag midventral cirri of urostyline ciliates (hence, Gonostomum's previous incorrect classification). Furthermore, the cyst of G. affine, as revealed by TEM in this study, is unlike any other observed to date in the Oxytrichidae. Similar ultrastructural information on the cysts of Trachelostyla and Perisincirra is needed.

Morphogenesis accompanying division in Gonostomum is now well documented both in this study as well as the literature (Culberson, 1981; Hemberger, 1982) as is its general morphology and ecology (Foissner, 1982; Hemberger, 1982). The unique paroral membrane (misidentified as the endoral membrane by Foissner, 1982 and Hemberger, 1982 because of the unique cryptic placement of the latter) seems to be shared by other members of the family, especially Perisincirra similis and P. interrupta (Foissner, 1982). Morphogenesis in Trachelostyla (Kool, 1970) and Perisincirra (Hemberger, 1982) further support their placement with Gonostomum in a separate family.

While interfamilial relationships are the topic of a subsequent section of this dissertation, the possible origin of the family Gonostomidae is a major basis for its separation from the Oxytrichidae and should be mentioned here. It seems likely that Gonostomum affine
descended from ancestors very similar to *Trachelochaeta* of the family Amphisiellidae. Indeed, Hemberger (1982) made tacit allusion to this in his naming of a new *Trachelochaeta* species: *T. gonostomoida*. Loss of the single longitudinal cirral row of a *T. gonostomoida*-like ancestor, a reasonable evolutionary possibility (Poljanski and Raikov, 1976) would result in a hypotrich much like the modern day *G. affine*. Hemberger (1982) also shows (but does not name) a paroral membrane in his illustration of *T. gonostomoida* which is essentially identical to that observed in *G. affine*. As a further note, much might be learned about the possible origin of the unusual cyst of *G. affine* through detailed study of *Trachelochaeta* cysts. It is reasonable to hypothesize that such cysts, if found, would reflect ultrastructurally a very recent common ancestry of *Gonostomum* and *Trachelochaeta*. While I believe it is possible, even probable, that the family Oxytrichidae has its origin in the Amphisiellid line, I believe its closest affinities are with some other branch.

**Oxytrichidae Ehrenberg, 1838**

**Diagnosis.** Hypotrichs typically having 18 F-V-T cirri arranged in an *Oxytricha*-like pattern (see Fig. 1). These cirri develop from 4-6 longitudinal kinetosomal streaks. Single rows of left and right marginal cirri are typically present (exception: *Pleurotricha* with 2 RMCR) as are 6 dorsal kineties and 3 caudal cirri.

**Genera.** Type: *Oxytricha* Bory de St. Vincent, 1852

(including *Steinia, Urosoma, Opisthotricha*)

**Stylonychia** Ehrenberg, 1830

(including *Histricus, Parahistricus*)

**Tachysoma** Stokes, 1887
Incertae sedis. Actinotricha Cohn, 1866

I include in this family only those oxytrichine species whose F-V-T ciliation is exclusively "sporadically" (from the old suborder name, Sporadotrichina) situated. Thus, species with linearly arranged ventral cirri of frontal origin which were included here previously (Onychodromus, Gastrostyla, Laurentiella, Gastrostyla, Paragastrostyla) were removed to other families. Pleurotricha is retained because the extra row of cirri (Fig. 16) is of marginal, somatic origin rather than frontal origin. Members of the family typically possess 18 F-V-T cirri: 8 in the frontal region, 5 post-buccal cirri, and 5 transverse cirri. Furthermore, the arrangement of these cirri is conserved throughout the family. The 8 frontally situated cirri are arranged in a "C" shaped pattern (Fig. 1). Three postbuccal cirri are situated close to the center of the ventral surface, while the other 2 are in close proximity to the transverse cirri. The transverse cirri are arranged in a "V" shaped pattern.

In members of the Oxytrichidae whose morphogenetic processes were studied, a characteristic developmental pattern was observed. In Oxytricha 5 F-V-T kinetosomal streaks are observed. Initially, these streaks are produced in serial array, but as development progresses streaks 3 and 4 migrate posteriorly to produce certain of the
postbuccal and transverse cirri. This process is repeated, with minor variations, in the other members of the family.

There was some confusion, historically, over the use of several genus names applied to Oxytricha-like species. Corliss (1979) recognized Histricus, Opisthotricha, Oxytricha, Steinia, Stylonychia, Tachysoma, and Urosoma as valid genera, while Kahl (1932) considered them subgenera of Oxytricha. Certainly, identifying characteristics for some of these deserve reconsideration because of their extensive overlap and vanishingly small differences.

I consider Tachysoma sufficiently distinct from the other Kahlian subgenera of Oxytricha to warrant its recognition as a valid genus. The absence (Hemberger, 1982) or reduced number and atypical development (see Results) of caudal cirri serve as bases for this decision. A slightly modified ventral cirral pattern with greater interspecific variability lends further credence to this idea.

I agree with Hemberger (1982) that Histricus and Parahistricus must be considered junior synonyms of Stylonychia. Cortical stiffness and flexibility of caudal cirri are too poorly quantified and too variable to serve as useful criteria for generic separation in this instance.

I am in tentative agreement with Borr and Hemberger (1982) that Opisthotricha, Urosoma, and Steinia should be considered members of the genus Oxytricha. Relative lengths of posterior marginal cirri (Opisthotricha) and slight posterior extension (Urosoma) are not sufficient criteria for generic separation. The hypertrophied paroral apparatus of Steinia was poorly described (Borr and 1972) and prior to this study, received no attention with regard to ultrastructural
detail. As I indicated earlier, *O. platystoma*, the type species of *Oxytricha*, possesses an hypertrophied paroral apparatus of uncertain similarity (Fig. 23) to other members of the subgenus *Steinia*. Additionally, *O. platystoma* exhibits cortical or somatic stiffness characteristic of the genus *Stylonchia*. *Steinia* is considered a valid genus by various authors (Corliss, 1979; Foissner, 1982). Such recognition, however, must result in considerable taxonomic confusion. The type species of the genus *Steinia* would be *S. platystoma* and the problem of the species' similarity to *Stylonchia* would have to be dealt with. Certainly these problems should not impede taxonomically progressive moves resulting in improved or more realistic categorization of this complex of hypotrichs. However, in the absence of detailed information delineating newly proposed generic boundaries and either avoiding or clearly explaining generic overlap, I believe that the more conservative route of subgeneric recognition of *Steinia* is warranted.

**Interfamilial Evolutionary Relationships**

Confusion over relative primitiveness and/or significance of various oxytrichine structural and developmental characteristics necessitates consideration of alternative interfamilial evolutionary schemes. In a "traditional" scenario (Fig. 24) the genera comprising the family Kahliellidae are recognized as the most primitive group of the suborder, primarily on the basis of their possession of numerous ventral longitudinal rows of relatively uniform cirri (Corliss, 1979; Borror and Evans, 1979; Tuffrau, 1979; Wicklow, 1982). Other families evolved from hypothetical Kahliella-like ancestors through reduction of cirral and cirral row numbers (oligomerization) accompanied by
hypertrophy and specialization of certain cirral groups (Poljansky and Raikov, 1976; Wicklow, 1982), especially those of the F-V-T system. This trend leads to the decreased numbers of longitudinal rows observed in the Amphisiellidae and culminates with the Oxytrichidae and Gonostomidae whose members lack ventral longitudinal cirral rows. The origin of the suborder under this scenario remains obscure, but members of the order Heterotrichida with longitudinal rows of cirri, oral paramembranelles (AZM) and a hypotrich-like UM (Plagiotoma) may share common ancestry with Kahliella.

Although the aforementioned "traditional" evolutionary scheme accounts for many morphologic characteristics of the suborder Oxytrichina, it is subject to debate. Fleury and Fryd-Versavel (1982) argued that Kahliella, though apparently primitive morphologically, exhibits non-primitive morphogenesis. The longitudinal rows of cirri on the ventral surface of Kahliella do not develop "within row" as is usual for somatic cirri, but form from 5 frontal kinetosomal streaks. Since relatively more primitive somatic development is observed, in part, in other oxytrichines (i.e. Amphisiellidae), alternative phylogenies must be considered.

A phylogenetic scenario favoring morphogenetic characteristics and the evolution of frontal ciliature from somatic ciliature is depicted in Fig. 25. A Cladotricha-like ancestor with scant frontal ciliature is considered to be at an intermediate stage in the evolution of frontal ciliature from somatic ciliature. The evolution of Amphisiellid ancestors continues that developmental trend. The Oxytrichidae and Gonostomidae arise as a result of similar evolutionary tendencies away from ventral cirral rows. I believe that the
dissimilar morphologies of these 2 families reflects a divergent, biphyletic origin from separate ancestral Amphisiellids.

The origin of the families Keronidae and Kahliellidae is uncertain. Their ventral surfaces are dominated by longitudinal rows of cirri and the development of these rows from kinetosomal streaks occurs in similar patterns. An evolutionary tendency toward this pattern could have occurred in either an Amphisiellid or Cladotricha-like ancestral line.

Recent additions to our understanding of morphology and morphogenesis in the Order Hypotrichida resulted in major subordinal systematic upheaval Fauré-Fremiet's (1961) bi-subordinal concept yielded to modern recognition of several suborders and additional refinements are expected. Systematics and taxonomy are dynamic disciplines. The systematic framework presented in this dissertation is not intended as an absolute or static representation of incontrovertable fact. It may, however, provide firm basis for further taxonomic consideration of the suborder Oxytrichina and its relationship to other hypotrich taxa.
LITERATURE CITED


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TABLE 1. An Abridged Protozoan Taxonomy

KINGDOM: Protista (in part)

PHYLUM: Sarcomastigophora Honigberg & Balamuth, 1963
PHYLUM: Labyrinthomorpha Levine, et al., 1980
PHYLUM: Apicomplexa Levine, 1970
PHYLUM: Microspora Sprague, 1977
PHYLUM: Ascetospora Sprague, 1978
PHYLUM: Myxozoa Grassé & Lavette, 1978
PHYLUM: Ciliophora Doflein, 1901

CLASS: Kinetofragminophorea Depuytorac, et al., 1974
CLASS: Oligohymenophorea Depuytorac, et al., 1974
CLASS: Polyhymenophorea Jankowski, 1967

ORDER: Heterotrichida Stein, 1859
ORDER: Odontostomatida Sawaya, 1940
ORDER: Oligotrichida Bütschli, 1887
ORDER: Hypotrichida Stein, 1859
TABLE 2. Disparate Systems of Hypotrich Taxonomy

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**TABLE 3. Measurements of Oxytricha fallax (Rollinsford, NH population)**

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* All linear measurements are in \( \mu \text{m} \).
TABLE 4. Measurements of *Oxytricha fallax* (Boulder, CO population)

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* All linear measurements are in \( \mu \)m.
TABLE 5. Measurements of *Oxytrichia quadrinucleata*

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* All linear measurments are in μm.
TABLE 6. Measurements of *Oxytricha similis*

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* All linear measurements are in μm.
TABLE 7. Measurements of *Stylonychia pustulata*

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* All linear measurements are in \( \mu m \).
TABLE 8. Measurements of *Tachysoma sp.*

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* All linear measurements are in μm.
TABLE 9. Measurements of *Gonostomum affine*

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* All linear measurements are in um.
TABLE 10. Measurements of *Pleurotricha lanceolata*

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<td>33-36</td>
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<td>15-24</td>
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<td>.02</td>
<td>.41-.48</td>
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* All linear measurements are in \( \mu m \).*
TABLE 11. Measurements of *Paraurostyla* sp. (Mexico City population)

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<th>Range</th>
<th>C.V.</th>
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<tr>
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<td>13.51</td>
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<td>1.90</td>
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<td>1-1</td>
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<tr>
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<tr>
<td>Number of Caudal Cirri</td>
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<td>.27</td>
<td>2-3</td>
<td>9.1</td>
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</tbody>
</table>

* All linear measurements are in μm.
<table>
<thead>
<tr>
<th>Measurement</th>
<th>n</th>
<th>$\bar{x}$</th>
<th>S.D.</th>
<th>Range</th>
<th>C.V.</th>
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<td>.45</td>
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<td>11.42</td>
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</tr>
<tr>
<td>Number of Cirri in Left Longitudinal Rows</td>
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<td>1-1</td>
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<td>Number of Right Marginal Cirri</td>
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<td>Number of Caudal Cirri</td>
<td>12</td>
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<td>0</td>
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* All linear measurements are in μm.
### Table 13. Cyst-Trophozoite Morphology Interrelationships

<table>
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<tr>
<th>Organism</th>
<th>Average Cyst Wall Thickness (T)</th>
<th>Average Cyst Radius (R)</th>
<th>Average Cyst Volume (CVol)</th>
<th>Average Trophozoite Volume (TVol)</th>
<th>T/R</th>
<th>CVol/TVol</th>
</tr>
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<tbody>
<tr>
<td><strong>Oxytricha fallax</strong></td>
<td>3 μm</td>
<td>24.5 μm</td>
<td>6.16 x 10^4 μm^3</td>
<td>5.38 x 10^4 μm^3</td>
<td>0.12</td>
<td>1.14</td>
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<tr>
<td><strong>Parurostyla sp.</strong></td>
<td>3 μm</td>
<td>25.5 μm</td>
<td>6.95 x 10^4 μm^3</td>
<td>1.58 x 10^5 μm^3</td>
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<td>0.44</td>
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<tr>
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<td>23.1 μm</td>
<td>5.16 x 10^4 μm^3</td>
<td>7.36 x 10^4 μm^3</td>
<td>0.13</td>
<td>0.70</td>
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<tr>
<td><strong>Pleurotricha lanceolata</strong></td>
<td>0.7 μm</td>
<td>28.5 μm</td>
<td>9.70 x 10^4 μm^3</td>
<td>1.38 x 10^5 μm^3</td>
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<td>0.70</td>
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<tr>
<td><strong>Stylonychia pustulata</strong></td>
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<td>17.5 μm</td>
<td>2.24 x 10^4 μm^3</td>
<td>1.18 x 10^5 μm^3</td>
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<td>0.19</td>
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<tr>
<td><strong>Gonostomum affine</strong></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>outer wall</td>
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<td>1.85 x 10^4 μm^3</td>
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<td>middle wall</td>
<td>0.7 μm</td>
<td>11.6 μm</td>
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<td>7.21 x 10^3 μm^3</td>
<td>0.06</td>
<td>0.90</td>
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<tr>
<td>inner wall</td>
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<td>5.6 μm</td>
<td>7.36 x 10^3 μm^3</td>
<td>7.21 x 10^3 μm^3</td>
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Table 14. Implications of level of organizational complexity

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<th>High</th>
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<td>Kinetid Ultrastructure</td>
<td>Cirrus Ultrastructure</td>
<td>Oral Macrostructure</td>
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<td>Membranelle Ultrastructure</td>
<td>Preoral &quot;membrane&quot; Ultrastructure</td>
<td>Global Ciliary Pattern</td>
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<td>Examples</td>
<td>Membrane Particle Patterns</td>
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<td>Examples</td>
<td>Kinetosome Replication</td>
<td>Patterns of Developmental</td>
<td>Patterns of Cirral Migration</td>
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<td>Examples</td>
<td>Development</td>
<td>Streak Development</td>
<td>Migration</td>
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<td>Examples</td>
<td>Polymerizing Development</td>
<td>Oligomerizing Development</td>
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<td>Ancient</td>
<td>Moderate</td>
<td>Recent</td>
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<td>Appropriate Levels For Systematic Application</td>
<td>Class----&gt; Order</td>
<td>Order------&gt; Genus</td>
<td>Genus------&gt; Species</td>
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Table 15. Comparative Hypotrich Cyst Structures

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<th>T/R</th>
<th>CVol/TVol</th>
<th>Layers</th>
<th>Cyst Wall Layers</th>
<th>Cyst Sculpturing</th>
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<td><strong>non-kinetosome resorbing species</strong></td>
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<td>Faure-Fremiet et al. (1954)</td>
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<td>-</td>
</tr>
<tr>
<td><strong>kinetosome resorbing species</strong></td>
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<td></td>
<td></td>
<td></td>
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<td>Gastrostyla steinii</td>
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<td>0.44</td>
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<td>-</td>
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<td>1.14</td>
<td>4</td>
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<tr>
<td>S. pustulata</td>
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<td>0.19</td>
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<td>Pleurotricha lanceolata</td>
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<td>0.70</td>
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</table>

protrusions
Figure 1. Representatives of morphological Group A of the Oxytrichina: (a) Oxytricha, (b) Stylonychia, (c) Tachysoma, (d) Gonostomum. Adoral Zone Membranelles, AZM; Paroral Membrane, PM; Endoral Membrane, EM; Frontal Cirri, FC; Post Buccal Cirri, PBC; Right Marginal Cirral Row, RMR; Left Marginal Cirral Row, LMR; Transverse Cirri, TC; Caudal Cirri, CC.
Figure 2. Representatives of morphological Groups B and C of the Oxytrichina: (a) Pleurotricha, (b) Paraurostyla, (c) Amphisiella
Figure 3. Diagrammatic representation of *Paraurostyla hymenophora* demonstrating ciliation typical of members of the suborder Oxytrichina; (a) ventral, (b) dorsal. Adoral Zone Membranelles, AZM; Paroral Membrane, PM; Frontal Cirri, FC; Post Buccal Cirri, PBC; Right Marginal Cirral Row, RMR; Left Marginal Cirral Row, LMR; Transverse Cirri, TC; Caudal Cirri, CC; Dorsal Kineties, DK.
Figure 4. *Oxytricha fallax* - ventral (a) and dorsal (b) aspects.
Figure 5. Morphogenesis during division in *Oxytricha fallax*. (a-e) ventral view, (f) diagramatic representation of origins of dorsal bristles and caudal cirri.
Figure 6. *Oxytricha quadrinucleata* - (a) ventral aspect showing oral region and prey organism, *Polytomella* sp. (x2434); (b) dorsal aspect showing dorsal bristles and caudal cirri (x709).
Figure 6 (continued). *O. quadrinucleata* - (c) early opisthe oral primordium developing at a distance from transverse cirri (x2145); (d) later stage showing 5 frontal streaks typical of *Oxytricha* (x715); (e) higher magnification of 6b demonstrating apparent non-participation of postbuccal cirrus 3 in production of opisthe frontal streaks (x1729); (f) late divider, beginning of cytokinesis; an endoral membrane is apparent at this stage (x624).
Figure 7. *Oxytricha similis* - (a) ventral aspect (SEM) showing typical *Oxytricha* arrangement of oral, F-V-T, and marginal ciliature (x1296); (b) dorsal view showing 6 rows of dorsal bristles (x1206); (c) enlarged view of a typical *O. similis* oral area showing short EM and PM, and raised RBO (also visible in 7a) (x3762); (d) nigrosin stained specimen showing development of 5 frontal streaks in addition to PM and EM streaks (x2200).
Figure 8. *Stylonychia pustulata* - (a) nigrosin stained interphase cell showing typical placement of ventral ciliature (x1768). (b) SEM micrograph of ventral surface of early divider (x1153). OP is forming in postbuccal area. Note: cell possesses 9 frontal cirri rather than the usual 8. (c) Composite photomicrograph of nigrosin stained cell in early-mid division (x1407). EM, PM, and 5 F-V-T streaks are visible. Buccal cirrus is being produced at anterior end of PM streak. (d) SEM micrograph of reorganizing cell (x997). Note partial redifferentiation of AZM.
Figure 9. *T. saltans* - (a) ventral aspect; (b) dorsal aspect.
Figure 10. Photomicrographs of protargol stained specimens of *Tachysoma sp.* - (a) Interphase cell showing typical arrangement of ventral ciliature. Note anteriorly displaced transverse cirrus (T1) and the 4 macronuclei (x2423) (b) Early divider showing OP and dedifferentiation of parental F-V-T cirri to produce a single latitudinal field of kinetosomes (x2200). (c) Early divider with F-V-T field becoming organized into diagonal streaks (x2089). (d) Early divider slightly later than 10c. Note continued development of membranelles in opisthe oral primordium (x2150).
Figure 10 (continued). Protargol stained specimens of *Tachysoma sp.*
- (e) Composite photomicrograph demonstrating splitting of F-V-T streaks into proter and opisthe F-V-T streaks, separate patterns of left and right marginal cirral production, and placement and development of left dorsal kinety. Two caudal cirri are produced at its posterior end (x1822). (f) Mid-divider showing development of individual cirri (x2164). (g) Late divider at beginning of cytokinesis. F-V-T cirri are migrating in the typical "Oxytricha" pattern (x2114). (h) Recently separated member (opisthe) of a dividing cell. Parental cirri have not yet been resorbed (x2640).
Figure 11. *Gonostomum affine* - (a) ventral aspect; (b) dorsal aspect.
Figure 12. *Gonostomum affine* - (a) SEM micrograph of ventral surface of interphase cell (x1681). (b) Photomicrograph of protargol stained interphase cell (x1486). Note atypical PM (arrow) and arrangement of frontal cirri. (c) SEM micrograph of dorsal surface of interphase cell (x1469). Relicts of parental ciliary rows are evident (arrow). (d) SEM micrograph of paroral membrane (x16017). Note that cilia are well separated from one another.
Figure 12 (continued). *Gonostomum affine* development - (e) Photomicrographs of nigrosin stained early reorganizer (x1733). Five frontal streaks are apparent. (f) Photomicrograph of nigrosin stained late reorganizer (x1467). Cirral migration at this stage closely resembles that seen in *Oxytricha*. 
Figure 13. *Gonostomum affine* development. Diagrammatic representations based upon reorganizing cells, early dividers from my own collection, and the work of Hemberger (1982).
Figure 14. *Pleurotricha lanceolata* - (a) ventral aspect; (b) dorsal aspect.
Figure 15. *Pleurotricha lanceolata* - (a) SEM micrograph of interphase cell, ventral view (x732). (b) SEM micrograph of interphase cell, dorsal view (x912). (c) Development of right marginal cirral rows. Two kinetosomal streaks are produced within the outer row. Note also early development of dorsal kineties 5 and 6 (arrow) (nigrosin stained specimen) (x4550). (d) Photomicrograph of divider showing frontal streak production (x553).
Figure 16. Diagrammatic representation of ventral morphogenesis in *Pleurotricha lanceolata*. 
Figure 17. Paraurostyla sp. - (a) ventral aspect; (b) dorsal aspect.
Paraurostyla sp. — (a) SEM micrograph showing ventral surface of interphase cell (x526). Relict cirri (r) are apparent in the right posterior area. Smaller ciliates are the food organism, *Tetrahymena pyriformis*. (b) SEM micrograph showing ventral surface of interphase cell (x623). This cell is unusual in having no postbuccal cirri and only 2 transverse cirri. (c) SEM micrograph of oral region (x1783). Note the elongate membranellar cilia (mc). (d) SEM micrograph of dorsal surface of interphase cell (x612).
Figure 18 (continued). Paraurostyla sp. – (e) SEM micrograph of opisthe oral primordium (OP) and UM field (UM) (x1560). (f) SEM micrograph of early divider (x2434). Frontal streak proliferation is beginning. The left longitudinal row has begun to dedifferentiate and produce 2 streaks (arrows) in a "V"-shaped pattern. (g) Photomicrograph of nigrosin stained divider, slightly later than seen in 16f (x1673). Again, the "V"-shaped proliferation of kinetosomes is evident as is the developmentally non-participating right longitudinal row. (h) Photomicrograph of nigrosin stained divider (x1633). Cirral development in longitudinal streaks is apparent.
Figure 18 (continued). *Paraurostyla* sp. - (i) SEM micrograph of frontal field of proter showing 5 frontal streaks (1-5), and PM and EM streaks (x1179). (j) SEM micrograph of mid-division cell (x569). Portions of 3 "generations" of right longitudinal rows are present (arrows)(k) SEM micrograph of frontal field of opisthe showing development similar to 18i (x1354). UM field is beginning to separate into PM and EM streaks. (l) SEM micrograph of divider in cytokinesis (x617). Again, portions of 3 "generations" of right longitudinal rows are present (arrows).
Figure 19. SEM micrographs of hypotrich cysts - (a) *Oxytricha fallax* (x1198), (b) *O. quadrinucleata* (x1409), (c) *Paraurostyla* sp. (x1195), (d) *Stylochua pustulata* (x1714), (e) *Gonostomum affine* (x2070), (f) *Pleurotricha lanceolata* (x1183).
Figure 20. TEM micrographs of hypotrich cyst walls - (a) *Oxytricha quadrispirella* (x8057), (b) *O. quadrispirella* (x76563), (c) *Pleurotricha lanceolata* (x32927), (d) *Paraurostyla sp.* (x13538). Legend: ectocyst, EC; mesocysts, M; endocyst, En; granular layer, g; space inside spine, S; mitochondria, Mi.
Figure 2j. Cyst wall development in *Stylonchia pustulata* - (a) early development showing ectocyst and cirral base (x38889), (b) early development showing ectocyst and cirrus in cytoplasmic groove (x12414); (c) later development showing various cyst wall layer precursors (x40161); (d) stage similar to 19c showing detail of ectocyst and developing mesocyst (x66875). Legend: cirrus, C; autophagic vacuole, a.v.; mesocyst precursor, MP; endocyst precursor, EnP; granular layer, G.P.
Figure 22. EM micrographs of *Gonostomum affine* cysts - (a) SEM micrograph of cyst showing papillary caps (arrows) (x2307); (b) TEM cross section of cyst showing 3 cyst walls and dense protoplast (x2545); (c) TEM micrograph of papilla and cap (x8143); (d) TEM micrograph of cyst walls and their constituent layers. Legend: papillary cap, PC.
Figure 23. Diagrammatic representations of oral areas of (a) *Oxytricha platystoma* (after Kahl, 1932) and (b) *Oxytricha quadrinucleata*. 
Figure 24. Evolutionary diagram based upon the "traditional" correlation of possession of multiple longitudinal ventral rows of cirri with relative primitiveness.
Figure 25. Evolutionary diagram based upon possible relative primitiveness of Cladotricha-like organisms possessing multiple longitudinal cirral rows of somatic (rather than frontal as with Kahliella) origin.