

THE SIGNIFICANCE OF CYTOLOGICAL CHARACTERISTICS
AS REVEALED BY PROTARGOL SILVER STAINING IN
EVALUATING THE SYSTEMATICS OF THE CILIATE
SUBORDER TINTINNINA

by
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ABSTRACT

Title of Thesis: The Significance of Cytological Characteristics as Revealed by Protargol Silver Staining in Evaluating the Systematics of the Ciliate Suborder Tintinnina

David Carl Brownlee, Master of Science, 1977

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The present systematics of the tintinnid ciliates is based on the shape, size, and composition of the lorica as established by Kofoed and Campbell. Construction of a classification based on a restricted set of characteristics, such as those pertaining only to the lorica in the tintinnid ciliates, may lead to an artificial or unnatural scheme. This lorica based classification also prohibits phylogenetic comparisons of the tintinnids to other ciliate groups whose taxonomy is based on cytological characteristics. In an attempt to demonstrate the value and necessity of employing cytological characteristics in constructing the taxonomy of the tintinnid ciliates, the cytology of representative species was examined using the protargol silver-impregnation technique.

Specimens were collected from a wide range of environments, including marine, brackish, and fresh water habitats which ranged from tropical to temperate latitudes. Eleven species comprising ten genera and representing seven families were chosen to represent the suborder in this preliminary analysis.

The examination of the stained species provided the first precise description of somatic ciliation patterns, a more complete understanding of the buccal organization, and insight into the biological processes of these ciliates. Using these observations, comparisons are made to other ciliate groups and a preliminary analysis of evolutionary trends in the tintinnid ciliates is supported. It is suggested that a revision of the placement of certain genera within the families of tintinnids is necessary and that such changes should be based on both cytology and morphology of the lorica.

DEDICATION

Dedicated to my parents and Stella Grahm for their love, support, and encouragement.

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LIST OF ABBREVIATIONS

<u>Abbreviation</u>	<u>Definition</u>
AC	accessory comb
AM	anterior ciliary margin
An	anlage
AZM	adoral zone of membranelles
CM	cilia of the membranelle
CP	capsule
CV	coefficient of variation
Cy	cytopharynx
DK	dorsal kinety
F	fiber
G	granules
GT	giant ciliary tuft
Kx	kinety number x
kx	kinetosomal row of the membranelar base number x
LF	left ciliary field
LL	left lateral fiber
M	membranelle
Ma	macronucleus
MB _x	base of membranelle number x
Mi	micronucleus
n	sample size
OP	oral plug

<u>Abbreviation</u>	<u>Definition</u>
Pg	proximal plug
PK	posterior kinety
PM	paroral membrane
PP	primary pectinelle
PR	preoral ring
R _h	upper limit of range
R _l	lower limit of range
RF	right field
FL	right lateral fiber
SD	standard deviation
SE	standard error
SEM	scanning electron microscopy
T	tentaculoid
TEM	transmission electron microscopy
VK	ventral kinety

INTRODUCTION

The tintinnid ciliates are a major component of marine and brackish planktonic communities and frequently become numerically important in freshwater environments. They form a link in the food chain from phytoplankton and bacteria to the larger zooplankton.

Tintinnids characteristically secrete a lorica and attach themselves to a single spot near its posterior end. The shapes, sizes, and structural peculiarities of the loricae are very diverse and are the basis for species identification. Many species agglomerate foreign particles, including sand grains, diatom frustules, and coccoliths to their lorica, whereas others secrete their entire test. They swim and feed by using a large spiral of membranelles which can extend beyond the oral aperture of the lorica.

There is a long history of investigations into the taxonomy, morphology, biology, ecology, and fossil history of tintinnids. Many technological advances have been made through the years which have furthered the study of tintinnids. Such advances include the improvement in the optics of light microscopy and in staining methods, the implementation of scanning electron microscopy (SEM) and transmission electron microscopy (TEM), and the successful cultivation

and subsequent live observations of tintinnids. Despite the voluminous literature and advances in technology, there are still some serious deficiencies and many unsolved problems in the systematics of tintinnids.

History

A brief history of tintinnid systematics is given to show the development of and the problems and deficiencies in the systematics of these ciliates.

PRE-1900. Müller¹ (1776) was the first to describe a tintinnid, and he named it Trichoda inquilinus. This genus included a diverse group of organisms. Schrank² (1803) recognized the tintinnids as a cohesive group, gave this group the genus name Tintinnus, and made Tintinnus inquilinus the type species. Before the twentieth century, nine more genera and many species were established by investigators such as, Ehrenberg³ (1854), Stein⁴ (1867), Haeckel⁵ (1873), Fol⁶ (1881a), Daday (1887), Brandt⁷ (1896), Jörgensen (1901). All taxonomic distinctions were based on the morphology of the lorica.

¹As cited in Fol (1881b).

²Ibid.

³As cited in Loeblich and Tappan (1968).

⁴Ibid.

⁵Ibid.

⁶Ibid.

⁷Ibid.

In addition to the taxonomic contributions, the cytology of tintinnids also was being investigated. Claparède and Lachmann⁸ (1858) gave the first account of the cytology of tintinnids. In their observations they even noted small lobes (today known as tentaculoids) between the membranelles. Further cytological characterizations; such as, the shape and position of the peristome, infundibulum, membranelles, and anlage, were presented by Fol⁹ (1881a), Entz (1886), and Daday (1887). Apstein (1893) described conjugation in a tintinnid. The above reports on cytology, based on light microscopy without the aid of stains, laid the groundwork for understanding the morphology of tintinnids, but the resolution of fine details of the morphology were limited without the technologies of staining and electron microscopy.

1901 TO 1925. Between 1901 and 1925, sixteen more genera were established, bringing the number of genera to twenty-six. Jörgensen (1924) worked on the Mediterranean tintinnids and contributed many of the new genera of this time period. Brandt (1906), Laackmann¹⁰ (1910) and Cleve¹¹ (1902) also established new genera. By the end of this time period, only three families of tintinnids were in

⁸Fol. (1881b).

⁹Ibid.

¹⁰Leoblich and Tappan (1968).

¹¹Ibid.

existence; i.e., the Tintinnidae Claparède and Lachmann 1858, Codonellidae Haeckel 1873, and Dictyocystidae Haeckel 1873. Family distinctions and species identifications were based on the morphology of the lorica.

Brandt (1906, 1907), Entz (1909), and Fauré-Fremiet (1924) produced the most notable cytological studies of this time period. Entz (1909) sectioned hematoxylin stained specimens in the study of their morphology. This was an important step forward in the examination of tintinnid morphology, as the stain produced greater resolution of cellular components, and the sectioning removed the visual interference of the lorica and heavily stained cytological parts. But the somatic ciliation and infraciliary structures are stained poorly if at all with hematoxylin, and thus the somatic ciliation patterns were not described in complete detail. Fauré-Fremiet (1924) made careful observations on several tintinnids and demonstrated a variety of ciliation patterns. His observations, based on light microscopy without the aid of staining, were limited by the interference of the lorica and the lack of a stain to increase resolution. Based on these observations, Fauré-Fremiet suggested that the ciliation patterns of tintinnids were similar to oligotrichs and that the tintinnids probably evolved from oligotrich-like ancestors.

Entz (1909), Brandt (1906, 1907), and Fauré-Fremiet (1924) recognized the importance of cytological characteristics in constructing a natural classification, and suggested one based solely on the lorica is artificial and only

provisional. They suggested that characteristics; such as, number of membranelles, number of macronuclei and micronuclei, placement of the point of attachment to the lorica and disposition of somatic cilia could be used to construct a classification.

1926 to 1950. Kofoed and Campbell dominated the field of tintinnid taxonomy between 1926 and 1950. Together they produced two monographs (1929, 1939) in which they revised and updated the taxonomy of the tintinnids. Noting the insufficient data on cytological characteristics, they nevertheless followed the historical approach and based their taxonomic scheme for the tintinnids strictly on the architecture of the lorica. They often attributed species designation to specimens which vary in only minute details of the lorica. Kofoed (1930) and Kofoed and Campbell (1939), in defense of the use of the morphology of the lorica for constructing a classification and phylogeny, suggested that the lorica represents the particular behavior of a tintinnid. A phylogenetic scheme of the tintinnids, based on the morphology of the lorica, was presented by Kofoed and Campbell (1939). In their 1939 monograph, Kofoed and Campbell recognized 750 species in 62 genera and established 10 new families which raised the total number of families to 13. Other investigators who made contributions to tintinnid taxonomy in this time period include Hada (1938), Busch¹² (1949), Balech (1948), and

¹²Leoblich and Tappan (1968).

Strand¹³ (1926).

In addition to the taxonomic contributions, the cytology of tintinnids also was being investigated. Campbell (1926, 1927) described the general morphology of two species of tintinnids and gave an account of the now defunct neuro-motor apparatus of nervous coordination. Campbell (1931) gave a description of the membranelles of a tintinnid species. Entz (1927) described the structure and function of the membrellar system of a tintinnid and later (1935) discussed the nuclear organization of the same species. These studies were based on live and hematoxylin stained specimens and faced the same problems of earlier studies.

1952 TO PRESENT. Since the monographs of Kofoed and Campbell, the taxonomic publications on tintinnids have dealt mostly with new specific and generic descriptions, and the reduction of previously described genera and species by synonymy (Burkovsky, 1973; Balech, 1975). Balech (1951, 1975), Corliss (1960), Hada (1970), and Laval-Peuto (1977) made taxonomic contributions during this time period. Only four new extant genera were established during this time period. Three more genera were renamed (Corliss, 1960). In contrast to the sparsity of taxonomic papers in recent years, there is an increasing amount of work on tintinnids which has taxonomic implications. The structure and ultra-structure of the lorica and cytosome, the reproductive biology of

¹³Leoblich and Tappan (1968).

cultured specimens, and the ecology of tintinnids have been described for some species. New techniques including SEM, TEM, and the Bodian protargol silver-impregnations method have been employed.

Cosper (1972) and more recently Gold and Morales (1976a,b) have employed SEM as a taxonomic tool. Gold and Morales suggest that the size, shape, composition, and distribution of the particles agglomerated to the lorica of many tintinnids may be species specific, and thus of taxonomic importance.

Hedin (1976a) published the first account of a silver impregnation stain of tintinnids and compared the cortex as revealed by the protargol stain to the same observed by SEM. The implementation of ^a protargol silver-impregnation method by Hedin (1975) was a major advance in tintinnid taxonomy, but it was not exploited fully by him and has not been used in any other published account on tintinnids.

The ultrastructure of several tintinnids has been presented recently. Laval (1971, 1972, 1976) studied several species of tintinnids in detail with TEM and has discussed the phylogenetic relationships of the tintinnids to other polyhymenophoran groups of ciliates. She stated that more information on the somatic ciliation patterns was necessary before a better understanding of these relationships can be reached. TEM studies also were conducted by Hedin (1975, 1976b). He concluded that many of the ultrastructural characteristics of the cell body were conservative among the

species that he and Laval have studied.

The biology of tintinnids, including modes of reproduction, division rates, lorica formation, and conjugation, can, in addition to morphology, provide important taxonomic information. The successful cultivation of several tintinnids by Gold (1966, 1968, 1970, 1971, 1973) allowed careful observations of tintinnids under controlled conditions. This is an important step forward for studies of tintinnid biology and systematics.

Biernacka (1952), Gold (1970, 1971, 1973), and Gold and Pollinger (1971) reported on reproduction of tintinnids. Laval-Peuto (1977) made a striking discovery in following the life cycle of a Favella sp. in culture. She found that Favella, under certain conditions, could produce two different lorica forms. The one form is identical to the lorica of the parent cell (Favella form) and the second form of the lorica has been previously associated with the genus Coxliella (Coxliella form). The Favella form and the Coxliella form have been observed to conjugate. These two lorica forms, proven by Laval to be produced by the same species, are not only representative of different genera but they also belong to different families. This work demonstrates the importance of controlled live observations on the life cycle of tintinnids and suggests that lorica morphology alone can lead to serious taxonomic errors.

PROBLEMS AND DEFICIENCIES IN TINTINNID SYSTEMATICS.

Despite the numerous studies on tintinnids through the years

and the major advances in technology in recent times, two serious problems still remain in the systematics of the tintinnids. The first is the exclusive use of the lorica morphology in constructing the classification and phylogeny within this ciliate group. This is a direct result of the second problem which is a lack of cytological characterization of most species. These deficiencies restrict phylogenetic comparisons of the tintinnids to other ciliate groups and hinder the construction of a natural classification within the tintinnids.

Though a classification can be constructed, based on lorica peculiarities, it probably will not represent a natural classification. The phylogeneticist Mayr (1969) and the more recent pheneticists Sneath and Sokal (1973) agree that a classification based on a set of characteristics pertaining to only one aspect of any group of organisms can lead to an unnatural classification. Laval-Peuto's (1977) study on Favella (mentioned above) demonstrates very well that data on lorica form, alone, can lead to erroneous taxonomic decisions.

In addition to the variability in lorica form discussed by Laval, the lorica dimensions also vary with environmental conditions (Heald, 1911; Gold, 1974; Gold & Morales, 1974, 1975). Thus, it is clear that the present systematics based on lorica morphology should not be accepted without question but must be tested by using a wide range of characteristics.

The organization of the ciliary and infraciliary components of the somatic and buccal regions have proven to be valuable characteristics in the study of systematics within and among the majority of other ciliate groups. Corliss (1974) emphasized the importance of the Chatton-Lwoff and Bodian protargol silver-impregnation techniques in revealing these characteristics and considered the application of these techniques as an essential step forward for ciliate systematics. These techniques have been used with increasing frequency in recent years in morphological and taxonomic studies of ciliates; however, only one tintinnid species has been described so far by using one of the two available methods.

Because of a lack of information on tintinnid somatic ciliation and other cytological characteristics as revealed by silver impregnation, my objective was to describe and compare a representative number of tintinnids with the Bodian protargol silver-impregnation technique. In addition, my results were compared to past studies on tintinnids that utilized light microscopy, SEM, and TEM. The observed cytological differences and trends between and among the various species are discussed in relation to their possible phylogenetic significance. These trends and differences are used to test the phylogeny of Kofoed and Campbell (1939) that is based on lorica morphology. Emphasis is placed on: (1) the application of the Bodian protargol stain to tintinnid morphology, biology, and systematics; and (2) the

significance of cytological characteristics in constructing the taxonomy and phylogeny of the tintinnid ciliates.

MATERIALS AND METHODS

Sampling

Specimens were collected from marine, brackish, and fresh water habitats which ranged from subtropical to temperate latitudes. The fresh-water specimens were collected from the Ohio River, the brackish water tintinnids from the sea-water flow through system at the Chesapeake Biological Laboratory, Solomons, Maryland and the marine species on one of three cruises in the Atlantic Ocean. Cruise I was off the Mid-Atlantic States (Maryland, Delaware, and Virginia) and conducted by the Environment Protection Agency, Annapolis, Maryland, between February 5-9, 1975. It was conducted on the Coast Guard Cutter Alert. Cruises II and III were conducted by Dr. Rita Colwell and her colleagues aboard the R. V. Eastward. During Cruise II, March 22-25, 1975, samples were collected in Miami Harbor and along the east coast of Florida north of Miami in the Gulf Stream. Cruise III provided samples from San Juan Harbor, Puerto Rico, and two other offshore stations between February 12-14, 1976.

Eleven species of tintinnids, thought to be representative of the group, were selected from these collections. The 11 species belong to 10 genera and represent 7 of the 13 families of tintinnids. The species considered are: Tintinnidium mucicola in the family Tintinnidiidae, Codonella cratera, Tintinnopsis baltica, and Tintinnopsis subacuta in

in the family Codonellidae, Stenosemella steini in the family Codonellopsidae, Climacocylis scalaroides in the family Coxliellidae, Favella panamensis in the family Ptychocylididae, Protorhabdonella in the family Rhabdonellidae, and Amphorellopsis acuta, Eutintinnus pectinis, and Salpingacantha sp. in the family Tintinnidae.

The sampling locations with brief descriptions, and the exact dates and times of sampling are given for each species in Table I. The temperature, salinity, and total depth of each station is given for each species in Table II. The data for C. cratera did not accompany the samples and has not yet been forwarded to me by the collector. This data will be furnished as soon as it is received.

Samples were collected on the three cruises at 5 meters depth by pump (Little Giant submersible pump). Two twenty liter carboys were filled from the pump. The samples were then poured through a 10 μ m mesh nytex net. The concentrate was placed into 250 ml nalgene bottle and an equal amount of Bouins fixative to concentrate was added. The samples were then brought to the laboratory for further concentration and staining.

A 10 μ m net also was used to filter an appropriate volume of sample water from the constant-flow system at the Chesapeake Biological Laboratory. Again, an equal volume of Bouins to sample concentrate was used as a fixative.

The Ohio River samples were mailed from Ohio in ca. 10 ml vials and were fixed in 1-4% formalin.

Table I. Sampling Sites.

Species	Cruise Station	Location	Latitude	Longitude	Date	Time
<i>Tintinnidium mucicola</i>	I-1	Neritic, Delaware	38°50.8'	74°48.1'	2/5/75	1029
<i>Codonella cratera</i>	-	Ohio River	-	-	-	-
<i>Tintinnopsis baltica</i>	I-1	Neritic, Delaware	38°50.8'	74°48.1'	2/5/75	1029
<i>Tintinnopsis subacuta</i>	-	Chesapeake Bay	-	-	6/11/77	2300
<i>Stenosemella steini</i>	III-1	San Juan Harbor	-	-	2/14/76	1400
<i>Climacocylis scalaroides</i>	II-2	Florida, Gulf Stream	26°16'	80°03'	3/22/75	1240
<i>Favella panamensis</i>	III-1	San Juan Harbor	-	-	2/14/76	1400
<i>Protorhabdonella simplex</i>	II-2	Florida, Gulf Stream	26°16'	80°03'	3/22/75	1240
<i>Amphorellopsis acuta</i>	II-1	Miami Harbor	-	-	3/22/75	0715
<i>Eutintinnus pectinis</i>	I-2	Pelagic, Delaware	39°03.5'	73°43.3'	2/9/75	1805
<i>Salpingacantha</i> sp.	II-2	Florida, Gulf Stream	80°03'	80°03'	3/22/75	1240

Table II. Physical-Chemical Parameters

Species	Depth (meters)	Temperature (°C)	Salinity (°/oo)
<i>Tintinnidium mucicola</i>	16.4	3.56	35.77
<i>Codonella cratera</i>	-	-	-
<i>Tintinnopsis baltica</i>	16.4		35.77
<i>Tintinnopsis subacuta</i>	3	-	-
<i>Stenosemella steini</i>	5	-	-
<i>Climacocylis scalaroides</i>	115	24.4	36.14
<i>Favella panamensis</i>	5	-	-
<i>Protorhabdonella simplex</i>	115	24.4	36.14
<i>Amphorellopsis acuta</i>	-	24.7	-
<i>Eutintinnus pectinis</i>	49.4	6.98	37.48
<i>Salpingacantha</i> sp.	115	24.4	36.14

Embedding and Staining

Prior to staining, the ciliates were concentrated by sedimentation and centrifugation and were attached to albuminized coverslips (embedded) for easy handling. A modified Bodian Protargol silver impregnation method of staining (E. B. Small, unpublished) was employed. The staining method is similar to the methods used by Kozloff (1945) and Tuffrau (1967a). The step-by-step procedures for embedding and protargol staining used here are given in Appendix I.

SEM Preparation and Examination

All specimens were fixed in either 2.5% glutaraldehyde or Bouins fixative except C. cratera which was fixed in dilute formalin. Specimens were freeze dried on a vacuum evaporative tissue dryer employing a Peltier cold stage (Pierce-Edwards Tissue Dryer, Edwards Vacuum, Ltd.) following the methods of Small and Marszalek (1969). All specimens were observed and photographed on a Cambridge Mark IIA scanning electron microscope except C. cratera which was examined with an AMR 1000A scanning electron microscope.

Microscopy and Measurements

All protargol stained preparations were observed through a compound microscope (Carl Zeiss Inc.). All measurements for which statistical parameters are given were made with a calibrated filar ocular micrometer (E. Leitz Inc.). The mean (\bar{X}), range (lower limit, R_1 ; upper

limit, R_h), standard deviation (SD), standard error (SE), coefficient of variation (CV), and sample size (n) are given for each measurement in Appendix II. In the text of the results, the measurements are given as $\bar{X} \mu\text{m}$ ($\pm\text{SE}$, R_l-R_h , n). All measurements given in approximate (ca.) values, such as length of cilia, were measured with a standard ocular micrometer.

Measurements of lorica dimensions include maximum length, maximum oral diameter, maximum width, if different from maximum oral diameter, and other dimensions that are appropriate to a particular species. All measurements were made from the outer most edges of the lorica.

Cytological measurements are taken of the maximum length, diameter of the adoral zone of membranelles (AZM), maximum width, and nuclear dimensions including length and width of the macronuclei and the diameter of the micronuclei. The length is defined as the distance from the base of the membranelles to the most aboral end. The diameter of the AZM is the distance between the most distant membranelar bases as measured from the most exterior portion of each. The maximum width was measured if it was larger than the diameter of the AZM. Other measurements were made on features particular to certain species.

Meristic data also were collected on each specimen. Number of kineties, macronuclei, micronuclei, and membranelles were recorded for each species. The median (Med) value and the range were given for these data in the

following form, $Med (R_1-R_h)$.

In addition to the measurements and counts, derived values from these data also were obtained. The ratio of the length to the oral diameter of the lorica (length/oral diameter) was used by Kofoed and Campbell (1929 and 1939) as a taxonomic character. This ratio is thus given for each species. As an index of the number of kineties per unit area at the oral margin and at the maximum width, the number of kineties is divided by the length of the circumference at the oral margin ($\# \text{ kineties}/\pi \cdot \text{diameter of the AZM}$) and at the maximum width ($\# \text{ kineties}/\pi \cdot \text{maximum width}$), respectively.

Species Descriptions

A description of the lorica is presented briefly with the dimensions recorded as stated above and notes were made on the types of agglomerated particles when present. A historical review of the literature pertaining to all of the tintinnids considered, except of course the unidentified Salpingacantha sp., is given by Kofoed and Campbell (1929). New information made available by either SEM or the pro-targol staining of the lorica is presented.

The patterns of somatic ciliation and the configuration of the AZM and nuclei are described for each species. Comments are made concerning the developing oral primordium (anlage), the lorica-forming granules, and the developmental states of the macronucleus, but a detailed account of the

morphogenesis of these structures is not included.

Photographs were taken to demonstrate features of both the lorica and the cell body. Drawings were made to present a more complete and three-dimensional image of the body of the ciliate. A drawing tube attached to the microscope was used to make the preliminary drawings of representative specimens. A ventral and dorsal view were drawn for each species. Final drawings were made by biological illustrators under the supervision of the author.

RESULTS

Introduction

To provide a foundation upon which the following species descriptions can be constructed, the body plan of a generalized tintinnid is presented (Fig. 1a-d). This model tintinnid is based on a composite of the species considered. New morphological terms are introduced and defined where necessary. Following this general account, the morphology of each species will be described in relation to the model. The species descriptions are presented according to their closeness of fit to the generalized tintinnid.

Generalized Tintinnid

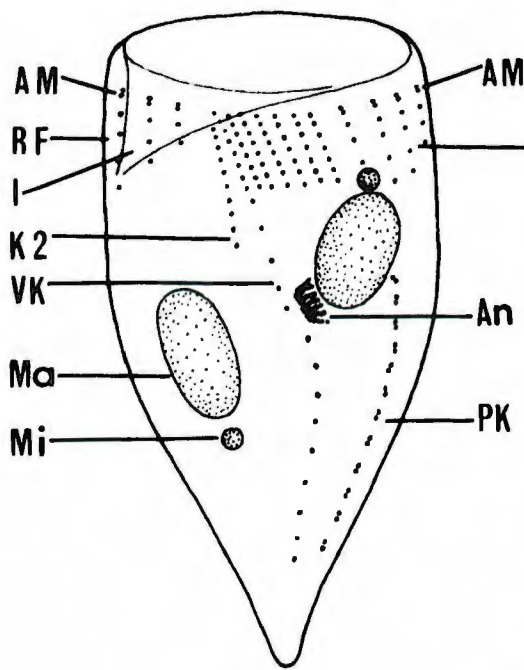
The cell body of living tintinnids is usually conical or funnel-shaped. Often there is an elongate slender peduncle which attaches the ciliate to its lorica. The body increases in width from the peduncle to the oral margin. Tintinnids contract when fixed and are found in different states of contraction on slides of stained specimens. Thus, the stained specimens and the figures based on them are less conical and more cylindrical or spherical than they are in the living state.

SOMATIC CILIATION. As the somatic ciliation of tintinnids has not been reported on in detail previously, it is necessary to provide some terminology and to provide a system for orientation.

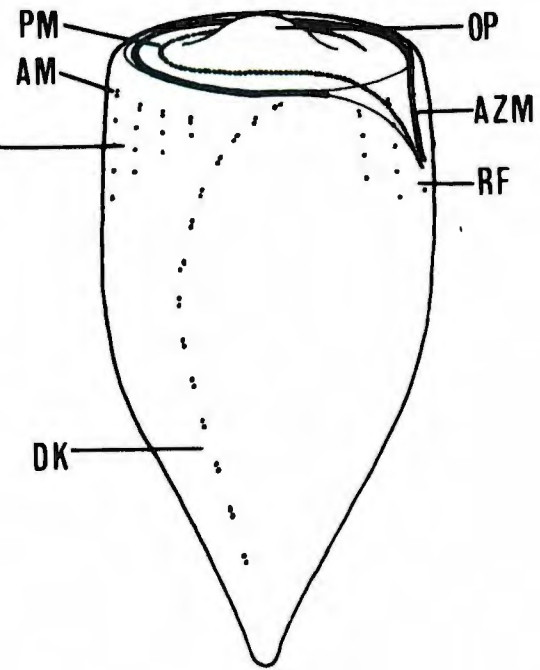
The position in which the oral primordium or anlage (An) develops is the point of reference used in the following

Figure 1

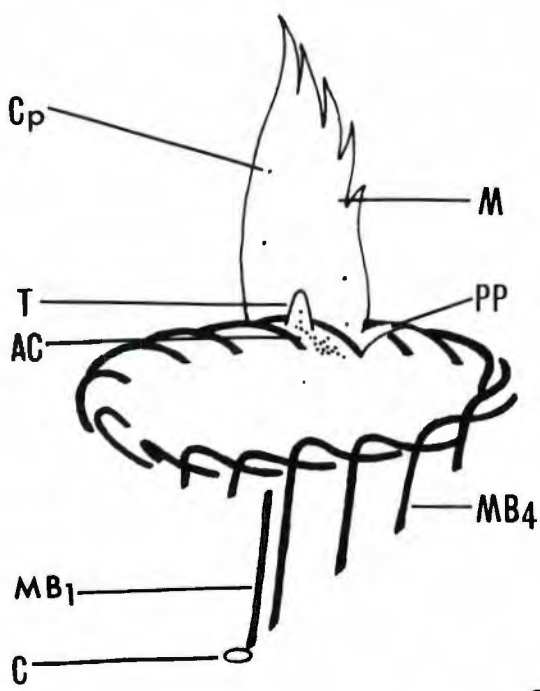
Drawings of a generalized tintinnid: a. ventral aspect, b. dorsal aspect, c. lateral view of buccal structures, d. oral view of buccal structures. AM, anterior ciliary margin; An, anlage; I, infundibulum; K2, kinety number two; Ma, macronucleus; Mi, micronucleus; PK, posterior kinety; VK, ventral kinety; RF, right ciliary field; LF, left ciliary field; DK, dorsal kinety; AZM, adoral zone of membranelles; PM, paroral membrane; OP, oral plug; Cp, capsules; T, tentaculoid; AC, accessory comb; MB₁, base of membranelle number one; MB₄, base of membranelle number four; C, cytostome; M, membranelle; PP, primary pectinelle.



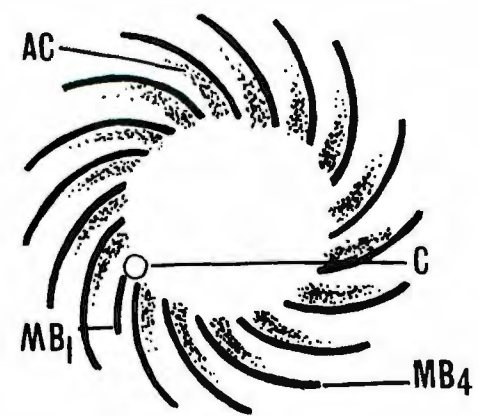
a



b



c



d

descriptions. The side upon which the An develops is by convention, the ventral side (Deroux 1974). The An develops about half way down the cell's length near a single bipolar kinety (Fig. 1a). This kinety is termed the ventral kinety (VK). Kinetosomes have not been seen, as yet, to proliferate off of the VK to form the primordium; therefore, the term stomatogenic kinety is not applied at this time. The right and left sides are now defined as to the organisms right or left of the VK. The An often forms just to the left of the VK.

In addition to the VK there are three other ciliary components. These are the right ciliary field (RF), dorsal kinety (DK), and the left ciliary field (LF), located to the right, opposite, and to the left of the VK, respectively. In most species there also is a single kinety located posterior to the LF, termed the posterior kinety (PK). The numbering convention of Chatton et al. (1931) can be applied to the numbering of the kineties in tintinnids in the following way. The first kinety to the right of the oral primordium, the VK, is kinety one (K1). The remaining kineties are numbered consecutively from left to right (as viewed from within the organism) from the VK. Thus the RF consists of kineties 2-x, the DK is kinety x+1, and the LF consists of kineties (x+2)-n. The PK is not given a number. The circle inscribed by the majority of the anterior kinetids of the LF and RF is termed the anterior ciliary margin (AM) (Fig. 1a,b).

BUCCAL MORPHOLOGY. The major components of the buccal area are the peristome (often with a raised oral plug), the cytostome-cytopharynx complex, the adoral zone of membranelles (AZM) with associated fiber system, tentaculoids and accessory combs, and the paroral membrane (PM) (Fig. 1a-d).

The peristome surrounds the infundibular cavity which is circular at its lip or most anterior end and funnels posteriorly to the right and ventral (Fig. 1a). The cytostome-cytopharynx complex is located at the posterior end of the infundibulum, directly interior to the area of the RF and dorsal to the VK. In many species there is a cytoplasmic bulge on the ventral wall of the peristome termed the oral plug by Campbell (1926) (Fig. 1b). This cytoplasmic flap can be seen to stroke back and forth in the living animal. In certain species of the Tintinnidae this area is extremely large extending well anterior to the membranelles. The oral plug tapers off to both sides and on the right side appears to be associated with the paroral membrane, which is described later.

The proximal ends of the membranelles of the AZM form a leiotropic (sinistral) spiral (Fig. 1c) which begins within the infundibulum near the cytostome. The spiral courses up the right ventral wall of the peristome to a position just below the ventral portion of the peristomial lip. The spiral continues to the left around the inside of the lip, courses around and past the dorsal side, and terminates at a position just to the right and anterior to the beginning of the spiral. The distal end of the first membranelle ends on the inner edge

of the peristomial lip (Fig. 1c). The distal ends of the remaining membranelles pass over the peristomial lip and stop at the external edge of the lip. The distal ends of the membranelles, excluding the first membranelle, form a circle on the peristomial lip (Fig. 1c,d).

The infraciliary bases of the membranelles are composed of three rows of kinetosomes, two long rows and a short row located on the distal end. These kinetosomes give rise to the cilia of the membranelles anteriorly and a complex fiber system posteriorly. These fibers from adjacent membranelles join posteriorly and parallel to the AZM forming the preoral ring.

Found between the membranelles of some tintinnids are raised cytoplasmic extensions called tentaculoids (Campbell 1926). There is one tentaculoid associated with each membranelle and they are located on the inside of the membranelle where the membranelle curves over the peristomial lip. The tentaculoids vary in shape and size in different species.

The accessory combs of Campbell (1926), when they are present, are found from near the proximal end of a membranelle up to the tentaculoid. They stain darkly with protargol and appear very granular.

Dark staining granules are observed on the membranelles, and in the tentaculoids and accessory combs of certain species of tintinnids. These are interpreted to be the haptocyst-like "capsules torquées" described by Laval (1971,1972).

The kinetosomes of the paroral membrane (PM) are rarely observed in these protargol stained specimens. Occasionally

portions of the PM appear as granular lines, but more often the PM appears as a deeply staining line. This line is interpreted to be the PM. This assumption is supported by the works of Deroux (1974), Grain (1972), Grim (1974), and Laval (1972). (See the discussion for further treatment of this evidence.)

The PM begins just above and dorsal to the cytopharynx area opposite the first membranelle. It moves anteriorly and to the right continuing around to the dorsal side. The PM, in some cases, continues around to the ventral side and across the ventral side of the oral plug.

NUCLEAR STRUCTURE. The nuclear components of tintinnids are variable in number, shape, and size, but, they are frequently composed of 2 macronuclei and 2 micronuclei (Fig. 1a). In some species there are connections between two interphase macronuclei such that there is a pair or several pairs of macronuclei in one cell. Reorganization bands and condensation of the macronuclei are observed during division.

Tintinnopsis baltica Brandt 1896

Lorica

The lorica is made of arenaceous particles cemented together with the lorica matrix (Fig. 3a,c). In Fig. 3c the proteinaceous matrix has been stained with protargol and can be seen to outline the attached particles. The lorica has a slightly flaring oral brim with an average diameter of $37.0\ \mu\text{m}$ (± 0.41 , 33.2-41.3, 20). The brim is followed posteriorly by a nuchal constriction $31.4\ \mu\text{m}$ ($\pm .35$, 29.3-33.5, 11) across. The breadth then increases to form the bowl which is $34.5\ \mu\text{m}$ (± 0.48 , 30.6-42.4, 23) in diameter and which is pointed at the aboral end. The average total length is $62.3\ \mu\text{m}$ (± 1.84 , 52.6-83.4, 19) which is equal to 1.68 oral diameters. The diameter of the nuchal constriction is the least variable of the measurements of the lorica with a CV equal to 3.37%.

Cytology

The cell body of this species is contracted down into the lorica in stained specimens (Fig. 3b). It is cylindrical anteriorly with a maximum width of $23.4\ \mu\text{m}$ (± 0.86 , 15.1-29.5, 21) and conical posteriorly. The length of the contracted cell body is $34.3\ \mu\text{m}$ (± 0.98 , 28.9-43.9, 19). The diameter of the AZM is $19.3\ \mu\text{m}$ (± 0.22 , 17.5-21.7, 22). A peduncle attaches the cell body to the posterior end of the lorica (Fig. 3b).

SOMATIC CILIATION. T. baltica has 32 (30-34) kineties. In addition to the VK and the DK there are 7 (6-9) kineties in the RF, and 22 (21-24) in the LF. The kinetal density index is 5.28/10 μm at the oral margin and 4.35/10 μm at the maximum width.

The VK (Fig. 2a,3d) begins anterior to the AM, extends posteriorly from right to left, and ends near the aboral end. The kinetids, composed of single ciliferous kinetosomes, are tightly packed anteriorly and become progressively more distant from each other posteriorly. The cilia of the anterior kinetids are longer than those of the posterior kinetids.

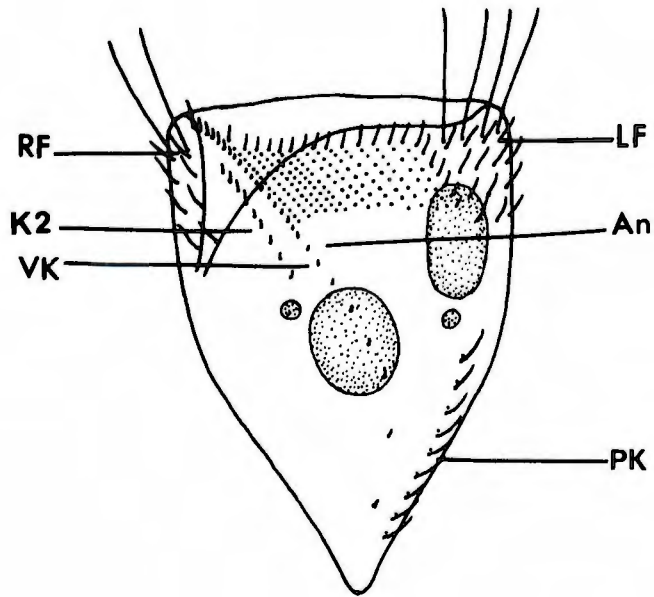
The anlage develops at the cortex, adjacent to the VK, and posterior to the LF (Fig. 2a). In early stomatogenesis the anlage consists of a group of unorganized nonciliferous kinetosomes.

The second kinety (Fig. 2a;3d) begins posterior to the AM and the anterior most portion of the VK, lies almost parallel to the VK, and extends posteriorly for over one-half of the cell length. The kinetids have single ciliferous kinetosomes.

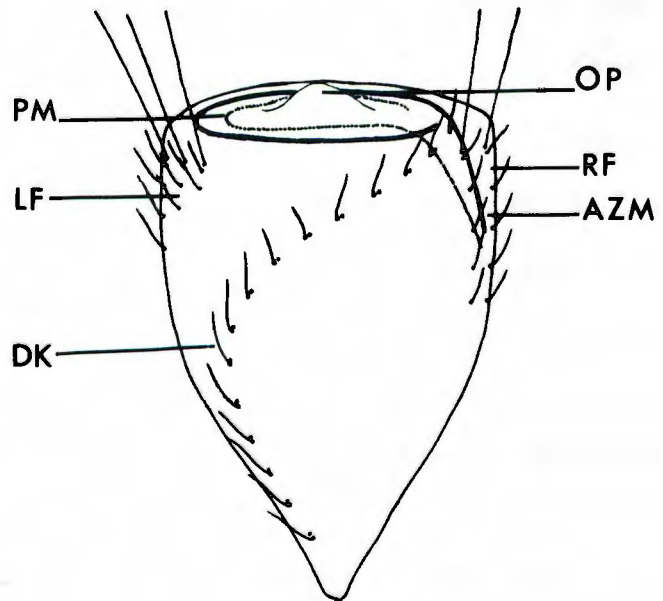
The other kineties of the RF and the kinetosomes within these kineties are evenly spaced (Fig. 2a,b;3e). The lengths of these kineties are between one-fourth and one-half of the total cell length. The kinetids of these kineties have single ciliferous kinetosomes except the most anterior kinetid of each which has two kinetosomes, both ciliferous. The anterior cilium of the double kinetids is long (ca. 10 μm) in comparison to the posterior cilium of the same kinetid (ca. 2-3 μm).

Figure 2

Drawings of ventral (a) and dorsal (b) aspects of Tintinnopsis baltica. RF, right ciliary field; LF, left ciliary field; VK, ventral kinety; PK, posterior kinety; K2, kinety number two; An, position of anlage; DK, dorsal kinety; AZM, adoral zone of membranelles; PM, paroral membrane; OP, oral plug. ca. 2,300X.



a

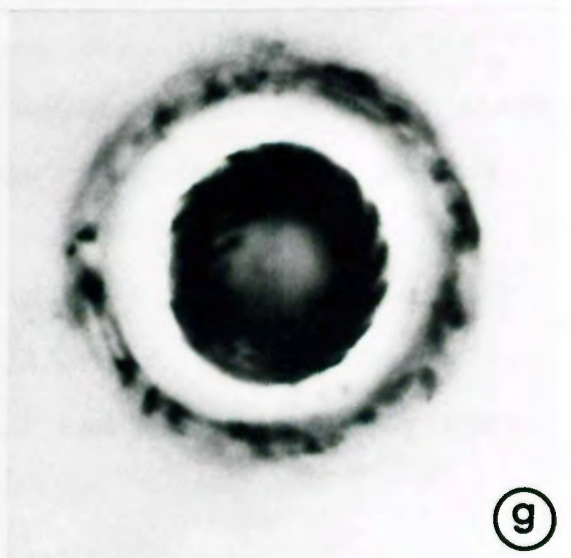
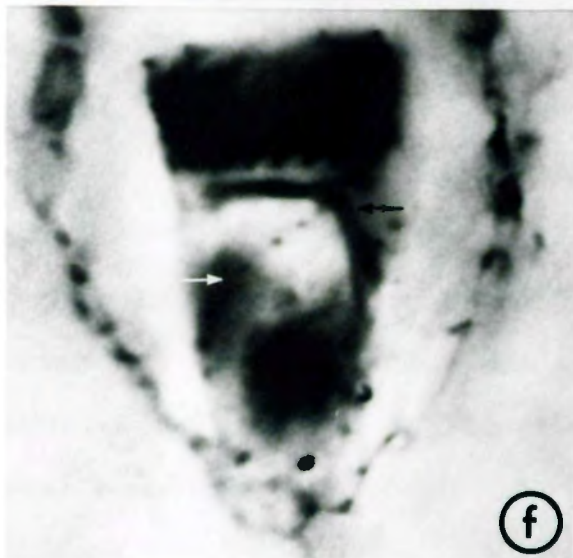
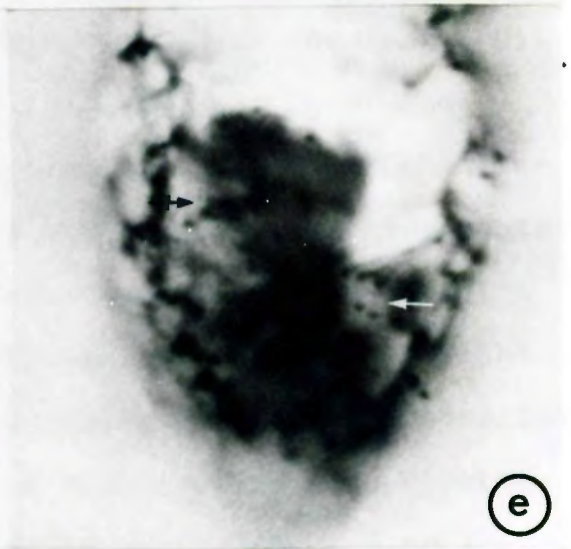
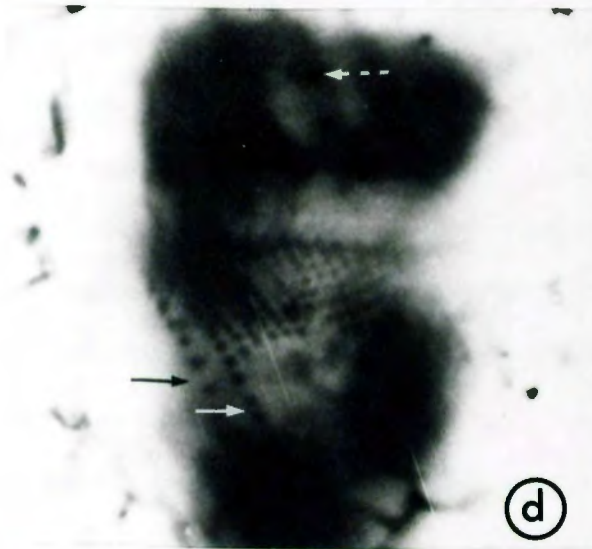
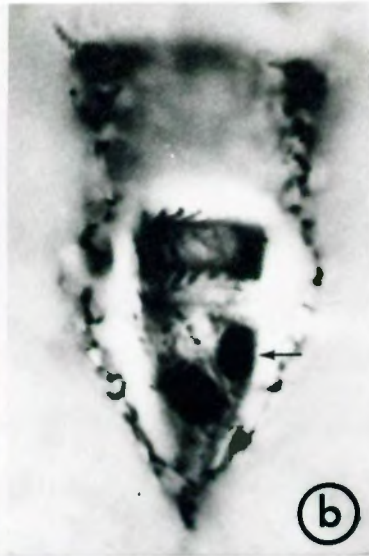
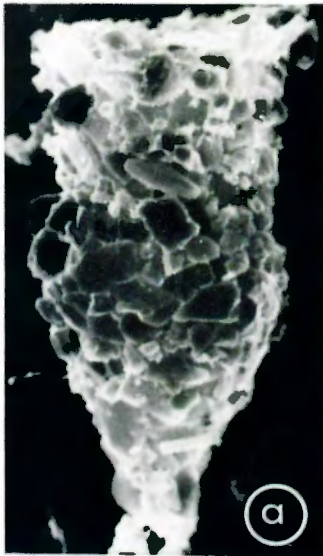


b

Figure 3

Photomicrographs of the lorica, somatic ciliation, and buccal area of Tintinnopsis baltica.

- a. Lorica. 990X, SEM
- b. Outline of lorica and general body form.
Black arrow, macronucleus. 1,410X. (Note also the proximal ends of the membranelles ascending the peristomial wall.)
- c. Lorica matrix surrounding arenaceous particles. 1,150X.
- d. Ventral aspect of cell body. Black arrow, kinety 2; solid white arrow, ventral kinety; broken arrow, capsule on membranelle. The left field lies to the animals left of the ventral kinety. 2,600X.
- e. Right dorsal aspect of cell body. White arrow, kinetosomes of dorsal field; black arrow, anterior kinetosomes of the dorsal kinety. 1,890X.
- f. Dorsal aspect of cell body. White arrow, dorsal kinety; black arrow, paroral membrane. 1,890X.
- g. Oral view of lorica (exterior) and AZM (interior). 1,660X.



The cilia of the remaining kinetids of the RF are ca. 2-4 μm long.

The dorsal kinety (Fig. 2b,3f), composed of 19 (15-22) kinetids, courses across the dorsal side from the right anterior to the left posterior. It is directed in the opposite direction of the VK and toward the LF. It begins anterior to the AM and extends down to near the posterior end of the cell. The kinetids have two kinetosomes, the posterior one ciliferous.

The 22 (21-24) kineties of the LF (Fig. 2a,b,3d) and the kinetids within these kineties show a gradient from loose to tight spacing from the first kinety ($K(x+2)$) to the last (K_n). There is also a gradient of tight to loose spacing of the kinetosomes from anterior to posterior especially for the latter kineties of this field. The lengths of the kineties range from very short (one kinetid) to about one-fourth the total length of the cell. The last 15-17 kineties angle from right anterior to left posterior and the last kinety, K_n , is parallel to the VK. The kinetids consist of single ciliferous kinetosomes except the anterior most kinetid on the first 5 to 7 kineties which have two kinetosomes, both ciliferous. The cilia of the double kinetids are comparable in length to those of the RF. The cilia of the single kinetids are ca. 2-4 μm long.

The PK (Fig. 2a) contains 9 (8-10) kinetids each with 2 kinetosomes, the posterior one ciliferous. The PK begins posterior to kineties 5-7 of the LF and terminates near the aboral end.

BUCCAL MORPHOLOGY. The infundibulum extends posteriorly for almost one-half of the cell length. It narrows to the right ending at the cytostome-cytopharynx complex which is located interior to the RF and dorsal to the VK. There is a prominent oral lobe (Fig. 2a) on the ventral side of the peristomial wall in the infundibulum.

The AZM (Fig. 2g) consist of 17 membranelles. The proximal ends of the first five membranelles are located in the infundibulum (Fig. 3b). The proximal end of the first membranelle is located ventral to and near the cytostome-cytopharynx complex while the ends of the next four membranelles are found ascending the ventral wall of the peristome. The next ten membranelles spiral around the peristome with their proximal ends located just inside the peristomial lip. The proximal ends of the last two membranelles descend slightly back into the infundibulum and they are located anterior and to the right of the proximal end of the first membranelle. The distal end of the first membranelle, which is shorter than the others, ends on the interior edge of the peristomial lip. The distal ends of the remaining membranelles cross over the peristomial lip from right to left (as viewed from within the cell) to the exterior edge of the lip.

The PM (Fig. 2b) begins at the dorsal side of the cytostome-cytopharynx complex and extends anteriorly and to the right along the peristomial wall. On the dorsal side of the cell, the PM is located posterior and parallel to the peristomial lip. The PM continues in this position around the left

side, then crosses over the ventral side of the oral plug.

Darkly stained capsules are distributed along the cilia of the membranelles, between the membranelar bases, and throughout the cytoplasm. They are $0.86\text{ }\mu\text{m}$ (± 0.018 , $0.73\text{--}0.92$, 10) in diameter, and six such capsules have been observed on a single membranelle. No tentaculoids have been seen but the capsules between the membranelar bases may represent the accessory combs.

NUCLEAR STRUCTURE. There are two macronuclei and two micronuclei in the interphase cells (Fig. 2a,3b). The macronucleus is irregularly ovoid with a length of $8.47\text{ }\mu\text{m}$ (± 0.41 , $6.89\text{--}11.8$, 11) and a width of $5.63\text{ }\mu\text{m}$ (± 0.35 , $3.40\text{--}6.70$, 11). The micronuclei are spherical with a diameter of $1.9\text{ }\mu\text{m}$ (± 0.043 , $1.74\text{--}2.20$, 11). Reorganization bands in and condensation of the macronuclei occur in dividing cells.

Codonella cratera (Leidy 1877) Vorce 1881

Lorica

The lorica of C. cratera (Fig. 5 a-d) is composed of arenaceous material cemented together with the lorica matrix. The lorica consists of an oral brim $36.2\text{ }\mu\text{m}$ (± 0.56 , 31.5-39.5, 19) in diameter, followed posteriorly by a cylindrical tube $32.5\text{ }\mu\text{m}$ (± 0.37 , 30.4-35.1, 20) in width and $25.1\text{ }\mu\text{m}$ (± 1.72 , 12.8-36.0, 14) in length. Posterior to the cylindrical tube is the bowl of the lorica which is $41.1\text{ }\mu\text{m}$ (± 0.51 , 36.9-46.1, 20) across and rounded posteriorly (Fig. 5c). The total length of the lorica is $58.4\text{ }\mu\text{m}$ (± 0.98 , 52.8-65.0, 17) and the length to oral diameter ratio is 1.61. There are several spiral ridges on the inside of the oral brim and cylinder portion of the lorica which are revealed by SEM (Fig. 5b). These ridges may or may not be expressed externally.

The lorica of C. cratera lacks the secondary structure, nuchal groove or shelf characteristic of the genus Codonella and has spiral turns in the collar which are not characteristic of Codonella. The taxonomic position of C. cratera is therefore in question.

Cytology

In stained specimens, the cell body exists in various states of contraction. In the extreme case the cell body becomes almost spherical (Fig. 5c) but other specimens are less spherical (Fig. 5e) or even cylindrical (Fig. 5f). The length and width measurements are therefore rather variable with

their CV equal to 17.7 and 11.7, respectively. The length of the cell body is $27.1 \mu\text{m}$ (± 0.77 , 1.16, 20.3-35.9, 17) and the width is $27.1 \mu\text{m}$ (± 0.77 , 19.8-31.8, 17). Slightly less variable than either the length or width is the diameter of the AZM which is $18.8 \mu\text{m}$ (± 0.42 , 16.7-22.7, 17) which has a CV of 9.26. The peduncle attaches internally to the posterior end of the lorica.

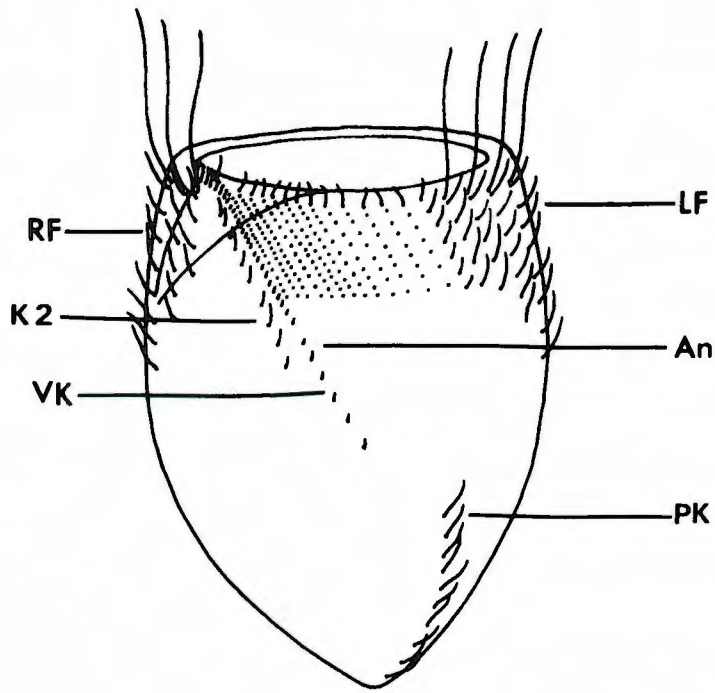
SOMATIC CILIATION. The somatic ciliation of C. cratera is very similar to that of T. baltica. There are 32 (30-33) kineties overall, with one VK, one DK, 8 (7-9) kineties in the RF, and 22 (19-23) kineties in the LF. The kinetal density index is 5.6/10 μm at the oral margin and 3.9/10 μm at the widest diameter of the cell body.

The VK begins just above the AM and extends posteriorly and to the left for about two-thirds of the cell length (Fig. 5f). The kinetids, all with single ciliferous kinetosomes, are tightly packed anteriorly but become more distant from each other posteriorly. The cilia of the anterior kinetosomes are longer (ca. 5 μm) than the posterior ones (ca. 3 μm).

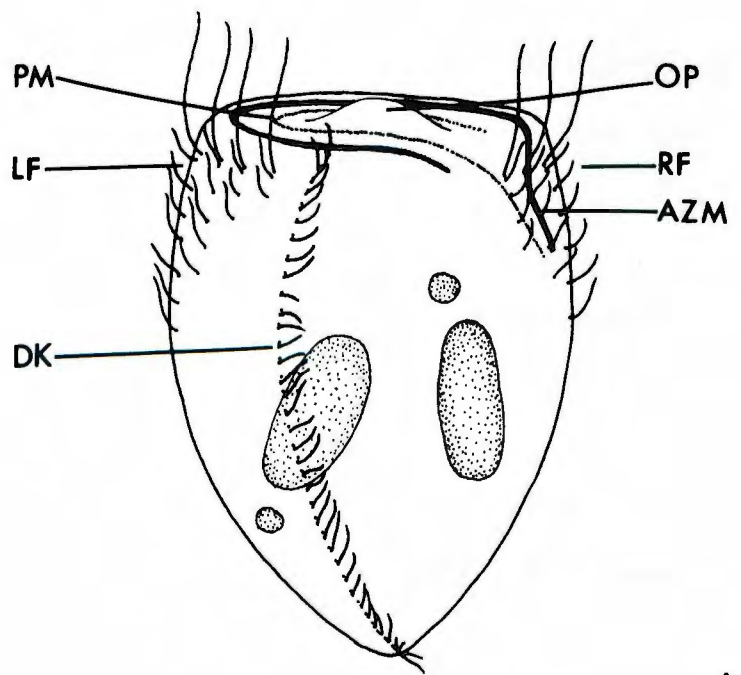
The first kinety of the RF is near and almost parallel to the VK and extends posteriorly for about one-half of the total length of the ciliate (Fig. 4a;5f). This kinety begins slightly posterior to the AM and the anterior most kinetosomes of the VK. The kinetids are composed of single ciliferous kinetosomes.

Figure 4

Drawings of ventral (a) and dorsal (b) aspects of Codonella cratera. RF, right ciliary field; LF, left ciliary field; VK, ventral kinety; PK, posterior kinety; K2, kinety number two; An, position of anlage; DK, dorsal kinety; AZM, adoral zone of membranelles; PM, paroral membrane; OP, oral plug. ca. 2,100X.



a

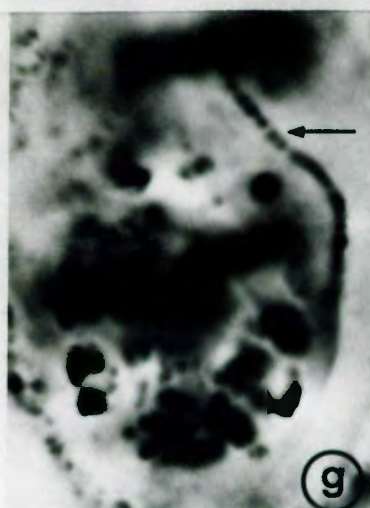
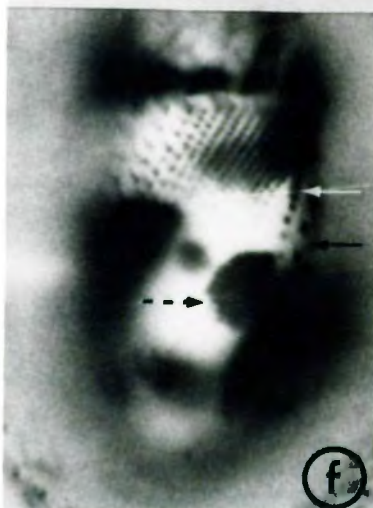
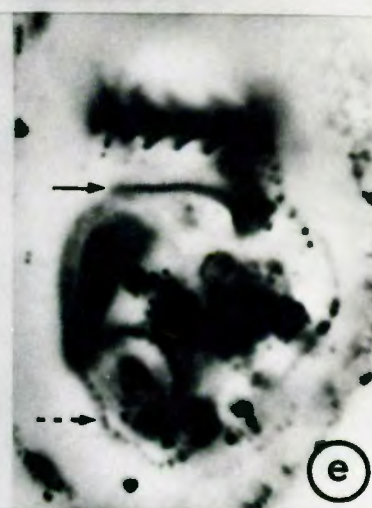
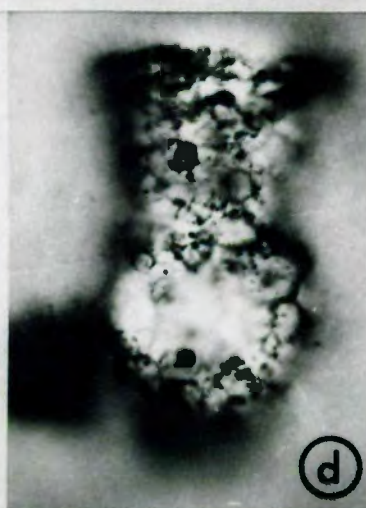
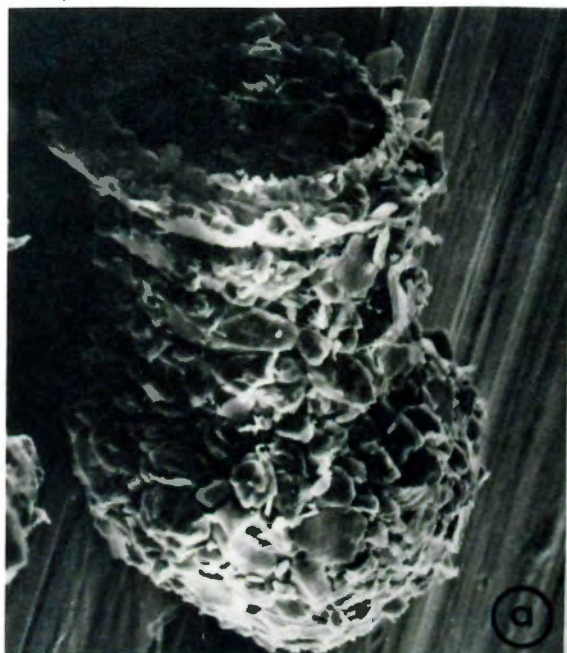


b

Figure 5

Photomicrographs of the lorica, somatic ciliation, and buccal area of Codonella cratera.

- a. Lorica. 1,500X, SEM. (Note oral brim and expanded bowl region.
- b. Oral view of lorica with specimen contracted inside. White arrow, long cilium originating from the anterior ciliary margin of the right ciliary field. 1,700X, SEM. (Note spiral ridges on the inside of lorica.)
- c. Outline of lorica and general body form. Black arrow, macronucleus. 890X.
- d. Lorica matrix outlining arenaceous particles. 905X.
- e. Right dorsal aspect of cell body. Solid black arrow, paroral membrane; broken arrow, posterior end of dorsal kinety. 1,470X.
- f. Ventral aspect of cell body. White arrow, ventral kinety; solid black arrow, K2; broken arrow, anlage. 1,860X. (Inverted)
- g. Dorsal aspect of cell body. Black arrow, anterior portion of dorsal kinety. 1,860X.
- h. Right dorsal aspect of cell body. White arrow, right ciliary field. 1,860X.



The remaining kineties of the RF (Fig. 4a,b;5h) extend about half way down the length of the ciliate and curve slightly toward the right side. The kinetids have single ciliferous kinetosomes except the most anterior one which has two kinetosomes, both ciliferous. The cilium of the anterior kinetosome of the double kinetid is ca. 12 μm long and the cilium of the posterior kinetosome of the same kinetid is ca. 3 μm long. The anterior cilium of these double kinetids are often seen touching the lorica (Fig. 5b). The cilia of the single kinetid of the RF are ca. 3 μm long.

The DK extends the entire length of the ciliate. It courses first to the ciliates left side or toward the first kineties of the LF, then continues posteriorly (Fig. 4b;5e,g (inverted)). The 29 (25-39) kinetids of the DK are double, with the posterior kinetosome ciliated. The length of the cilia are ca. 3 μm . The greatest distance between any pair of kineties is between the DK and the most dorsal portion of the RF (Fig. 4b). Between these kineties is a nonciliated dorsal area.

The kineties of the LF show a gradient of decreasing interkinetal distance from the first to the last kinety (Fig. 4a,b;5f). The first eight kineties are much more widely spaced than the remaining ones. The spacing of the kinetosomes within the kineties of the LF is greater in the posterior half. The kineties range from very short (two kinetids) to about half of the total length of the cell. The first couple kineties are very short, the next few kineties increase in length to almost half of the cell length, and the remaining

kineties decrease to approximately one-third of the cell length for the remaining kineties.

The kinetids of the LF have single ciliferous kinetosomes except the first eight kineties in which the most anterior kinetid has two kinetosomes, both ciliferous. The cilia from the anterior kinetosomes of the double kinetids are long ca. 12 μm . The posterior cilia of the double kinetids and the cilia of the remaining kinetids in these eight kineties are ca. 3 μm long. The cilia of the other kineties of the LF are shorter, ca. 1-2 μm long.

The PK is positioned in the posterior half of the cell below the area of transition from tight to loose packing of the kineties of the LF (Fig. 2c). The 11 (9-13) kinetids of the PK have single ciliferous kinetosomes.

BUCCAL MORPHOLOGY. The infundibulum extends posteriorly for about one-third of the cell length. It funnels to the right ending at the cytostome-cytopharynx complex which is located interior to the RF and dorsal to the VK. There is an oral plug on the ventral wall of the peristome but this is less developed than in T. baltica.

The AZM is arranged as in T. baltica with the proximal end of the first membranelle located in the infundibulum near and ventral to the cytostome-cytopharynx complex. The proximal ends of the next four membranelles are also in the infundibulum but are arranged consecutively more anterior on the ventral wall of the peristome. The proximal ends of the remaining

membranelles, excluding the last two, are located around the inner edge of the peristomial lip. The proximal ends of the last two membranelles descend slightly into the infundibulum. Sixteen membranelles were counted in the AZM based on lateral views, but because of a lack of oral views, this number is uncertain.

The PM (Fig. 5b;5e) begins at the dorsal side of the cytostome-cytopharynx complex and extends anteriorly and to the right along the peristomial wall. On the dorsal side of the cell, the PM is located posterior and parallel to the peristomial lip. The PM continues in this position around the left side, then crosses over the ventral side of the oral plug.

No tentaculoids, accessory combs, or capsules were observed in these specimens. There were however lorica forming granules which have a diameter of $0.92\ \mu\text{m}$ (± 0.022 , 0.83-1.1, 10). These granules were observed to aggregate around the opisthe oral primordium during division. They were not observed in non-dividing cells.

NUCLEAR STRUCTURE. In the nondividing forms, there are two macronuclei and two micronuclei (Fig. 4b,5c). The macronuclei are irregularly ovoid with an average length of $12.1\ \mu\text{m}$ (± 0.58 , 8.9-20.0, 22) and an average width of $6.64\ \mu\text{m}$ (± 0.19 , 4.73-8.40, 23). The nuclei are heavily stained and thus no internal structure could be seen. Reorganization bands in and condensation of the macronuclei have been observed in dividing forms. The micronuclei have an average diameter of $3.36\ \mu\text{m}$ (± 0.18 , 2.07-4.31, 12) and are found in close proximity to the macronuclei.

Tintinnopsis subacuta Jorgensen 1899

Lorica

The lorica (Fig. 7a) is composed of a long cylindrical tube with a posterior expansion or bowl which then closes to a pointed aboral end. Sand grains and diatom frustules are cemented to this lorica (Fig. f,d). The sand grains of the bowl region are larger than those on the cylindrical portion. There is no oral brim and the diameter of the oral opening is $35.5 \mu\text{m}$ (± 0.518 , 29.9-39.8, 23). The bowl obtains a maximum diameter of $42.0 \mu\text{m}$ (± 0.558 , 35.6-47.2, 23). The total length is $92.6 \mu\text{m}$ (± 1.27 , 78.9-102, 22) and the length of the cylindrical portion of the test, $45.2 \mu\text{m}$ (± 0.958 , 37.4-50.0, 14), is about one half the total length. The length is 2.59 times longer than the oral diameter.

Cytology

The shape of the contracted body is most often cylindrical (Fig. 7a;c;8a,b) but in cases of extreme contraction the posterior end is rounded (Fig. 8c). The length of the cell body is $48.0 \mu\text{m}$ (± 1.34 , 35.3-58.8, 22) and the width is $26.7 \mu\text{m}$ (± 0.711 , 20.9-31.8, 22). Due to the contractility of these organisms the length and width are variable with CV values of 13.1 and 12.5, respectively. A less variable measurement is the diameter of the AZM which is $20.7 \mu\text{m}$ (± 0.380 , 16.9-23.5, 22) and has a CV value of 8.63. The peduncle was contracted into the cell upon fixation and thus the point of attachment is not given.

SOMATIC CILIATION. There are 38 (35-40) kineties, with one VK, one DK, 11 (10-13) kineties in the RF and 24 (22-27) kineties in the LF. The kinetal density index is 5.42/10 μ m at the oral margin and 3.77/10 μ m at the greatest diameter of the cell. A PK also exist posterior to the LF.

The VK begins at the peristomial lip, courses down the body of the cell from right to left, and covers approximately two-thirds of its length (Fig. 6a;7c;8c). Originating from a length of the VK, ca. 6-12 μ m from its anterior end is a group of coalesced cilia of extreme length, 71.8 μ m (\pm 8.52, 29.3-99.7, 8) termed the giant ciliary tuft (Fig. 6a;7c,d). The kinetids that give rise to these cilia are closely packed and could not be resolved or counted. This tuft of cilia becomes progressively narrower and can split into fine groups distally (Fig. 7d). In the living organism, this tuft can be seen to move in an undulatory fashion, and is often in contact with the exterior surface of the lorica.

The anlage arises about half way down the cell length and just to the left of the VK (Fig. 6a;8c). It begins as a cluster of unorganized kinetosomes at the cell cortex.

The second kinety (K2), as in T. baltica and C. cratera, lies near and almost parallel to the VK. K2 begins posterior to the AM and the anterior most kinetosomes of the VK, and continues posteriorly ending just anterior to the end of the VK (Fig. 6a;7c). The kinetids are more closely packed at the anterior end than at the posterior end of this kinety. All the kinetids have single ciliferous kinetosomes.

Figure 6

Drawings of ventral (a) and dorsal (b) aspects of Tintinnopsis subacuta. GT, giant ciliary tuft; RF, right ciliary field; LF, left ciliary field; VK, ventral kinety; PK, posterior kinety; K2, kinety number two; An, position of anlage; DK, dorsal kinety; AZM, adoral zone of membranelles; PM, paroral membrane; OP, oral plug. ca. 1,700X.

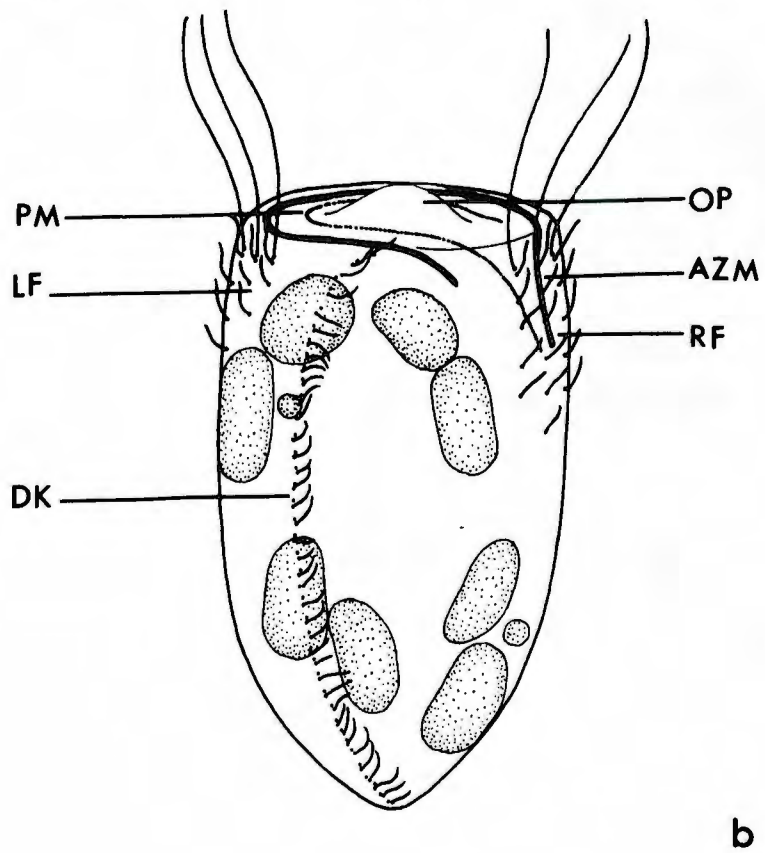
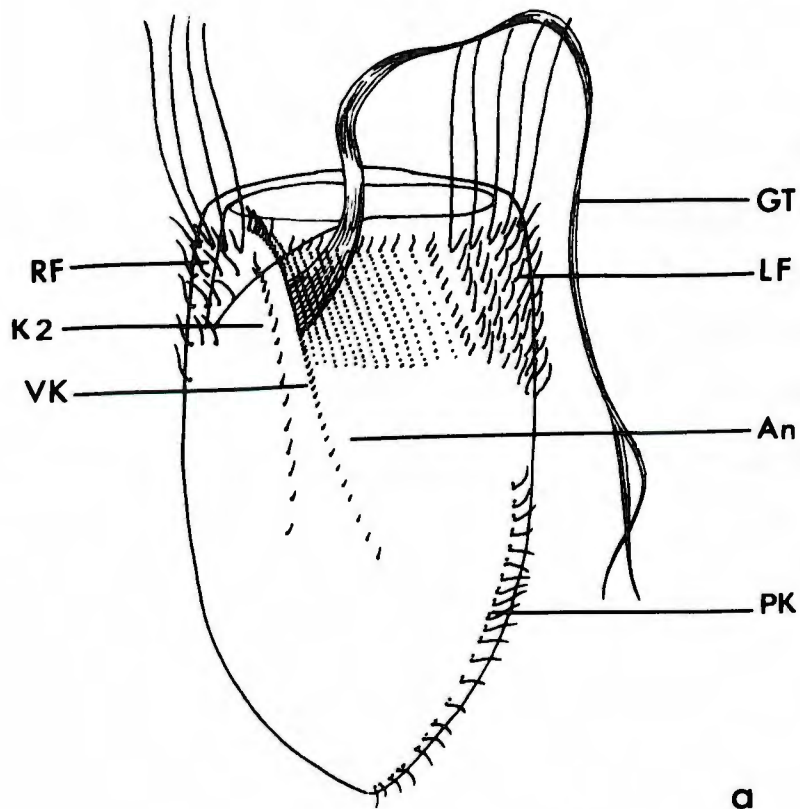


Figure 7

Photomicrographs of the lorica, somatic ciliation, and buccal area of Tintinnopsis subacuta.

- a. Outline of lorica and general body form. Black arrow, long cilium originating from the anterior ciliary margin of the right ciliary field. 1,030X. (Note the proximal ends of the membranelles ascending the peristomial wall.)
- b. Lorica matrix with diatom frustules and arenaceous particles attached. White arrow, diatom frustule. 1,500X.
- c. Ventral aspect of cell body and origin of the giant ciliary tuft. Solid black arrow, K2; broken arrow, ventral kinety; white arrow, giant ciliary tuft originating from the ventral kinety. 2,280X. (Note paired macronuclei.)
- d. Distal end of the giant ciliary tuft (black arrows). 1,620X. (Note split at terminal end of tuft and diatom frustule attached to posterior surface of the lorica.)

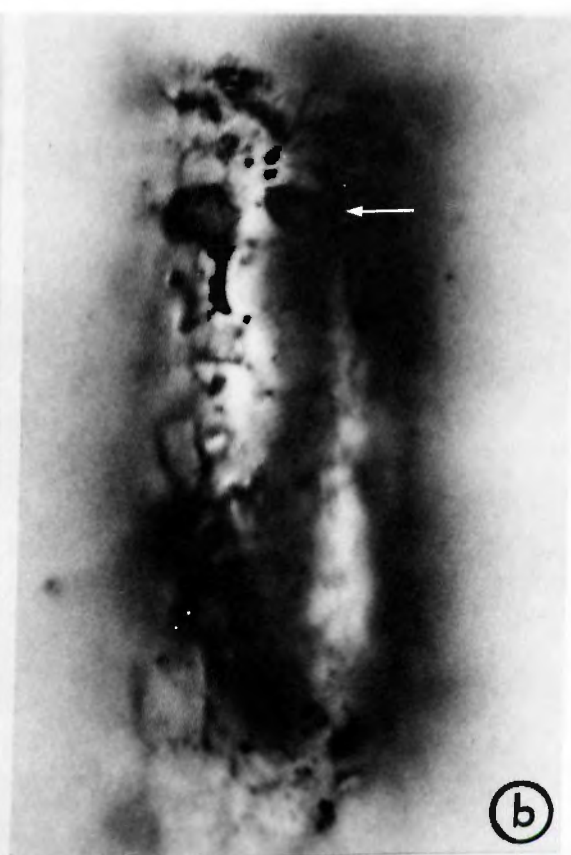
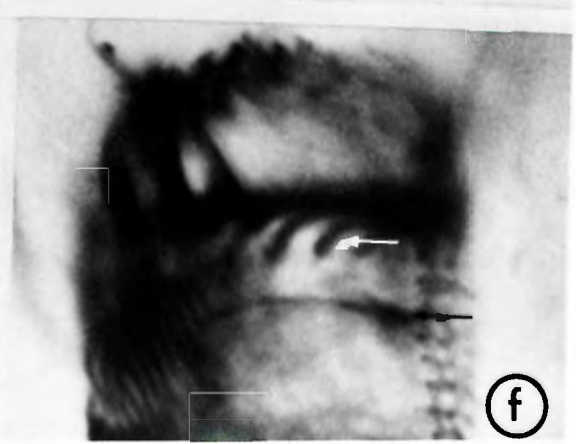
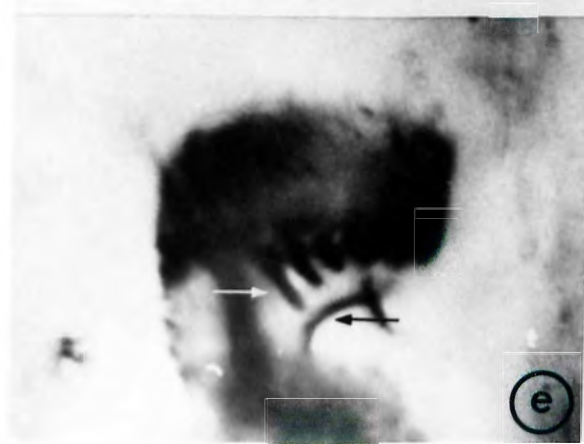
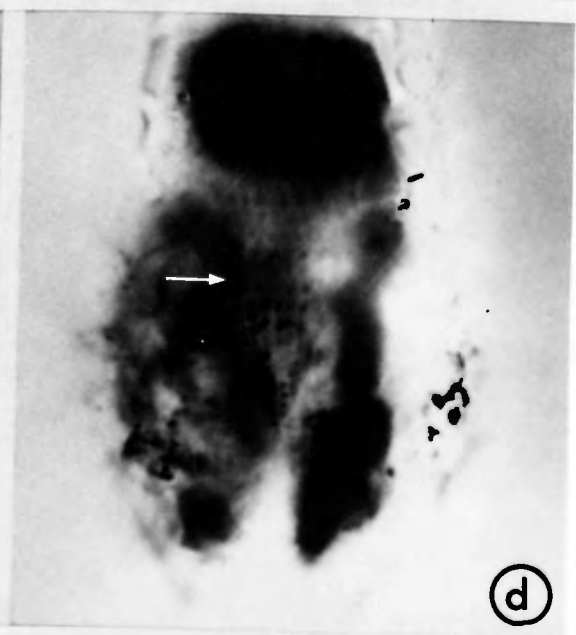
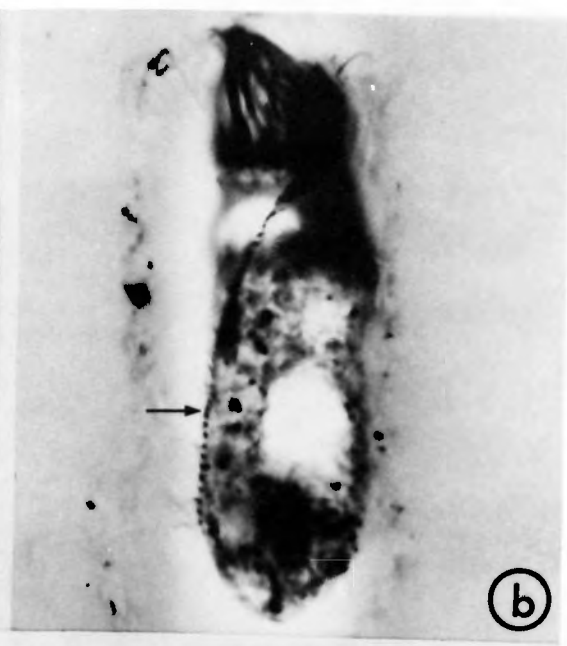
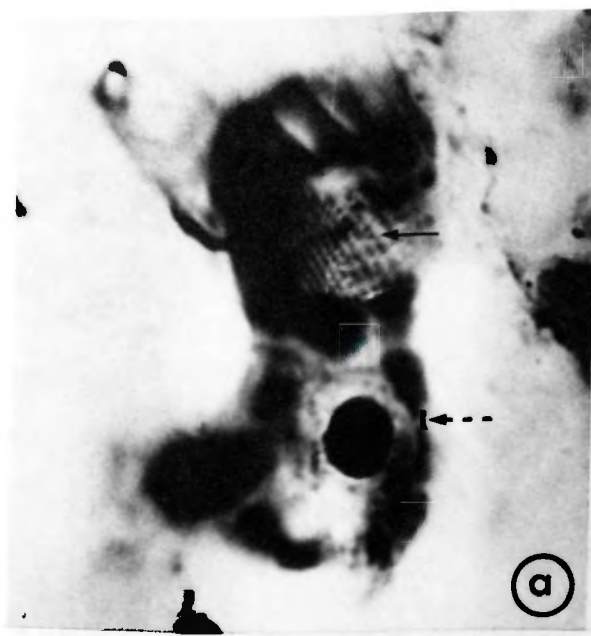


Figure 8

Photomicrographs of somatic ciliation and buccal area of Tintinnopsis subacuta.

- a. Left ventral aspect of the cell body. Solid black arrow, left field in area of transition from loose to tight packing of kineties; broken arrow, posterior kinety. 1,630X.
- b. Dorsal aspect of cell body. Black arrow, dorsal kinety. 1,070X.
- c. Ventral aspect of cell body of dividing form. White arrow, anlage. 1,500X. (Note ventral kinety to the right of the anlage and the left ciliary field above the anlage.)
- d. Right side of cell body of a dividing form. White arrow, right ciliary field. 1,310X. (Note division furrow at posterior end of field.)
- e. Lateral view of the bases of the membranelles. (inverted) White arrow, proximal end of the last membranelle of the AZM; black arrow, paroral membrane. 1,890X. (Inverted)
- f. Left ventral aspect of the bases of the membranelles. White arrow, proximal end of membranelle along inner edge of peristomial lip; black arrow, paroral membrane. 1,890X.



The remaining kineties of the RF are shorter in length than K2 and exist as an intact field to the right of K2 (Fig. 6a,b;8d). The kineties and kinetids within the kineties are evenly spaced. The kinetids which lie on the AM are composed of two kinetosomes, both ciliiferous. The cilium of the anterior most kinetosome of each double kinetid is long (up to 34 μm) and is fairly stiff (Fig. 7a). The cilium on the posterior kinetosome of these kinetids was short (2-3 μm) (Fig. 6a,b;7a).

The DK, consisting of 42 (28-58) kinetids, extends the entire length of the cell body from anterior to the AM to the posterior end. It angles from the right anterior side to the left posterior for the first half of the body length, and continues directly posterior for the last half of the cell length. The kinetids have double kinetosomes, the posterior one ciliated. The cilia are ca. 3-5 μm long.

The 24 (22-27) kineties of the LF exhibit a gradient from left to right of loose to tight packing of kineties and of kinetosomes within kineties. The first 8-10 kineties of this field are widely spaced and have two kinetosomes per kinetid in the anterior most kinetid of each kinety. The anterior kinetosomes of these kinetids have the very long stiff cilia like those of the RF. The remaining kinetids of these 8-10 kineties are single and have cilia ca. 2-3 μm long. The other kineties of the LF are more tightly packed and all kinetids are single. The cilia of these kineties are less than 3 μm in length; the shortest cilia are found in the right most kineties. The first few kineties of the LF are short

(1-4 kinetids), the next few kineties are the longest in this field reaching about one-third of the total length, and the remaining kineties are about one-fourth of the cell length.

The PK (Fig. 6a;8a) consists of 22 (18-25) kinetids and the anterior most kinetids lie posterior to the area of transition between the tight and loose packing of the kineties of the LF. The kinetids possess two kinetosomes, the posterior one ciliferous.

BUCCAL MORPHOLOGY. The buccal morphology is very similar to T. baltica and C. cratera. The infundibulum descends posteriorly about one-third of the cell length from the peristomial lip. It funnels to the right ending at the cytostome-cytopharynx complex which is located just interior to the RF and dorsal to the VK. There is an oral plug on the ventral wall of the peristome.

The AZM is arranged with the proximal end of the first membranelle located in the infundibulum near and ventral to the cytostome-cytopharynx complex. The proximal ends of the next five membranelles are also in the infundibulum but are arranged consecutively more anterior on the ventral wall of the peristome (Fig. 7a). The proximal ends of the other membranelles excluding the last four are located around the inner edge of the peristomial lip (Fig. 8f). The proximal ends of the last four membranelles descend slightly into the infundibulum (Fig. 8e). The distal end of the first membranelle ends on the inside of the peristomial lip. The distal ends of the other membranelles cross over the peristomial lip and end on its exterior margin.

As there were no specimens viewed from the oral end, the exact number of membranelles could not be ascertained. The number of membranelles based on lateral views ranged between 17 and 20.

The PM begins at the dorsal side of the cytostome-cytopharynx complex and extends anteriorly and to the right along the peristomial wall (Fig. 8e(inverted)). On the dorsal side of the cell, the PM is located posterior and parallel to the peristomial lip. The PM continues in this position around the left side, then crosses over the ventral side of the oral plug (Fig. 8f).

Tentaculoids, which contained many capsules, were observed in only one specimen and were 10-12 μm long and 2 μm wide. No other capsules or lorica forming granules were observed.

NUCLEAR STRUCTURE. In most specimens there are eight macronuclei arranged in four pairs. In three of the twenty-two specimens there were three pairs of macronuclei. The macronuclei are 8.20 μm (± 0.699 , 5.74-12.3, 10) long and 4.69 μm (± 0.215 , 3.90-5.65, 10) wide. The micronuclei were closely associated with the macronuclei and were therefore difficult to observe and count. There was at least one micronuclei per pair of macronuclei and possibly one for each macronucleus. The micronuclei had a diameter of 1.85 μm (± 0.072 , 1.47-2.16, 10).

Stenosemella steini Jorgensen 1924

Lorica

The lorica is cup-shaped and is composed of agglomerated sand grains cemented to the lorica matrix (Fig. 10a,b,c,e). The outline of the sand grains (Fig. 10b,g,h) can be seen where the proteinaceous matrix of the lorica has stained with protargol. At the oral end of the lorica is a short hyaline collar, 24.8 μm (± 1.48 , 13.8-19.2, 9) across. In many specimens the oral opening, encircled by this collar, is filled with many long thin refractile structures which appears to act as a plug for this opening. To either side of the collar the lorica increases in breadth to 40.0 μm (± 2.09 , 28.4-54.0, 16). This increase in breadth, about 15 μm , is due mainly to an increase in thickness of the lorica wall to form shoulder like projections (Fig. 10e). The lorica obtains its maximum width of 48.7 μm (± 1.22 , 42.3-59.3, 21) near the middle of its length. The total length of the lorica is 52.9 μm (± 1.62 , 47.2-66.9, 16) which is 2.13 times larger than the oral diameter of the collar. The posterior end of the bowl is bluntly pointed (Fig. 10a,c).

Cytology

Specimens were caught in various stages of contraction. Some were extended beyond the lorica and were cylindrical in their anterior region (Fig. 10a,c,e), while many were contracted into their lorica and were almost spherical (Fig. 10f-h). Due to the contractility of these specimens the length,

30.3 μm (± 1.48 , 23.9-42.4, 21), and the width, 33.4 μm (± 1.84 , 24.8-65.4, 24) are quite variable with CV values of 21 and 27%, respectively. In contrast to T. baltica, C. cratera and T. subacuta, the diameter of the AZM, 25.9 μm (± 1.79 , 18.8-33.0, 11), is just as variable as the length and width. The measurements of the AZM have a CV equal to 23%. The peduncle of this species was contracted into the cell body and therefore its point of attachment is not given.

SOMATIC CILIATION. S. steini has 40 (34-42) kineties total, with one VK and one DK, and 8 (7-9) kineties in the RF and 29 (22-32) in the LF. The kinetal density index is 4.9/10 μm at the oral margin and 3.8/10 μm at the greatest diameter of the cell body.

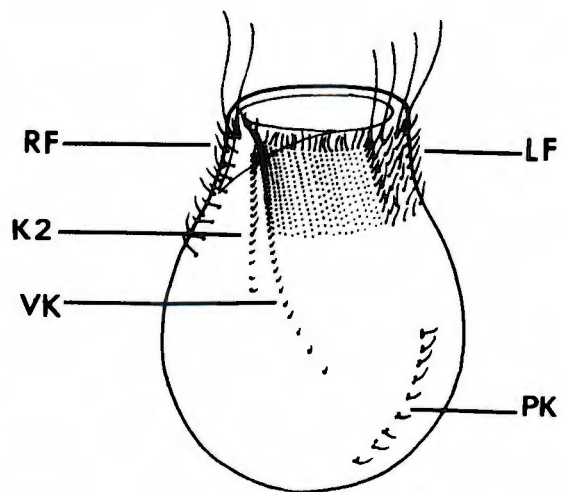
The VK begins anterior to the AM and extends posteriorly and to the left for about two-thirds of the cell length (Fig. 9a; 10e (inverted)). The kinetids, all with single ciliferous kinetosomes, are tightly packed anteriorly but become more distant from each other posteriorly. The cilia of the VK are ca. 3-4 μm long.

The first kinety of the RF, K2, is nearly parallel to the VK and extends about one half of the total length down from the oral margin (Fig. 5c, 8e (inverted)). This kinety begins slightly posterior to the other kineties. The kinetids are composed of single ciliated kinetosomes.

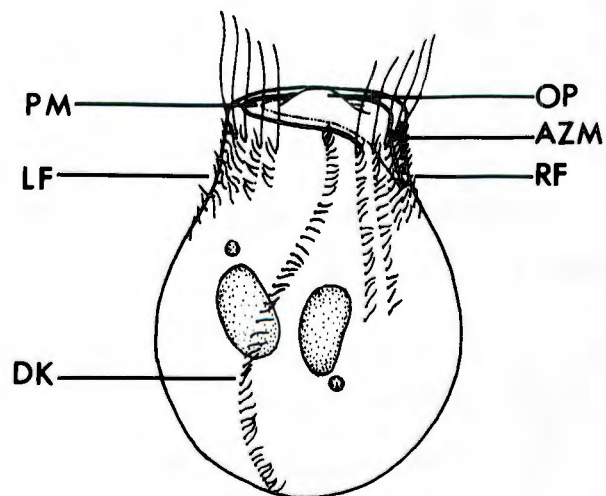
The remaining kineties of the RF begin at the AM, are evenly spaced with regularly spaced kinetosomes, and course posteriorly for one-third to over one-half of the cell length. The last two kineties are the longest and reach over one-half

Figure 9

Drawings of ventral (a) and dorsal (b) aspects of Stenosemella steini. RF, right ciliary field; LF, left ciliary field, VK, ventral kinety; PK, posterior kinety; K2, kinety number two; DK, dorsal kinety; AZM, adoral zone of membranelles; PM, paroral membrane; OP oral plug. ca. 1,300X.



a

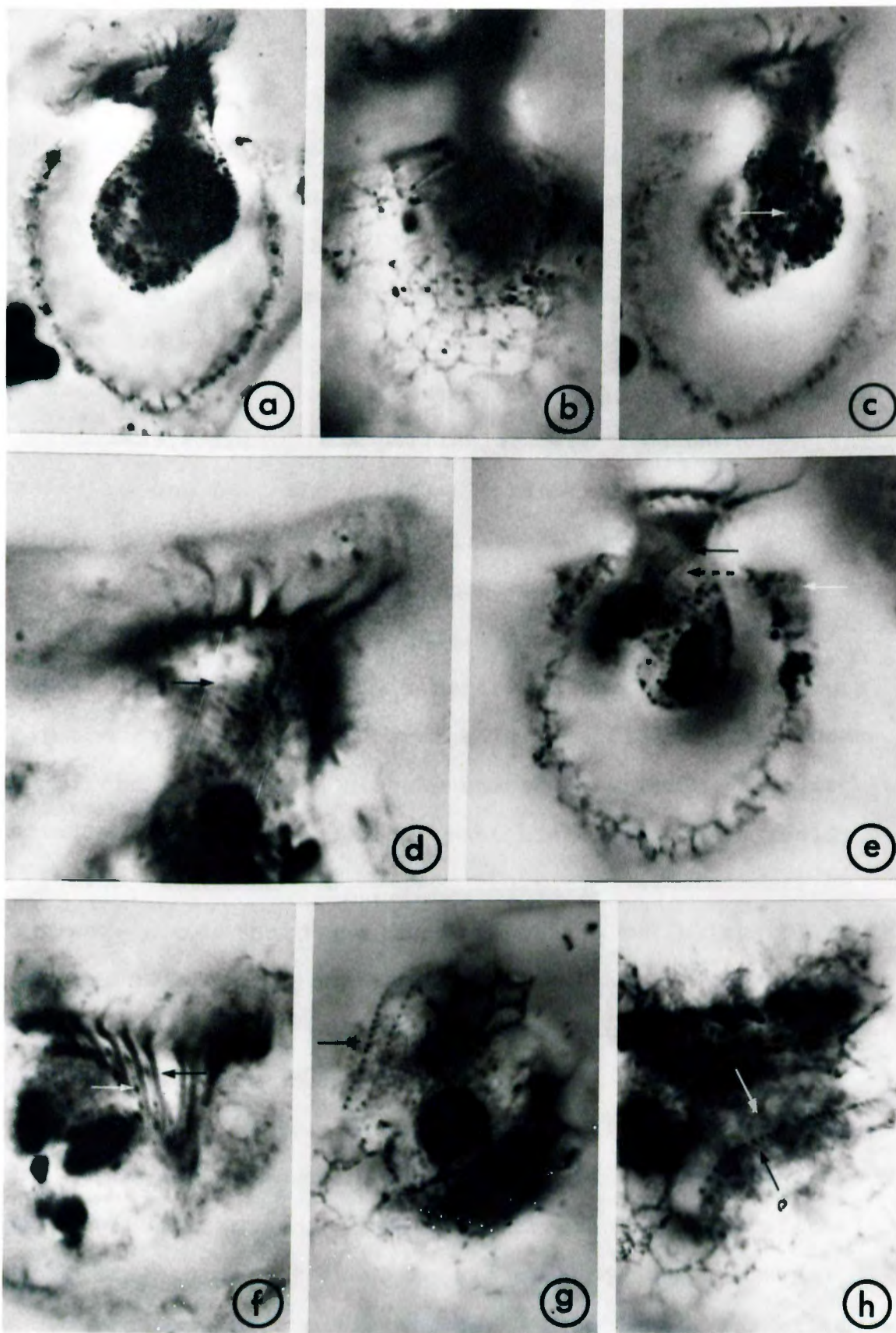


b

Figure 10

Photomicrographs of the lorica, somatic ciliation, and buccal area of Stenosemella steini.

- a. Outline of lorica and general body form. 905X.
- b. Lorica matrix outlining arenaceous particles. 1,260X.
- c. Lorica forming granules in cytoplasm near anlage. White arrow, lorica forming granules; black arrow, anlage. 972X.
- d. Left ventral aspect of cell body. Black arrow, left field in area of transition from loose to tight packing of kineties. 1,920X. (Inverted)
- e. Ventral aspect of cell body (inverted). Solid black arrow, ventral kinety; broken arrow, K2; white arrow, shoulder-like projections of lorica. 1,130X. (Inverted)
- f. Right ventral view of membranellar bases. Black arrow, proximal end of the third membranelle; white arrow, granules of accessory comb. 1,460X. (Inverted).
- g. Right dorsal aspect of cell body. Black arrow, posterior end of the last two kineties of the right field. 1,390X.
- h. Dorsal aspect of cell body. Black arrow, dorsal kinety; white arrow, dorsal furrow adjacent to the dorsal kinety. 1,280X.



of the distance to the posterior end (Fig. 9a; 10g).

The kinetids have single ciliferous kinetosomes except the most anterior one which has two kinetosomes, both ciliated. The cilium of the anterior kinetosome is ca. 12 μm long and the posterior cilium is ca. 3 μm long. The other kinetids have cilia ca. 3-4 μm long.

The DK extends the entire length of the ciliate (Fig. 9d). In contracted specimens the DK courses across the dorsal side from right anterior to left posterior in the direction of the LF (Fig. 10h). There is a pellicular groove to the right and parallel to the DK. The 42 (22-62) kinetids of the DK have single kinetosomes each with a cilium 2-3 μm long.

The distance between the kineties of the LF decreases from the first to the last kinety (Fig. 9a,b;10d (inverted),e (inverted)). The first 8-10 kineties of the LF are much more widely spaced than the others of this same field. The kinetosomes of the LF are more closely spaced anteriorly; this is especially evident in the right most kineties of this field. The kineties range in length from short (3-4 kinetosomes) to long (between one-third and one-half of the cells length). The first few kineties are short, the next two to the right are the longest in the LF, and the remaining kineties to the right are somewhat shorter than the long ones.

The kinetids of the LF have single ciliferous kinetosomes except the anterior most kinetids of the first eight kineties which have two kinetosomes, both ciliated. The cilia of the anterior kinetosomes of these double kinetids are ca. 8 μm long and the posterior cilia are ca. 2-3 μm long. The cilia

of the other kinetids of the LF are ca. 1-3 μm long, the shortest of these cilia are located in the right most kineties.

The PK is positioned in the posterior half of the cell below the area of transition from tight to loose packing of the kineties of the LF (Fig. 9a). The 9 (9-12) kinetids of the PK are double with cilia ca. 3 μm long arising only from the posterior kinetosome.

BUCCAL MORPHOLOGY. The infundibulum extends posteriorly from the peristomial lip to between one-third and one-half of the cell length. The depth of the infundibulum is a greater proportion of the cell length in highly contracted cells. The infundibulum funnels to the right and ends at the cytostome-cytopharynx complex which is located interior to the RF. There is a slight oral plug on the ventral wall of the peristome.

The AZM is arranged as in the model with the proximal end of the first membranelle located in the infundibulum near the cytostome-cytopharynx complex. The proximal ends of the next five or six membranelles are also in the infundibulum, and are arranged consecutively more anterior on the ventral wall of the peristome (Fig. 10f). The proximal ends of the remaining membranelles, excluding the last two, are located around the inner edge of the peristomial lip. The proximal ends of the last two membranelles descend slightly into the infundibulum. The distal end of the first membranelle is located on the inner edge of the peristomial lip. The other membranelles cross the peristomial lip and terminate distally on the outer margin of the peristomial lip. The AZM, observed

from an oral view in two specimens, consisted of 20 membranelles.

S. steini has triangular shaped tentaculoids without capsules located on the peristomial lip just interior to each membranelle as it crosses the lip (Fig. 1c). The tentaculoids are ca. 4 μm long and ca. 2 μm wide at its base. Beneath the tentaculoids are the argentophilic granules of the accessory combs. The granules of the accessory combs lie to the left of each membranelle and are distributed in two ways. When associated with the first 6-7 membranelles, the granules begin at the proximal end of each membranelle and end at the interior edge of the peristomial lip (Fig. 10f(inverted)). The granules associated with the other membranelles are concentrated at the proximal ends of these membranelles.

Lorica forming granules are observed in dividing cells and are associated with the developing oral primordium (Fig. 10c). The diameter of these granules is 0.83 μm (± 0.027 , 0.69-1.0, 10).

NUCLEAR STRUCTURE. In nondividing cells there are two macronuclei and two micronuclei (Fig. 9d). The macronuclei are irregularly ovoid with an average length of 10.8 μm (± 0.85 , 6.20-14.9, 10) and an average width of 5.93 μm (± 0.373 , 4.36-7.62, 10). Reorganization bands occur in the macronuclei of dividing cells. The micronuclei have an average diameter of 2.2 μm (± 0.18 , 1.2-3.0, 10) and are usually found in close proximity to the macronuclei.

Climacocylis scalaroides Kofoid and Campbell 1929

Lorica

The lorica matrix of C. scalaroides is arranged into many small polygons and does not contain foreign particles. The anterior opening of the lorica is $33.0\text{ }\mu\text{m}$ (± 0.693 , 29.1-35.5, 8) across. A prominent spiral ridge begins at the oral lip of the lorica and continues posterior for about one-half the length of the lorica. This ridge is expressed both internally and externally, and circles the lorica 3-7 times (Fig. 12a,b). The posterior end of the lorica is irregular and is often distorted in stained specimens (Fig. 12a). The total length of the lorica is $112\text{ }\mu\text{m}$ (± 0.739 , 77.8-136, 8) which is 3.40 times the length of the oral diameter.

Cytology

The specimens were observed in a contracted state and were cylindrical anteriorly and conical posteriorly (Fig. 12g,i). The length and width of the body are $39.4\text{ }\mu\text{m}$ (± 2.27 , 31.6-45.1, 7) and $21.1\text{ }\mu\text{m}$ (± 0.802 , 19.6-23.5, 7), respectively. The diameter of the AZM is $20.8\text{ }\mu\text{m}$ (± 0.488 , 19.2-22.4, 7) and has a CV of 5.75%. The variability of the measurements of the AZM, as expressed by the CV, is much lower than the values for the length and width, 15.2 and 10.0, respectively. The variability of the length and width is a result of the contractility of the cell. The peduncle of this species is attached to the side of the

lorica near the posterior end (Fig. 12i).

SOMATIC CILIATION. C. scalaroides has 29 (28-30) kineties overall, with one VK, one DK, 7 kineties in the RF, and 20 (19-21) in the LF. The kinetal index is $4.4/10\mu\text{m}$ at the oral margin and $4.37/10\mu\text{m}$ at the greatest diameter of the cell body.

The anterior end of the VK is peculiar in that it extends laterally above the AM of the RF (Fig. 11a, 12d). Posteriorly, the VK reaches between one-third and one-half of the cell length. The kinetids, all with single ciliferous kinetosomes, are more closely spaced anteriorly than posteriorly. The cilia of the VK are ca. $2-3\mu\text{m}$ long.

The first kinety of the RF, K2, is nearly parallel to the VK and extends about one-half of the total length down from the AM (Fig. 11a, 12d). This kinety begins slightly posterior to the other kineties. The kinetids are composed of single ciliated kinetosomes.

The remaining kineties of the RF begin just below the anterior portion of the VK, are evenly spaced with regularly spaced kinetosomes, and course posteriorly for about one-fourth of the cell length. The infraciliature, or at least some portion of the infraciliature, was revealed in these protargol stained specimens. The infraciliature of the RF consists of two lateral fibers to the left of the kinety and one longitudinal one just to the right of the kinetosomes. The lateral fibers are ca. $2\mu\text{m}$ in length and are at a 45 degree angle to the kinety, one directed

Figure 11

Drawings of ventral (a) and dorsal (b) aspects of Climacocylis scalaroides. My, myoneme; RF, right ciliary field; LF, left ciliary field; VK, ventral kinety; PK, posterior kinety; K2, kinety number two; An, position of anlage; DK, dorsal kinety; AZM, adoral zone of membranelles; PM, paroral membrane; OP, oral plug. ca. 1,600X

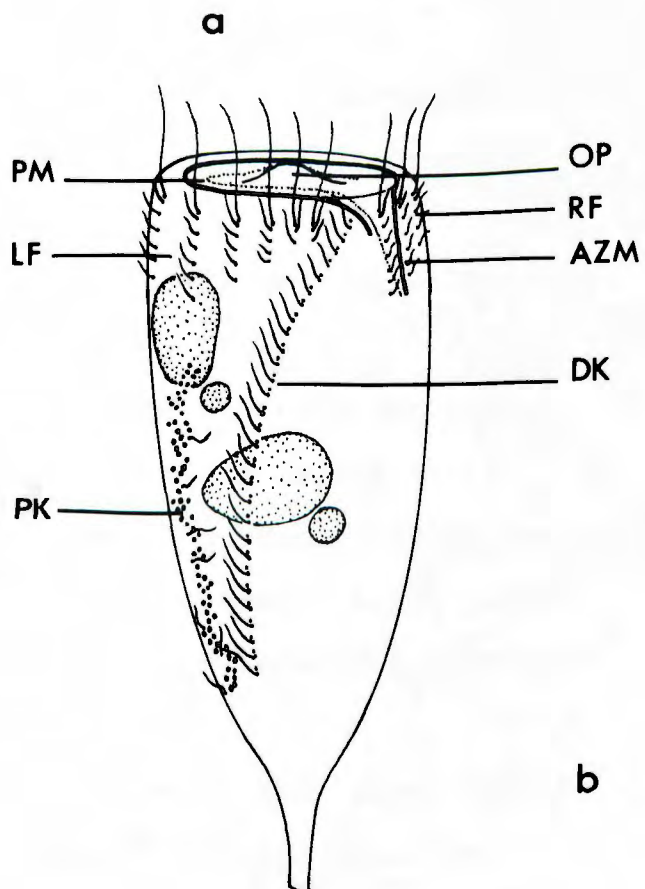
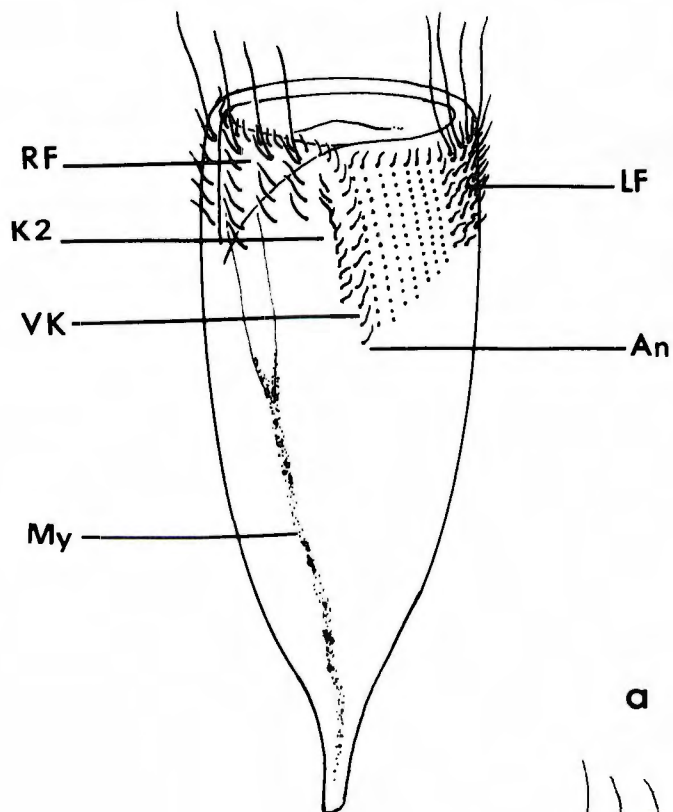
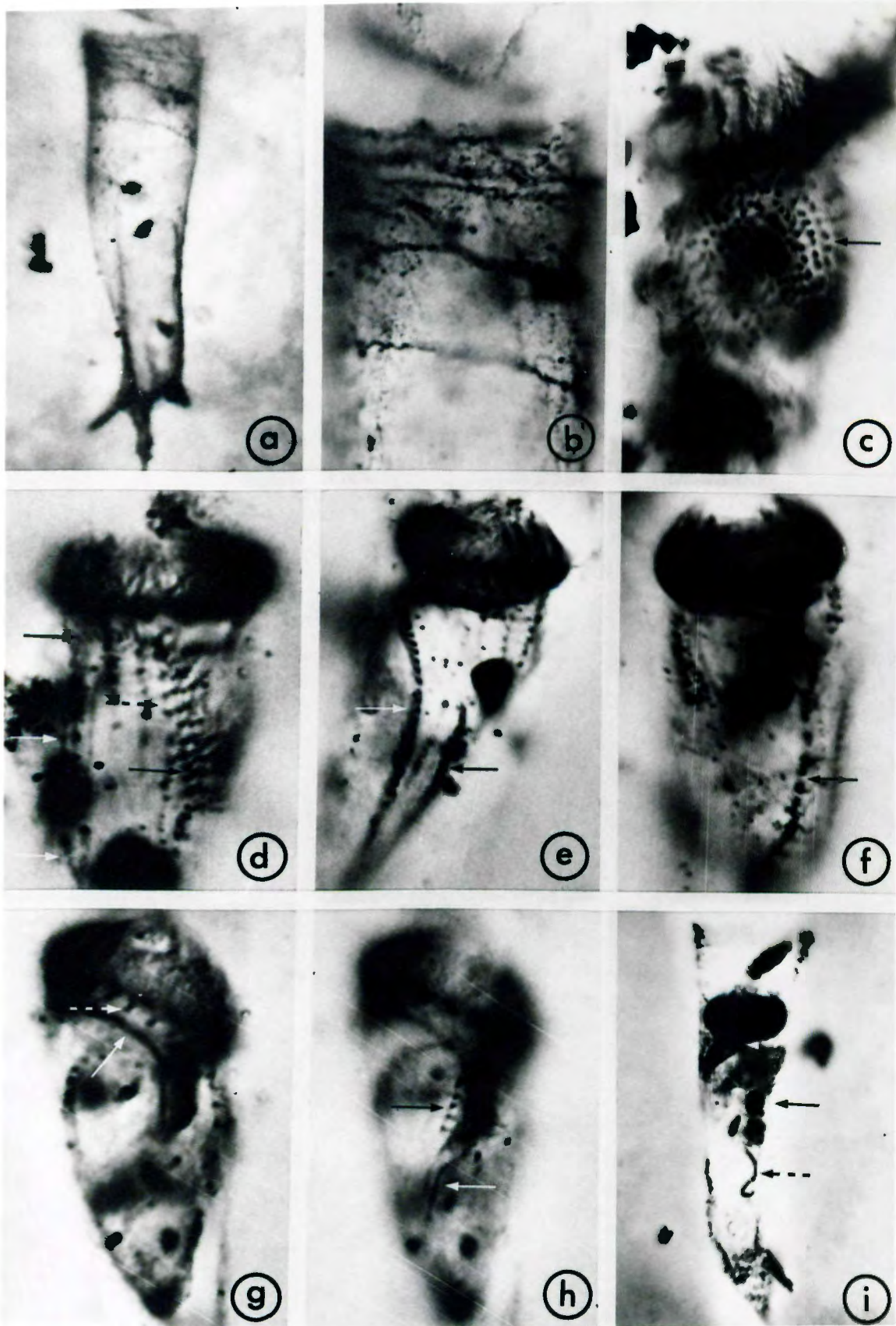


Figure 12

Photomicrographs of the lorica, somatic ciliation, and buccal area of Climacocylis scalaroides.

- a. Lorica. 639X. (Note the spiral ridge anteriorly and the irregular posterior end.)
- b. Anterior end of lorica with spiral ridge. 972X.
- c. Right ventral aspect of the cell body. Black arrow, left ciliary field.
- d. Ventral aspect of cell body. Solid black arrows, ventral kinety; broken black arrow, K2; white arrows, granular and fibrous structure, possibly myoneme. 1,860X.
- e. Left dorsal aspect of cell body. White arrow, dorsal kinety; black arrow, posterior kinety. 1,340X. (Inverted)
- f. Left ventral aspect of cell body. Black arrow, posterior kinety. 1,380X.
- g. Right dorsal aspect of the membranellar bases. White arrow, paroral membrane; broken arrow, proximal end of membranellar base. 1,470X.
- h. Right dorsal aspect of cell body. Black arrow, dorsal field; white arrow, fibers of cytopharynx. 1,490X.
- i. Outline of lorica and general body form. Solid black arrow, macronucleus and micronucleus; broken arrow, penduncle; white arrow, proximal ends of first several membranelles. 635X.



anteriorly and one posteriorly. The longitudinal fiber is directed anteriorly and appears continuous from kinetid to kinetid. The kinetids have single ciliferous kinetosomes except the most anterior kinetid which has two kinetosomes, both ciliferous. The cilium of the anterior kinetosome of the anterior kinetid is ca. 10 μm long and the posterior cilium is ca. 3 μm long.

The dorsal kinety [Fig. 11b, 12e (inverted)], composed of 30 (25-31) kinetids, courses across the dorsal side from the right anterior to the left posterior for the anterior third of the cell length. It then continues directly posterior for the remaining length of the cell. The kinetids have double kinetosomes and the posterior kinetosome is ciliated. The infraciliature of this kinety is the same as in the RF except that the anteriorly directed lateral fiber is twice as long as the posteriorly directed lateral fiber.

The distance between kineties of the LF decreased from the first to the last kinety [Fig. 11a,b; 12c,d,e (inverted)]. The kinetids of these kineties are more closely spaced anteriorly than posteriorly. This is especially evident in the right most kineties of this field. The first eight to ten kineties are more widely spaced than the others in this field. The kineties range in length from short (2-3 kinetosomes) to about one-third of the cell length. The first few kineties are the shortest. The kinetids of the LF have single ciliferous kinetosomes except the first

eight kineties in which the most anterior kinetid of each has two kinetosomes, both ciliated. The cilia of these kinetids are the same length as in the doublets of the RF, the anterior one ca. 10 μm and the posterior one ca. 3 μm . The cilia of the other kinetids of the LF are 2-4 μm long, the shortest ones located in the right most kineties. In the kineties with the anterior doublets, the infraciliature was like that of the RF. In the remaining kineties of the LF, the two lateral fibers were not present.

The PK [Fig. 11b, 12e (inverted), f] is positioned in the posterior half of the cell posterior to the beginning of the LF and near the DK. The 10 (6-16) kinetids of the PK are single with cilia ca. 4 μm long. Associated with the PK are numerous argentophilic granules which are larger in diameter than kinetosomes.

BUCCAL MORPHOLOGY. The infundibulum funnels to the right for about one-half the cell length ending at the cytostome-cytopharynx complex. The cytostome-cytopharynx complex is located interior to the RF (Fig. 12g,h). There is a small oral plug on the ventral wall of the peristome.

The AZM is arranged as in the model with the proximal end of the first membranelle located in the infundibulum near the cytostome-cytopharynx complex. The proximal ends of the next three to four are also in the infundibulum but are arranged consecutively more anterior on the ventral wall of the peristome (Fig. 12i). The proximal ends of the remaining membranelles, excluding the last two to three, are located

around the inner edge of the peristomial lip. The proximal ends of the last two to three membranelles descend into the infundibulum (Fig. 12g). The distal end of the first membranelle is located on the inner edge of the peristomial lip. The other membranelles cross the peristomial lip and terminate distally on the outer margin of the peristomial lip. The number of membranelles is estimated from lateral views of two specimens to be eighteen or nineteen. Until this species is viewed from the oral end, the exact number of membranelles remains a question. No tentaculoids or accessory combs were observed in these specimens.

NUCLEAR STRUCTURE. There are two macronuclei and two micronuclei in each cell (Fig. 11b). The macronuclei are irregularly ovoid with an average length of $7.14\text{ }\mu\text{m}$ (± 0.267 , 5.09–8.86, 14) and an average width of $4.75\text{ }\mu\text{m}$ (± 0.249 , 3.03–7.12, 14). The micronuclei have an average diameter of $1.7\text{ }\mu\text{m}$ (± 0.062 , 1.4–1.9, 11) and are usually found in close proximity to the macronuclei.

Eutintinnus pectinis (Kofoid 1905) Kofoid and Campbell 1939

Lorica

The lorica is hyaline, open at both ends, and has 21-24 small (3-4 μm) teeth on the oral margin (Fig. 14a). The oral diameter, 20.2 μm (± 0.616 , 15.9-24.3, 19) across, is larger than the diameter of the aboral opening, 12.5 μm (± 0.54 , 9.41-16.7, 16). Just anterior to the aboral opening is a slight constriction 11.2 μm (± 0.62 , 7.11-14.7, 13) across. The length of the lorica is 125 μm (± 2.70 , 109-150, 17) which is 6.19 times larger than the oral diameter.

Cytology

The cell body of E. pectinis is long, 57.4 μm (± 1.89 , 43.3-70.0, 19), and slender, 13.9 μm (± 0.24 , 11.8-16.3, 22) maximum width. The diameter of the AZM is 12.5 μm (± 0.16 , 11.2-14.2, 22) and the variability of this measurement is low, CV equal to 3.56. The peduncle was contracted into the cell body and thus its point of attachment to the lorica could not be ascertained.

SOMATIC CILIATION. This species has 20 (18-21) kineties total, with one VK, one DK comprised of two partial kineties, 7 (6-7) kineties in the RF, and 10 (8-11) kineties in the LF. In addition, there is a PK which lies posterior to the LF and is segmented. The kinetal density index is 5.09/10 μm at the oral margin and 4.59/10 μm at the greatest diameter of the cell body.

The VK begins at the AM and continues posteriorly to near the aboral end of the cell. This kinety is not continuous but is broken into several (4-5) segments with spaces between them (Fig. 13a).

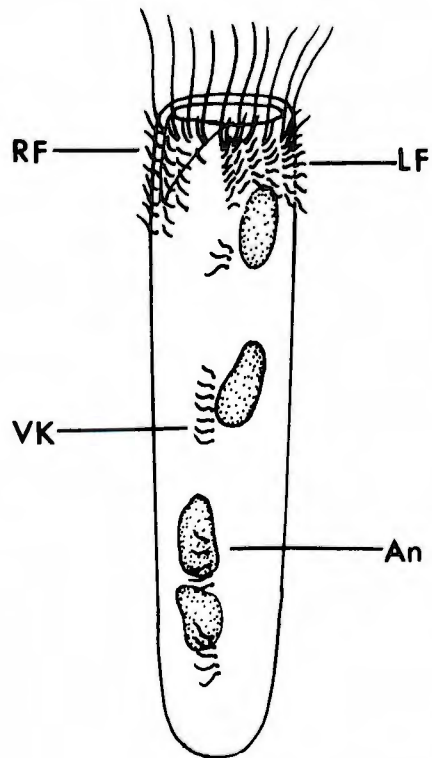
The kineties of the RF begin at the AM, are evenly spaced with regularly spaced kinetosomes, and course posteriorly for about one-fifth of the cell length (Fig. 13a,b; 14d,f). The kinetids have single ciliiferous kinetosomes except the most anterior kinetid of each kinety which has two kinetosomes, both ciliated. The anterior kinetosomes of the double kinetids have cilia ca. 8 μ m long and the posterior cilia of the same kinetids are ca. 2-3 μ m long.

The DK is composed of two overlapping kineties which together extend the entire length of the cell. The first part of the DK, DK₁, begins at the AM and passes posteriorly for just over one-half of the cell length. The kinetids of the DK₁ have single ciliated kinetosomes except the most anterior one which has two kinetosomes, both ciliated as in the doublets of the RF. The second part of the DK, DK₂, begins just below the first kinety of the LF and continues posteriorly to the aboral end of the cell (Fig. 13b, 14c). The kinetids of DK₂ have single ciliiferous kinetosomes. The lengths of the cilia are 4-5 μ m long on these two kineties excluding the previously mentioned anterior kinetid of the DK₁.

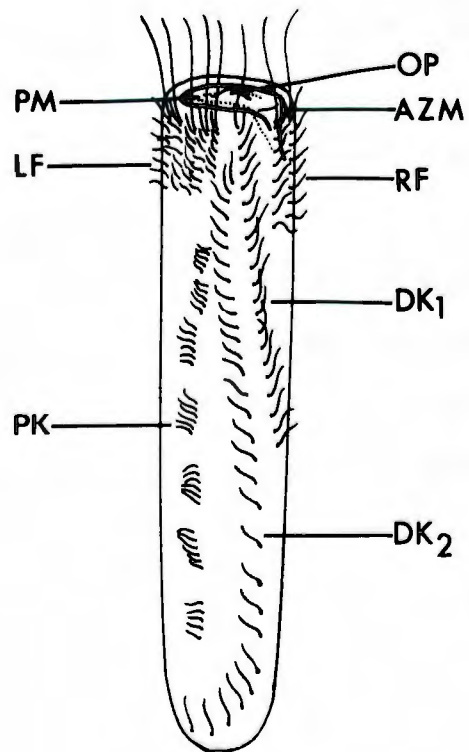
The kineties and the kinetosomes within these kineties in the LF are evenly spaced (Fig. 13a, 14b). The kinetids

Figure 13

Drawings of ventral (a) and dorsal (b) aspects of Eutintinnus pectinis. RF, right ciliary field; LF, left ciliary field, VK, ventral kinety; PK, posterior kinety; An, position of anlage; DK₁, dorsal kinety part 1; DK₂, dorsal kinety part 2; AZM, adoral zone of membranelles; PM, paroral membrane; OP, oral plug. ca. 1,300X.



a

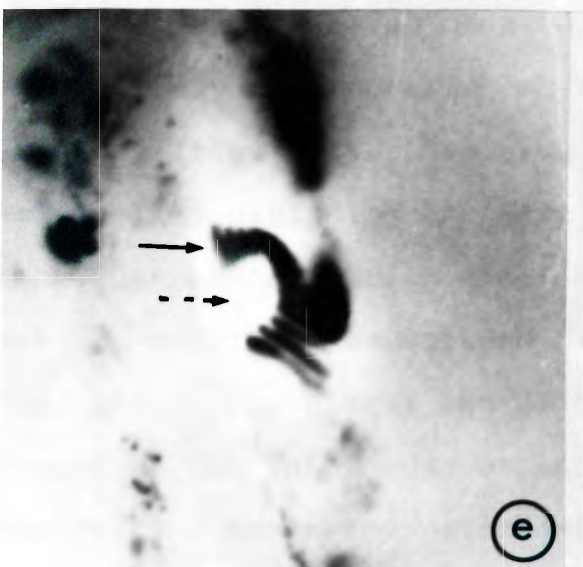
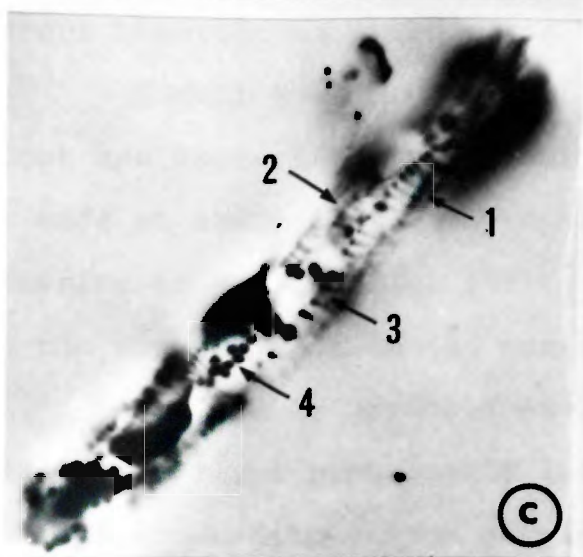
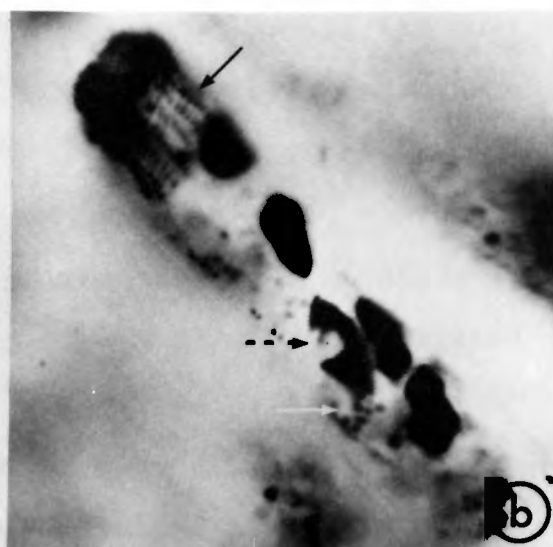
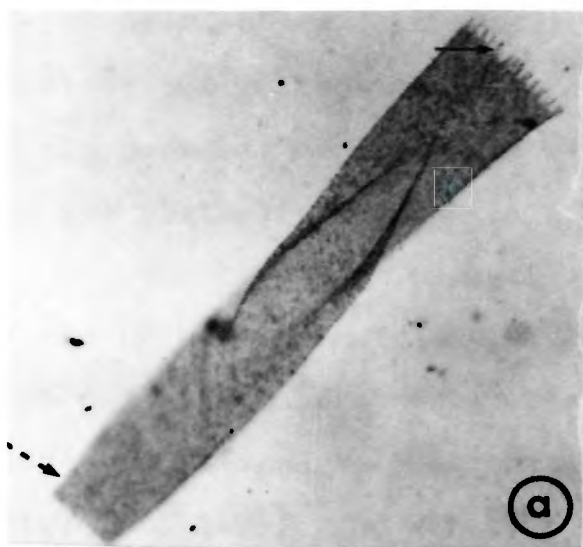


b

Figure 14

Photomicrographs of the lorica, somatic ciliation, and buccal area of Eutintinnus pectinis.

- a. Lorica. Solid arrow, oral teeth of lorica; broken arrow, posterior constriction. 689X.
- b. Ventral aspect of the cell body. Solid black arrow, left ciliary field; broken arrow, anlage; white arrow, lorica forming granules. 1,340X.
- c. Left dorsal view of cell body. Arrow 1, dorsal kinety part one; arrow 2, segment of posterior kinety; arrow 3, dorsal kinety part 2; arrow 4, lorica forming granules. 1,340X.
- d. Dorsal aspect of cell body. Black arrow, right ciliary field. 2,240X.
- e. Anlage. Solid arrow, AZM; broken arrow, paroral membrane. 2,240.
- f. Right dorsal aspect of cell body. Solid black arrow, right ciliary field; broken arrow, proximal ends of the first few membranelles; white arrow, proximal end of the last membranelle. 1,863X.



of the LF have single ciliiferous kinetosomes except the most anterior one which has two kinetosomes, both ciliated. As in the doublets of the RF, the anterior cilium is ca. 8 μm and the posterior one is ca. 2-3 μm long.

The PK begins posterior to the first few kineties of the LF and to the right of DK₂. This kinety is segmented into 6-7 kinetal fragments which extend posteriorly in a staggered fashion to near the aboral end of the cell (Fig. 13b, 14c). The kinetids are composed of single ciliiferous kinetosomes. The cilia are ca. 2-3 μm long.

BUCCAL MORPHOLOGY. The infundibulum funnels to the right and posteriorly for about one-fifth of the cell length. It ends at the cytostome-cytopharynx complex which is located interior to the RF (Fig. 14f). There is a slight oral plug on the ventral wall of the peristome.

The AZM is arranged as in the model with the proximal end of the first membranelle located in the infundibulum near the cytostome-cytopharynx complex. The proximal ends of the next three are also in the infundibulum but are arranged consecutively more anterior on the ventral wall of the peristome (Fig. 14f). The proximal ends of the remaining membranelles excluding the last two are located around the inner edge of the peristomial lip. The proximal ends of the last two membranelles descend back toward the infundibulum (Fig. 14f). The distal end of the first membranelle is located on the inner edge of the peristomial lip. The other membranelles cross the peristomial lip and terminate distally

on the outer margin of the peristomial lip. In three specimens, the membranelles could be counted with accuracy and the number of membranelles was found to be 15. No tentaculoids or accessory combs were observed in these specimens.

NUCLEAR STRUCTURE. In nondividing cells there are four interconnected macronuclei and two micronuclei (Fig. 13a; 14b,c). The macronuclei are irregularly ovoid with an average length of $7.69\text{ }\mu\text{m}$ (± 0.35 , 6.01-11.5, 19) and an average width of $3.79\text{ }\mu\text{m}$ (± 0.11 , 2.75-4.41, 19). Reorganization bands occurred in the micronuclei of dividing cells. The micronuclei have an average diameter of $1.8\text{ }\mu\text{m}$ (± 0.10 , 1.3-2.3, 12) and one is usually associated with each pair of macronuclei.

Lorica-forming granules are observed in dividing cells concentrated near the developing oral primordium (Fig. 14b,c) but also can be found distributed throughout the cell. The diameter of these granules is $1.2\text{ }\mu\text{m}$ (± 0.06 , 0.83-1.6, 16).

Favella panamensis Kofoid and Campbell 1929Lorica

F. Panamensis secretes its entire lorica, no foreign particles are attached. The lorica matrix is arranged into many small polygons from less than one to two micrometers in diameter. There is a prominent rim $9.31\ \mu\text{m}$ (± 0.29 , 6.77-11.3, 19) from the oral opening (Fig. 15a). Anterior to this rim, the polygons of the lorica matrix are less than or equal to $1\ \mu\text{m}$, and posteriorly they are 1-2 μm in diameter. The maximum width, $101\ \mu\text{m}$ (± 1.99 , 85.6-123, 23), is at the oral diameter. The width decreases to $80.0\ \mu\text{m}$ (± 2.14 , 63.9-105, 23) at the bowl region then the width decreases sharply to form an aboral spine with 2(0-6) spiral turns (Fig. 16a). The length of the spine, $46.8\ \mu\text{m}$ (± 2.76 , 20.9-71.3, 23), is the most variable of the measurements made on the lorica, with a CV value of 28.2%. The total length of the lorica is $213\ \mu\text{m}$ (± 5.32 , 162-254, 22) and the length to oral diameter ratio is 2.10.

Cytology

Specimens of F. panamensis were observed, contracted and extended (Fig. 15b). In the extended state the cell body was conical, while in contracted specimens it was rounded. The length of the cell body, $80.7\ \mu\text{m}$ (± 7.87 , 40.2-169, 15), is therefore quite variable with a CV value of 37.8%. The maximum width of the cell is $65.7\ \mu\text{m}$ (± 2.28 , 39.1-79.1, 15) and the diameter of the AZM is $60.3\ \mu\text{m}$ (± 2.28 , 34.3-71.6, 15).

The penducle attaches internally to the posterior end of the lorica (Fig. 16).

SOMATIC CILIATION. F. panamensis has ca. 90 kineties overall with one VK, 2 or 4 DKs, 46 (34-55) kineties in the RF, and 39 (30-50) in the LF. The kinetal density is 4.75/10 μ m at the oral margin and 4.36/10 μ m at the widest diameter of the cell body.

The VK begins just above the AM and extends posteriorly and to the left for about one-fifth of the cell length [Fig. 15a,c (inverted)]. The kinetids, all with single ciliferous kinetosomes, are tightly packed anteriorly but become more distant from each other posteriorly. The cilia are 3-5 μ m long. The anlage forms below and just to the left of the VK (Fig. 15d).

The first kinety of the RF, K2, begins posterior to the AM and lies near the VK (Fig. 15a, 16c). The kinetids are composed of single ciliferous kinetosomes, ca. 3-5 μ m long.

The remaining kineties of the RF (Fig. 15a,b, 16c) extend posteriorly for one-fifth to one-fourth of the cell length. The kinetids of these kineties are arranged in paratenes. The kinetids have single ciliated kinetosomes except the most anterior one which has two kinetosomes, both ciliated. The anterior kinetosomes of the anterior kinetids possess cilia ca. 7-12 μ m long and the posterior cilium of this same kinetid is ca. 2 μ m long.

Figure 15

Drawings of ventral (a) and dorsal (b) aspects of Favella panamensis. RF, right ciliary field; LF, left ciliary field; VK, ventral kinety; PK, posterior kinety; K2, kinety number two; An, position of anlage; DK, dorsal kineties; AZM, adoral zone of membranelles; PM, paroral membrane; OP, oral plug. ca. 580X.

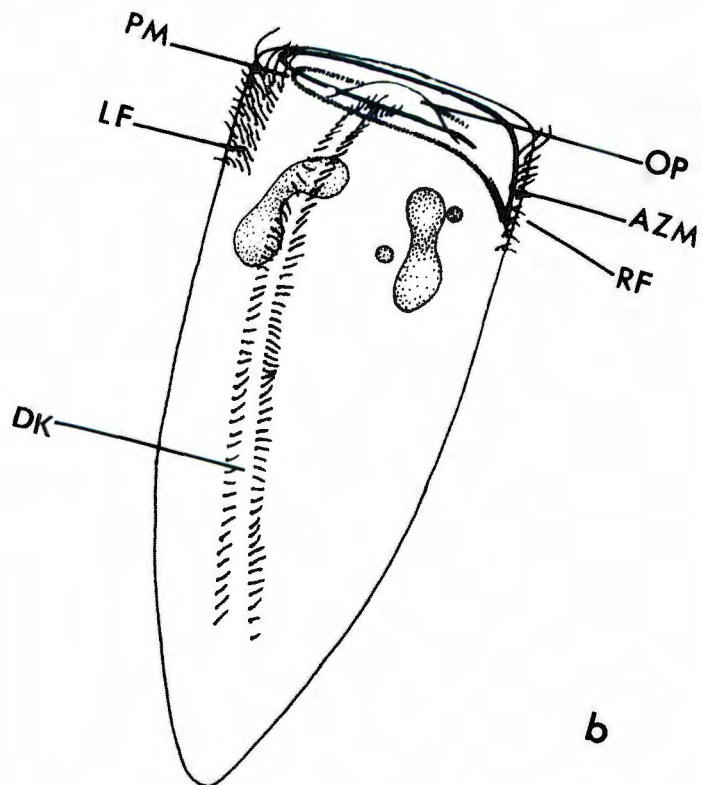
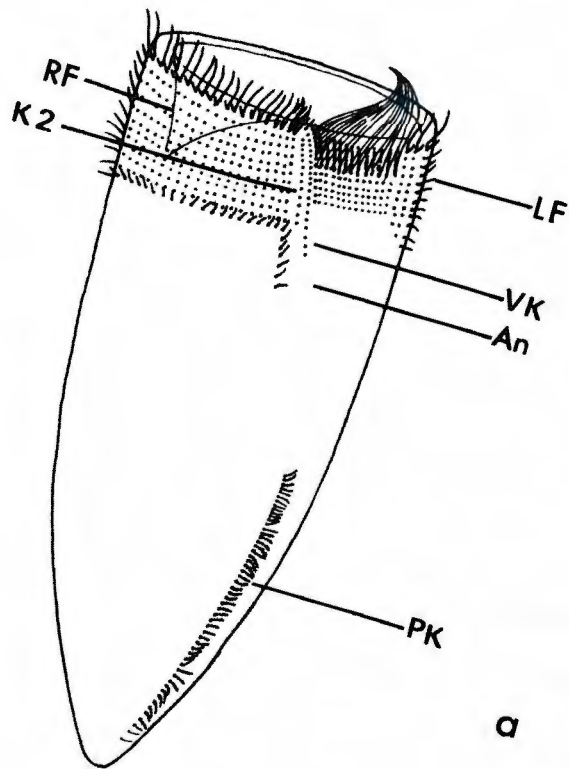
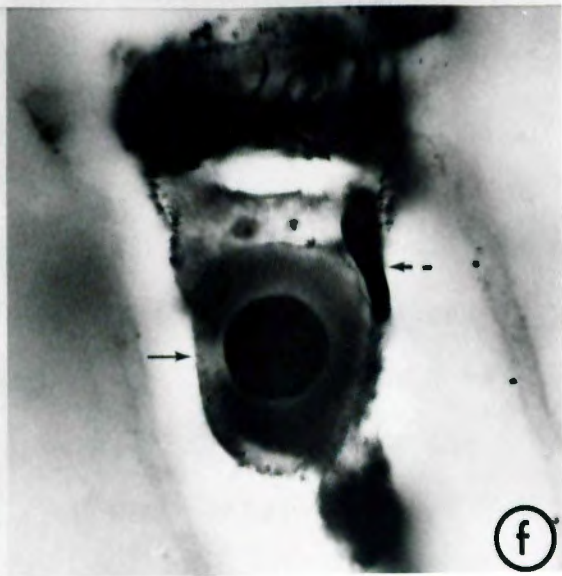
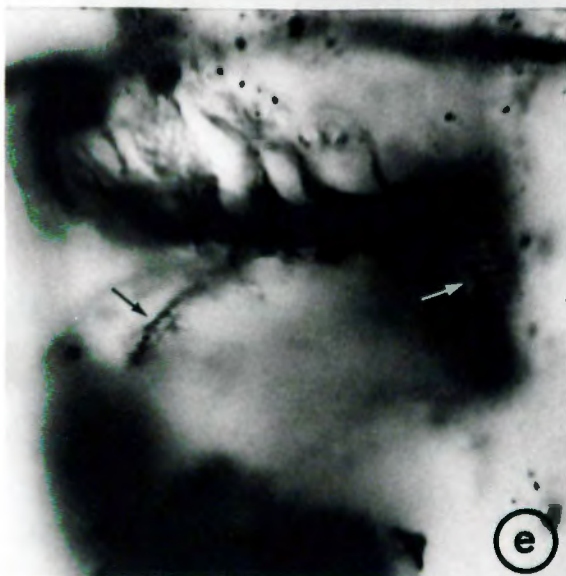
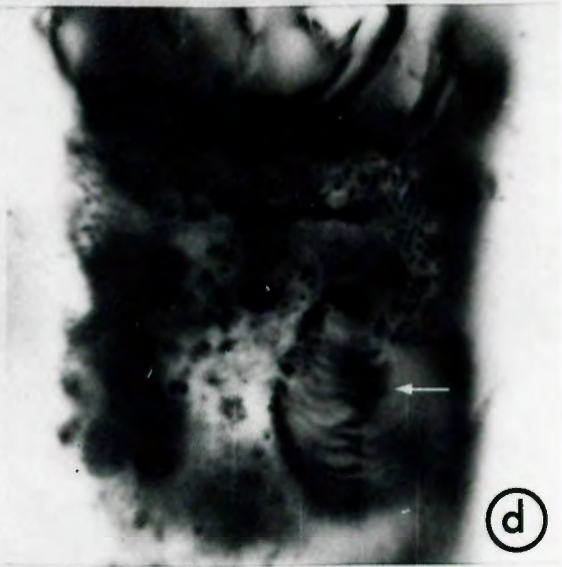
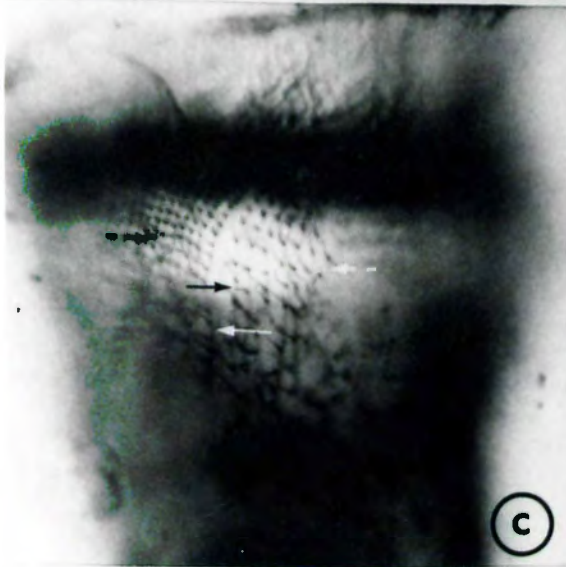
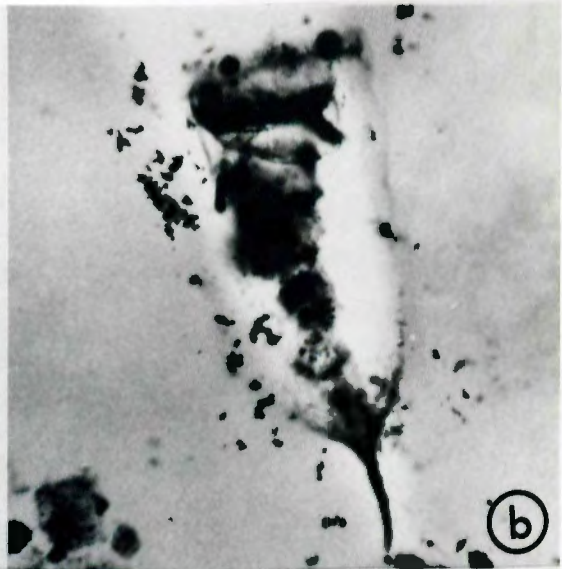
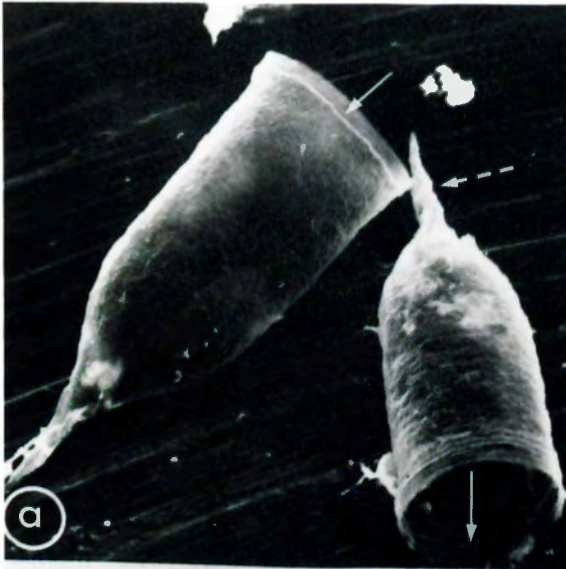


Figure 16

Photomicrographs of the lorica, somatic ciliation, and buccal area of Favella panamensis.

- a. Loricae. Solid arrows, annulations at anterior end of lorica; broken arrow, spiral turns in the aboral spine. 286X. SEM.
- b. Outline of lorica and general body form. 291X
- c. Ventral aspect of the cell body. Solid black arrow, K2; solid white arrow, ventral kinety; broken black arrow, left ciliary field; broken white arrow, right ciliary field. 1,130X.
(Inverted)
- d. Ventral aspect of the cell body in a dividing form. White arrow, anlage. 959X.
- e. Dorsal aspect of the cell body. Black arrow, anterior portion of the dorsal kinety; white arrow, right ciliary field. 959X.
- f. Parasitized F. panamensis. Solid arrow, parasite; broken arrow, macronucleus. 527X.



There are usually two and sometimes four kineties in the position of the DK. These kineties angle from the right anterior to the left posterior in the anterior portion of their length, and continue directly posterior to near the aboral end (Fig. 15b, 16e). The kinetids are composed of single ciliated kinetosomes.

The LF shows a slight gradient from the first to the last kinety of decreasing distance between kineties. The last 8-12 kineties are tightly packed, and the kinetosomes in their anterior portion give rise to cilia ca. 20-25 μm long [Fig. 15a, 16c, (inverted)]. The kinetids of these last 8-12 kineties have single ciliated kinetosomes with cilia ca. 3-5 μm long. The kinetids of the other kineties of this field have single ciliferous kinetosomes except the most anterior kinetid which has two kinetosomes, both ciliated. The lengths of these cilia are as in the doublets of the RF, the anterior one ca. 7-12 μm and the short one ca. 3-5 μm long.

The PK is positioned in the posterior half of the cell below the area of transition from tight to loose packing of the kineties of the LF (Fig. 15a). The 28 (10-30) kinetids have single ciliferous kinetosomes.

BUCCAL MORPHOLOGY. The infundibulum is very large and cylindrical anteriorly, funnels to the right posteriorly, and ends near the cytostome-cytopharynx complex, which is located interior to the RF. The oral plug is within the infundibulum on the ventral wall of the peristome.

The AZM, composed of 17 membranelles, is arranged with the proximal end of the membranelle located in the infundibulum near and ventral to the cytostome-cytopharynx complex. The proximal ends of the next five or six membranelles are also in the infundibulum but are arranged consecutively more anterior on the ventral wall of the peristome (Fig. 18). The proximal ends of the remaining membranelles, excluding the last membranelle, are located around the inner edge of the peristomial lip. The proximal end of the last membranelle descends slightly into the infundibulum. No tentaculoids or accessory combs were observed among the membranelles.

Due to the large size of F. panamensis, the system of fibers associated with the AZM could be examined in detail. At the proximal end of the membranelles are the proximal plugs, composed of root-like fibers which originate from the kinetosomal bases of the membranelles (Fig. 17, 18a-d). Near the proximal plug, lateral fibers extend between adjacent membranelles (Fig. 17, 18d). Just anterior to the proximal plug, begin two of the three kinetosomal rows of the membranelle. The cilia arising from the first section of kinetosomes are joined together to form the primary pectinelles. The primary pectinelles are directed anterior and toward the infundibulum.

Continuing up and over the peristomial lip from right interior to left exterior (as viewed from within), the two rows of kinetosomes give rise anteriorly to the very long

Figure 17

Drawings of the membranelles and associated fibers of Favella panamensis. PP, primary pectinelle; Pg, proximal plug; RL, right lateral fibers; LL, left lateral fibers; PR, preoral ring; k_x , kinetosomal row of the membranelar base number x ; CM, cilia of the membranelle; CF, connecting fibers.

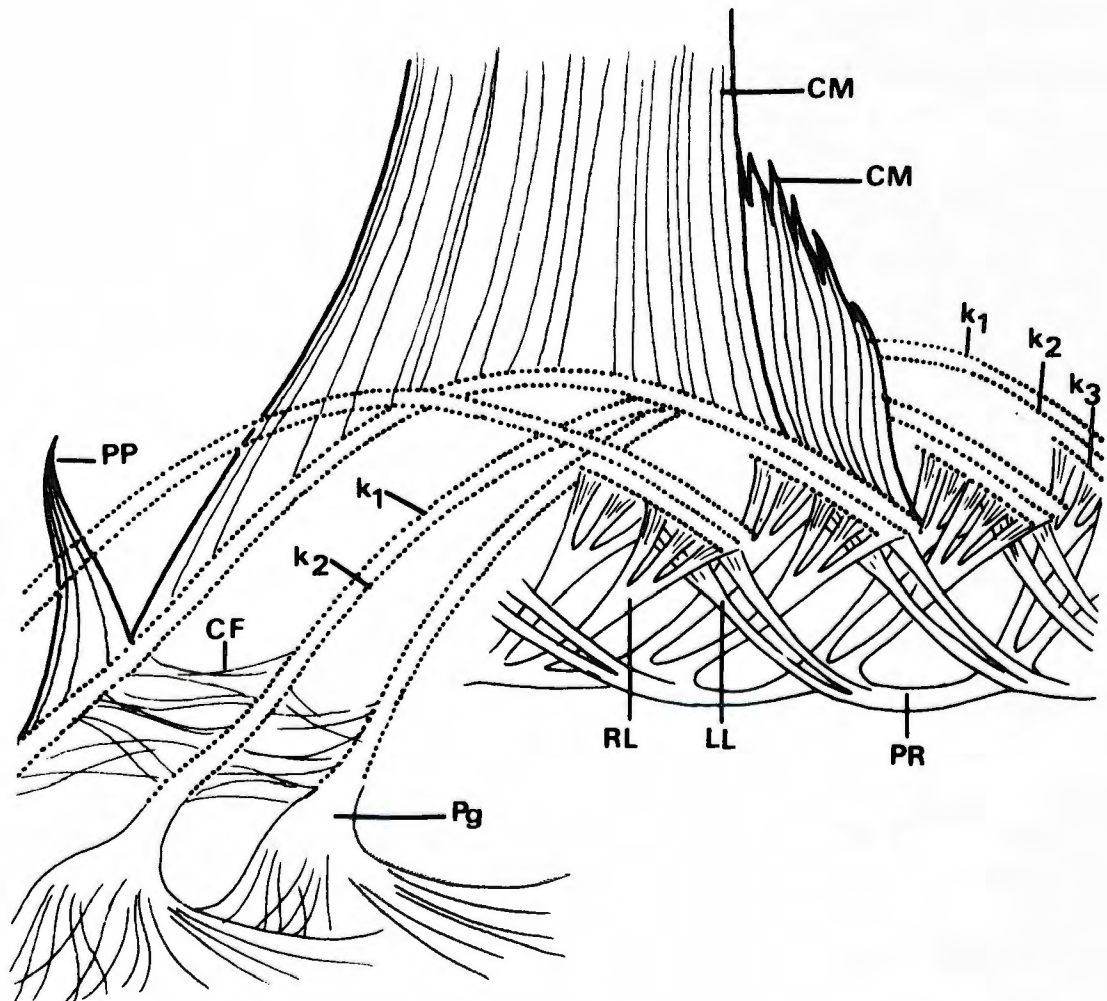
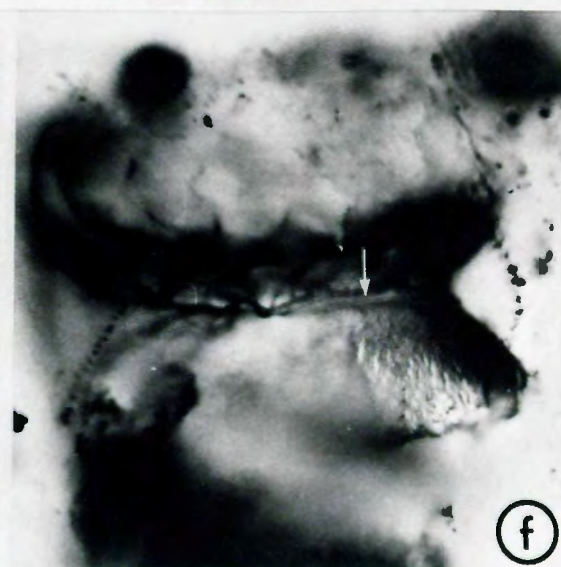
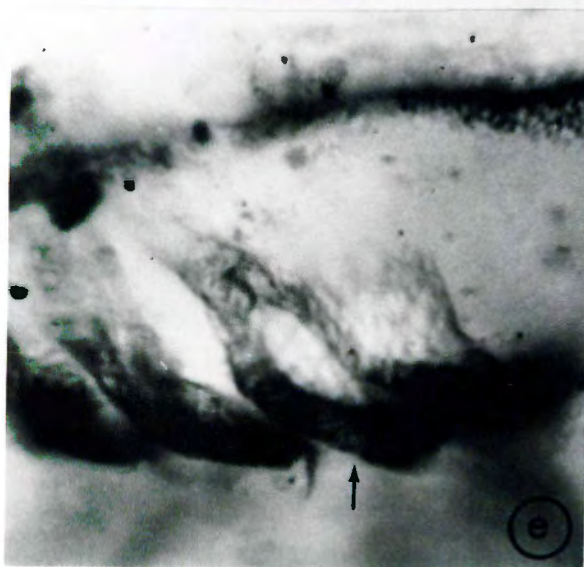
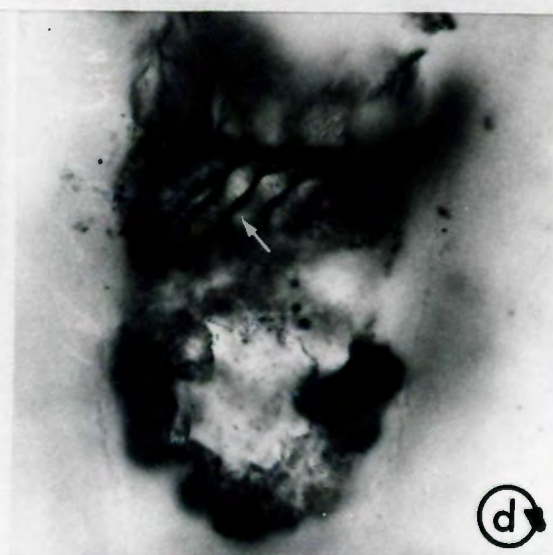
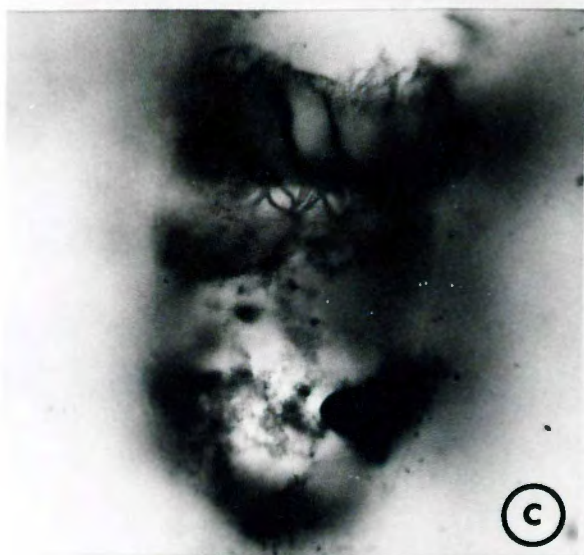
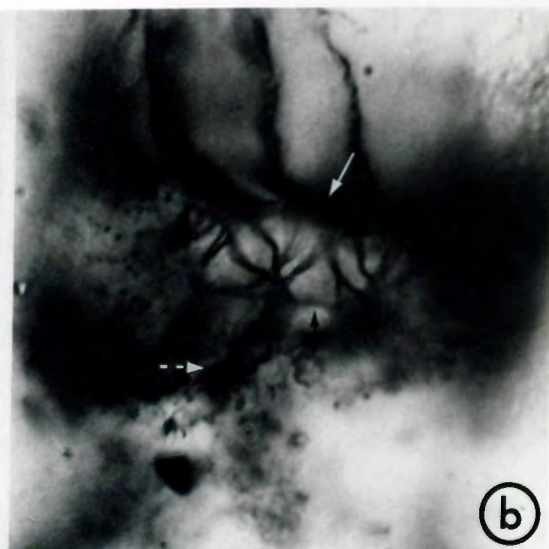


Figure 18

Photomicrographs of the membranelles and associated fibers of Favella panamensis.

- a. Fiber system originating from the distal end of a membranelle. Black arrows, right lateral fibers; solid white arrows, left lateral fibers; broken white arrow, proximal plug of a membranelle. 1,330X.
- b. Fiber system originating from the distal end of a membranelle. Black arrow, preoral ring; solid white arrow, base of a membranelle; broken arrow, proximal plug. 1,330X.
- c. Lower magnification of a and b, above. 662X.
- d. Fiber system at proximal ends of the membranelles. White arrow, proximal ends of the membranelar bases ascending the wall of the peristome. 662X. (Note fibers of the proximal plugs and the fibers between membranelles.)
- e. Membranelles. Black arrow, distal end of a membranelle with cilia. 1,670X.
- f. Paroral membrane. White arrow, the two long rows of kinetosomes in the paroral membrane. 959X. (Note the very long cilia attached to the posterior row of kinetosomes.)



conspicuous cilia of the membranelle. At the distal end of the membranelle, a third short row of kinetosomes is added to the right of the existing two. The cilia arising from these distal kinetosomes are longer than the primary pectinelles but are shorter than the other cilia of the membranelle (Fig. 17, 18e).

Extending posteriorly and medially from these distal kinetosomes are right and left lateral fibers (Fig. 17, 18a-c). The left lateral fibers cross over the right lateral fibers of the adjacent membranelles (Fig. 17, 18b). The left lateral fibers consist of two groups of fibers which fuse together distally. Near the kinetosomal bases, the right lateral fibers are composed of two groups of two to three fibers which fuse into two groups distally. These two larger groups again fuse to form one bundle of fibers. The distal ends of the right and left lateral fiber bundles, though passing in opposite directions, fuse to form a preoral ring (Fig. 17, 18b). The preoral ring makes a complete circle parallel to the peristomial lip. The proximal plugs of the first six to seven membranelles are located posterior to the preoral ring; whereas, the proximal plugs of the other membranelles are positioned anterior to the preoral ring.

The kinetosomes of the PM are organized like those of the membranelles with two long rows (k_1 and k_2) and one short row (k_3) of kinetosomes (Fig. 15b, 18f). The k_3 is located to the left of the k_1 and k_2 , and the three rows begin together near the cytostome-cytopharynx complex. The

PM courses from the cytostome-cytopharynx complex anteriorly and to the right and obtains a position parallel and near to the preoral ring at the right dorsal side. On the dorsal side, the PM is posterior and parallel to the peristomial lip.

The cilia of k_3 and k_2 are short; whereas, k_1 gives rise proximally to very long cilia (Fig. 18f) which can extend from one side of the infundibulum to the other.

NUCLEAR STRUCTURE. In the interphase cell, there are two macronuclei and two micronuclei. The macronuclei are dumbbell-shaped or elongate ovoids (Fig. 15b, 16f), with a length of $26.8 \mu\text{m}$ (± 1.65 , 13.5-32.0, 10) and a width of $8.67 \mu\text{m}$ (± 0.496 , 5.32-12.3, 15). Reorganization bands and condensation have been observed in the macronucleus during division. The two micronuclei, often juxtaposed to one of the two macronuclei, are $1.9 \mu\text{m}$ (± 0.097 , 1.5-2.3, 9) in diameter.

Tintinnidium mucicola (Claparède and Lachmann 1858) Daday 1887

Lorica

Particles of biogenic origin such as diatom frustules are attached to the lorica matrix (Fig. 20a). The lorica is sac-like with the maximum width, $44.1\text{ }\mu\text{m}$ (± 0.88 , 9.34-37.4, 22), near the posterior end. Anteriorly, the lorica is elongate and decreases in diameter. The length of this anterior extension of the lorica appears to be related to the age of the ciliate, the longest loricae are produced by specimens in late stomatogenic states. The length of the lorica, $83.5\text{ }\mu\text{m}$ (± 4.76 , 43.4-113, 20), is variable due to the variation in the length of the anterior extension which has a CV value of 34%.

Cytology

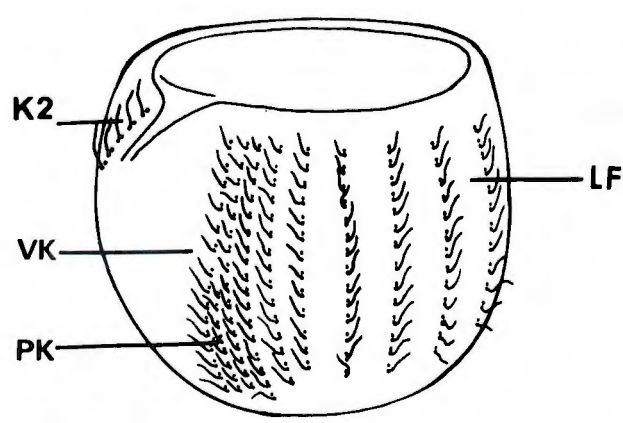
The cell body is rounded in fixed and stained specimens with a length of $20.9\text{ }\mu\text{m}$ (± 0.95 , 13.6-28.6, 20) and a width of $24.9\text{ }\mu\text{m}$ (± 0.416 , 22.2-29.7, 21). A peduncle and therefore its point of attachment were not observed.

SOMATIC CILIATION. There are 16 somatic kineties, one as a VK, no DK, 13 kineties in the LF and 2 kineties in the RF. In addition to these 16 kineties there is a PK located posterior to the left field. The kinetal density index is $2.3/10\mu\text{m}$ at the oral margin and $2.1/10\mu\text{m}$ at the maximum width. The kinetids of all the kineties have two kinetosomes, the anterior one ciliated.

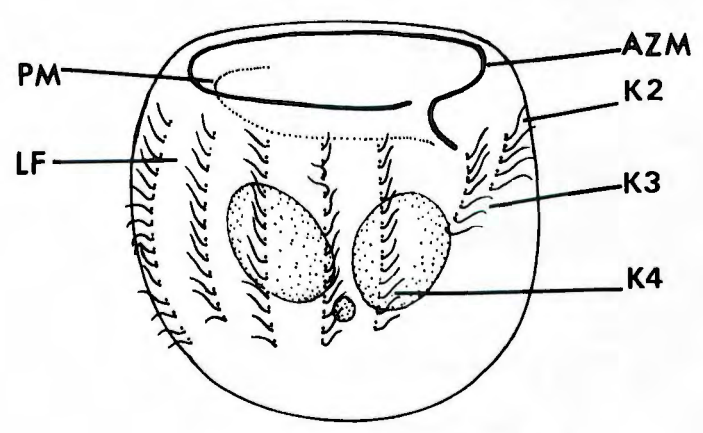
The VK begins at the AM, courses posteriorly down the length of the cell, and ends near the aboral pole (Fig. 19a, 20d). The length of the cilia are ca. $2\text{ }\mu\text{m}$. The anlage

Figure 19

Drawings of ventral (a) and dorsal (b) aspects of Tintinnidium mucicola. VK, ventral kinety; PK, posterior kinety; Kx, kinety number x; LF, left ciliary field; AZM, adoral zone of membranelles; PM, paroral membrane. ca. 2,200X.



a

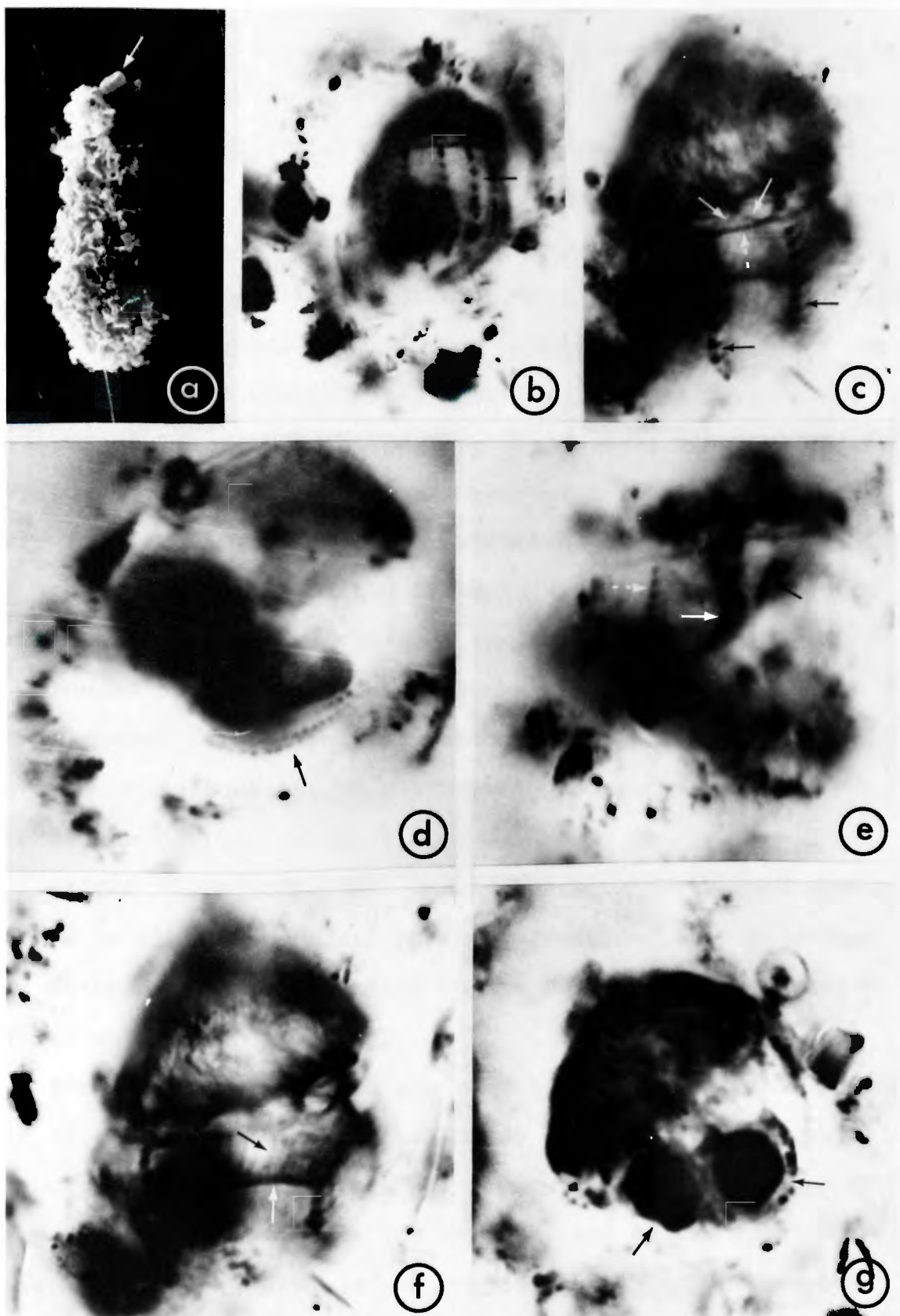


b

Figure 20

Photomicrographs of the lorica, somatic ciliation, and buccal area of Tintinnidium mucicola.

- a. Lorica. White arrow, diatom frustule. 445X. SEM.
- b. Left ventral aspect of cell body. Black arrow, kinety of the left ciliary field. 1,220X.
- c. Dorsal aspect of the cell body. Black arrows, kineties of left ciliary field; solid white arrows, lateral fibers originating from the distal ends of the membranelles; broken white arrow, preoral ring. 2,180X.
- d. Ventral aspect of the cell body. Solid black arrow, posterior portion of the first few kineties of the left ciliary field; broken black arrow, anlage. 1,940X.
- e. Right ventral aspect of the cell body. Black arrow, K2; solid white arrow, K3; broken white arrow, K4. 2,110X.
- f. Dorsal aspect of the cell body. White arrow, paroral membrane; black arrow, cilia of the paroral membrane. 2,180X.
- g. Nuclear structure. Black arrows, macronuclei. 1,920X. (Note dense cytoplasm around macronuclei.)



(Fig. 20d) develops beneath the cortex and adjacent to the VK.

The RF (Fig. 19a,b;20e) consist of two kineties, K2 and K3. K2 contains only 4-5 kinetids and lies at an angle from left anterior to right posterior. K3, with 5-10 kinetids, is longer than K2. K3 begins slightly more posterior than K2 and is curved to the right. The cilia of the RF have slightly longer cilia (ca. 3 μ m) than the other somatic cilia (ca. 2 μ m).

Unlike the model, the LF of T. mucicola covers about three-quarters of the cell circumference. The LF exhibits a gradient of loose to tight packing of kineties from the first (K4) to the last (K16). Kineties number 4-14 extend posteriorly from the AM for about three-fourths of the cell length. The last two kineties of the LF begin at the AM and course to near the aboral pole of the cell in line with the VK.

The PK begins about one-half the distance from the AM to the aboral pole between the VK and the last kinety of the LF. The PK follows the VK posteriorly to near the aboral pole of the cell.

BUCCAL MORPHOLOGY. The infundibulum is cup-shaped and narrows to the right ending at the cytostome-cytopharynx complex which is located interior to the RF. There is no oral plug on the peristomial wall.

The AZM is composed of the same number of membranelles (16) as there are kineties that begin at the AM. The proximal ends of the membranelles are all located on the inner edge of the peristomial lip except the proximal end of the first membranelle which begins near the cytostome-cytopharynx complex. No tentaculoids were observed. The preoral ring and associated

lateral fibers can be seen in Fig. 20c.

The PM (Fig. 19b;20f) begins at the cytostome-cytopharynx complex continues around the right side, and ends on the dorsal side of the peristome. The PM does not ascend the peristomial wall but remains perpendicular to the longitudinal axis of the ciliate. The fibers of the cytopharynx appear to originate from the proximal end of the PM.

NUCLEAR STRUCTURE. The two macronuclei are located posteriorly in a central mass of darkly staining cytoplasm (Fig. 19b;20g). The macronuclei are irregularly rounded to ovoid, $9.04\ \mu\text{m}$ (± 0.347 , 5.78-13.0, 23) by $6.45\ \mu\text{m}$ (± 0.178 , 4.54-7.85, 23). In one specimen, a fine strand connects the two macronuclei. This connection may be a consistent character but is difficult to see due to the juxtaposition of the nuclei and the darkly stained cytoplasm. Reorganization bands and condensation of the macronucleus are observed in dividing specimens. The micronuclei were rarely observed due to their proximity to the macronucleus. No more than one micronucleus was observed in the same specimen but the possibility of a second cannot be excluded due to the poor visibility in this area.

The following three species, Protohabdonella simplex, Amphorelloopsis acuta, and Salpingacantha sp., are represented on my slides by only a few stained specimens. These species are, therefore, not described in detail, but they are included for heuristic reasons. P. simplex represents the family Rhabdonellidae, while A. acuta and Salpingacantha sp. possess features different from the model tintinnid.

Protohabdonella simplex (Cleve 1900) Jorgensen 1924

Lorica

The lorica is 49.5 μm (n=1) long with an oral diameter of 32.7 μm (n=1) and has the characteristic ribs and small fenestrae of the family Rhabdonella (Fig. 22a). The length to oral diameter ratio is 1.51.

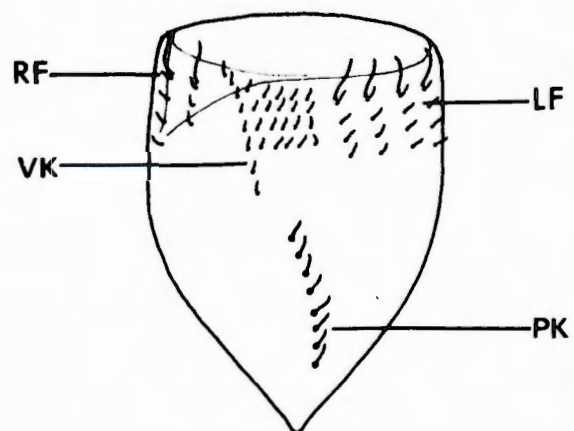
Cytology

SOMATIC CILIATION. The one specimen observed had 20 kineties, with one VK, one DK, 8 kineties in the RF, and 10 kineties in the LF. The kinetal density index is 2.49/10 μm at the oral diameter.

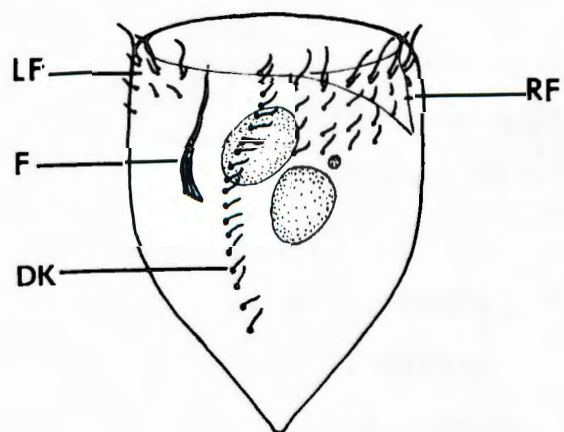
The somatic ciliation is very similar to the model (Fig. 21a,b, 22b). The VK courses posteriorly and to the left from just above the AM to about the midpoint on the ventral surface. The kinetids have single kinetosomes with cilia ca. 2-3 μm long. The 8 kineties of the RF and the kinetids within these kineties are evenly spaced. There are

Figure 21

Drawings of ventral (a) and dorsal (b) aspects of Protorhabdonella simplex. RF, right ciliary field; LF, left ciliary field; VK, ventral kinety; PK, posterior kinety; F, fibers; DK, dorsal kinety. ca. 1,650X.



a

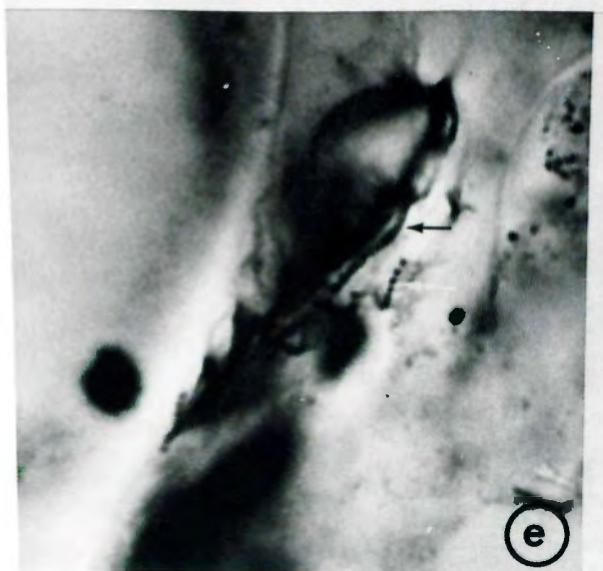
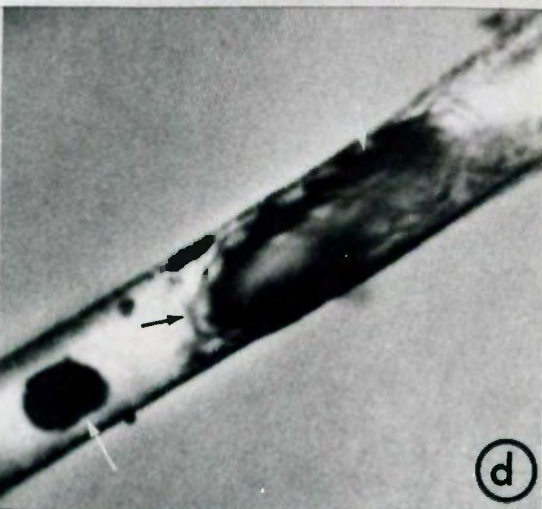
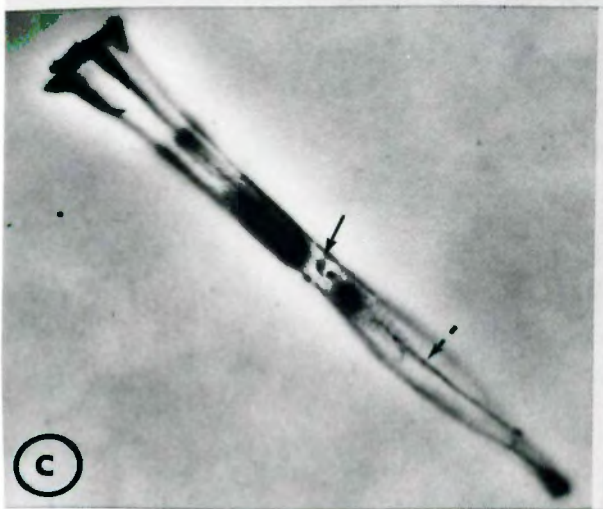
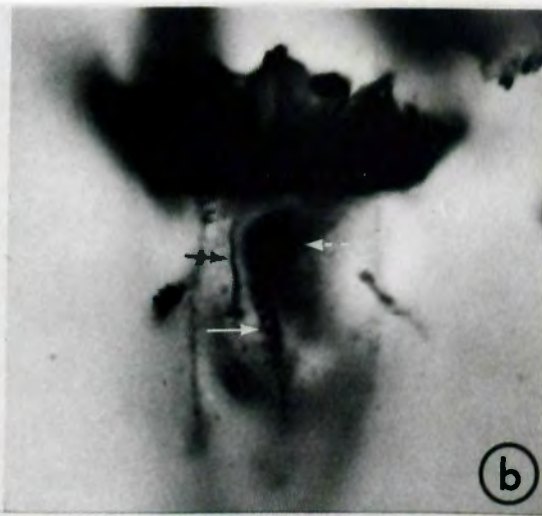
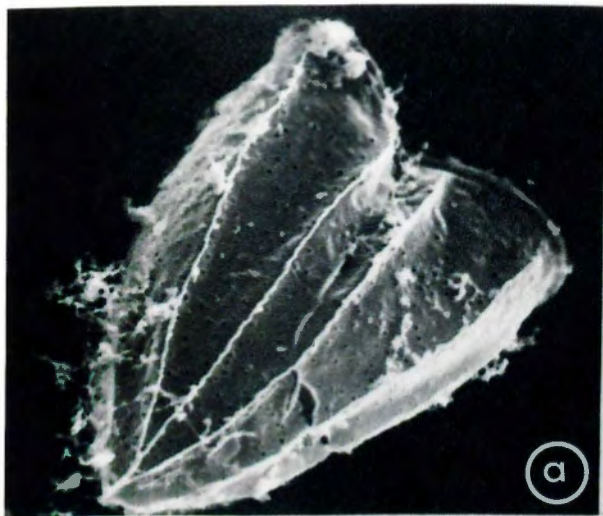


b

Figure 22

Photomicrographs of Protorhabdonella simplex,
Salpingacantha sp., and Amphorellopsis acuta.

- a. Lorica of P. simplex. 1,850X. (Note the ribs and small fenestrae, specimen is slightly crushed.) SEM.
- b. Dorsal aspect of the cell body of P. simplex. Solid white arrow, dorsal kinety; broken white arrow, macronucleus; black arrow, unidentified fibers. 1,260X.
- c. Lorica and ventral aspect of the cell body Salpingacantha sp. Solid arrow, ventral kinety; broken arrow, rib of lorica. 783X.
- d. Ventral aspect of Salpingacantha sp. Solid white arrow, macronucleus; broken white arrow, membranelar base; black arrow, preoral ring. 1,920X.
- e. Left ventral aspect of the cell body of A. acuta. White arrow, a kinety of the left ciliary field; black arrow, preoral ring. 1,390X.
- f. Ventral aspect of the cell body of A. acuta. Solid black arrow, paroral membrane; broken black arrow, macronucleus; solid white arrow, anlage; broken white arrow, base of membranelle. 1,400X.



2-4 kinetids per kinety, and all have single ciliferous kinetosomes except the anterior most kinetid which has two kinetosomes, both ciliated. The 20 kinetids of the DK were heavily stained but appeared to possess only one ciliferous kinetosome. The LF, containing 10 kineties, showed a gradient of loose to tight packing of the kineties from left to right. All kinetids in the LF have single kinetosomes except the anterior most kinetids of the first 5 kineties which have two kinetosomes, both ciliated. There are 2-4 kinetids in the kineties of the LF. The 8 kinetids of the PK stretch from just posterior and to the left of the last kinetid of the VK to the posterior end of the cell. There is a group of subpellicular fibers between the DK and the beginning of the LF (Fig. 21b, 22b).

BUCCAL MORPHOLOGY. The cilia of the AZM stained very dark and interfered with observations of the oral area. There were, however, 5 membranelles with their proximal ends ascending the peristomial wall of the infundibulum. This arrangement is the same pattern exhibited by the model tintinnid (Fig. 1c).

NUCLEAR STRUCTURE. There are two macronuclei set close together in the center of the cell. One micronucleus was observed, but others, if in close association with the macronuclei, may have been masked from view.

Amphorelloopsis acuta (Schmidt 1901) Kofoed and Campbell 1929

Lorica

The lorica is hyaline and elongate, has a flaring oral rim, and a pointed aboral end. The length is 107 μm ($n=1$) and the width is 20.5 μm which increases in width anteriorly to the oral brim, 37.1 μm across. (See Kofoed and Campbell 1929 for figure and further description.)

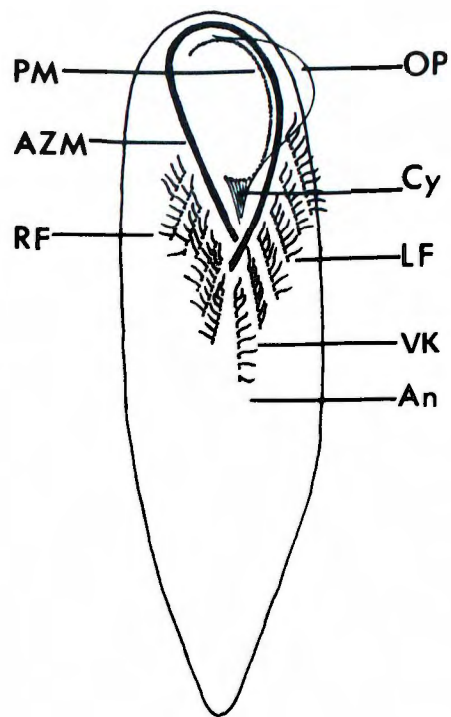
Cytology

SOMATIC CILIATION. The one specimen observed had 14 kineties, with one VK, one DK, 7 kineties in the RF and 5 kineties in the LF. The kinetal density index is 2.72/10 μm at the greatest width, and the kineties are concentrated on the ventral side. All kinetids have two kinetosomes, the anterior one ciliated, except the DK which also has two kinetosomes, but the posterior one is ciliated. All of the somatic cilia are ca. 2-3 μm long except those cilia of the DK which are ca. 5 μm long.

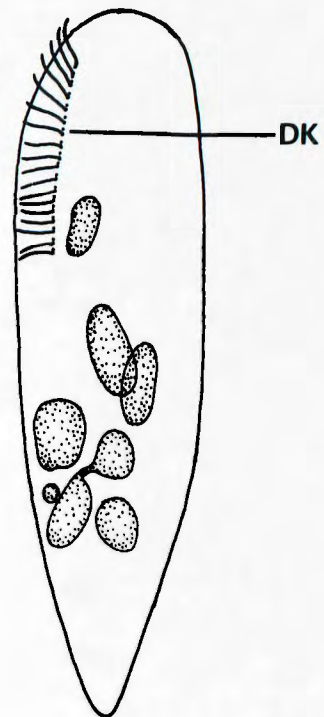
The VK, composed of 9 kinetids, is positioned more posterior than the other kineties (Fig. 23a). The anlage forms posterior and slightly to the left of the VK (Fig. 23a). The AM of the RF parallels the peristomial lip and angles anteriorly and to the right from the most anterior kinetid of the VK (Fig. 23a). There are 3-7 kinetids per kinety in the RF. The dorsal kinety, composed of 18 kinetids, lies on the left dorsal side of the cell near the first kinety

Figure 23

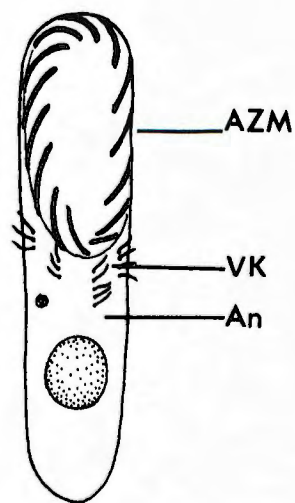
Drawings of ventral (a) and dorsal (b) aspects of Amphorelloopsis acuta, and the ventral (c) aspect of Salpingacantha sp. RF, right ciliary field; LF, left ciliary field; VK, ventral kinety; DK, dorsal kinety; An, position of anlage; AZM, adoral zone of membranelles; PM, paroral membrane; OP, oral plug; Cy, cytopharynx. A. acuta, ca. 1,300X; Salpingacantha sp., ca. 1,740X.



a



b



c

of the LF. The first kinetid of the DK is the most anterior positioned kinetid of this ciliate (Fig. 23b). The AM of the LF begins posterior to the first kinetid of the DK and continues posteriorly parallel to the peristomial lip. The AM ends near but anterior to the anterior most kinetid of the VK. In this specimen, the kineties of the LF were curved at their posterior ends (Fig. 22e). This is assumed to be due to the contraction of the cell and, therefore, these kineties are depicted as linear rows (Fig. 23a).

BUCCAL MORPHOLOGY. The infundibulum and AZM are compressed laterally, extended along the long axis, and have become more ventral in position (ventralization) in comparison to the model tintinnid (Fig. 22e,f; 23a). The AZM, composed of 14 membranelles, begins just interior to the RF and dorsal to the VK. Coursing anteriorly and to the right, the AZM curves around the peristome at the anterior end of the ciliate and returns toward, terminates near, and is slightly exterior to the first membranelle (Fig. 23a). A well defined preoral ring is associated with the AZM (Fig. 22e). The oral plug is well developed and extends from the anterior end of the infundibulum to the posterior end and is raised well beyond the plane of the AZM. The PM is positioned differently than in the PM of the model. The PM begins to the right and dorsal to the beginning of the AZM as in the model, but the PM then courses to the left, parallel to the AZM. The PM terminates at the anterior most portion of the inner edge of the peristomial lip (Fig. 22f, 23a). The proximal end

of the PM gives rise to the fibers of the cytopharynx (Fig. 23a).

NUCLEAR STRUCTURE. There are 7 macronuclei in this specimen (Fig. 23b). A fine connection exists between one pair of macronuclei. One micronucleus was observed.

Salpingacantha sp.

Lorica

The hyaline lorica (Fig. 22c) is long, 103 μm average length ($n=4$), and slender, 9.16 μm average width ($n=4$), and has a gradually flaring oral rim, 16.4 μm average diameter ($n=4$). The oral rim has five crests or teeth and posterior to each crest is a ridge which continues to the aboral end of the lorica and spirals to the left at the posterior.

Cytology

SOMATIC CILIATION. There are 6 ($n=2$) kineties with 2-5 kinetids per kinety. The kinetids are composed of single ciliiferous kinetosomes. The kinetal density index is 2.50/10 μm at the maximum width. The VK is the longest with 5 kinetids and is more posterior than the other kineties. The anlage develops posterior and to the left of the VK (Fig. 22c, 23c). The kineties on the dorsal side are the most anteriorly positioned kineties. There is no specialized kinety on the dorsal side to designate as the DK.

BUCCAL MORPHOLOGY. In comparison to the model tintinnid, the AZM and infundibulum, as in A. acuta, are compressed laterally, lengthened along the long axis, and have become more ventral in position. The first of the 13 membranelles of the AZM begins anterior and internal to the VK, is directed toward the right, and is shorter than the other membranelles (Fig. 23c, 22d). The AZM courses to the

right and follows the peristomial lip around the anterior end of the cell. The AZM circumscribes an oval with the first membranelle only slightly interior to the last membranelle. A preoral ring accompanies the AZM (Fig. 22d). No oral plug or PM were observed.

NUCLEAR STRUCTURE. There is one macronucleus and one micronucleus. The macronucleus has an average size of 6.0 by 4.0 μm (n=4) and the diameter of the micronucleus is 1.4 μm (n=1).

DISCUSSION

The characterization of the oral structures and especially the somatic ciliation patterns of tintinnids as revealed by the Bodian protargol silver impregnation technique, has opened up a new frontier in tintinnid taxonomy. Not only can a more natural classification be constructed within the tintinnids but the relationship of tintinnids to other ciliates can be investigated in a new light.

Tintinnid Morphology

SOMATIC CILIATION. The somatic ciliation patterns of these representative tintinnids are surprisingly consistent. A VK, RF, DK, LF, and PK are found in all of the species examined except three, A. acuta, T. mucicola, Salpingacantha sp. T. mucicola lacks a DK, A. acuta is without a PK, and the ciliation of Salpingacantha sp. is very reduced. The kinetal density indices of the species examined can be divided into two groups. T. mucicola, P. simplex, A. acuta, and Salpingacantha sp. have kinetal density values between 2-3 kineties/10 μ m and the other species examined have values of 4.4-5.4 kineties/10 μ m.

The ventral kinety (K1) which is the ciliary membrane of Faure-Fremiet (1924) and Campbell (1926), is longer than the kineties of the right and left ciliary fields and in T. baltica, C. cratera, T. subacuta, S. steini, E. pectinis, and T. mucicola the VK extends posteriorly over one-half of the cell length. The peculiar position of the anterior half of the VK in C.

scalaroides made it appear shorter than it really is. In general the VK is the longest kinety on the ventral surface.

The anlage forms just to the left of the VK about one-half way down the cell length in T. baltica, C. cratera, T. subacuta, S. steini, and E. pectinis. In C. scalaroides, F. panamensis, A. acuta, and Salpingacantha sp. the anlage develops below and to the left of the VK. In T. mucicola the anlage forms beneath the cortex interior to the VK.

The RF is composed of evenly spaced kineties with regularly spaced kinetosomes and the anterior kinetid of each kinety, except in Salpingacantha sp., is composed of two kinetosomes, both ciliated. The RF has not been described previous to this report. The RF is composed of 6-13 kineties except in T. mucicola and F. panamensis in which the number of kineties is 2 and 39 (30-50), respectively. The anterior double kinetid produces a long cilium from the anterior kinetosome in T. baltica, C. cratera, T. subacuta, S. steini, C. scalaroides, E. pectinis, F. panamensis, and P. simplex. The length of this cilium ranges from ca. 8-34 μ m in these species. Fauré-Fremiet (1924) observed these cilia on C. cratera (T. lacustris), T. campanula, T. bütschlii, Stenosemella ventricosa (T. ventricosa). These long and fairly stiff pairs of cilia of tintinnids and the bristles of oligotrichs, both originate from pairs of kinetosomes. These ciliary structures may be homologous but ultrastructural evidence must be obtained before any definite statements can be made.

The DK, found in every tintinnid examined except T. mucicola and Salpingacantha sp., is a conspicuous kinety often

running from the peristomial lip posteriorly to the aboral end of the cell. In E. pectinis the DK is split into two overlapping parts. The cilia of this kinety are usually longer than the other somatic cilia excluding the anterior double kinetids of some kineties. The DK is composed of kinetids with paired kinetosomes except in C. cratera, S. steini and E. pectinis, where the DK is single. The number of kinetids in the DK varies greatly within a species and appears to be related to the age of the cell; late stomatogenic stages have the greatest number of kinetids.

In T. baltica, C. cratera, T. subacuta, S. steini, C. scalaroides, F. panamensis, and P. simplex, the LF which is the same field as the lateral ciliary field of Fauré-Fremiet (1924) and Campbell (1926) can be divided into two subfields. The first subfield has widely spaced kineties and the anterior kinetid produces a long and a short cilium. The second subfield has closely spaced kineties and all of the kinetids produce single ciliferous kinetosomes. The cilia of the second subfield are often shorter than cilia of the first subfield. Fauré-Fremiet (1924) observed and figured the LF in T. campanula, and Stenosemella ventricosa (T. ventricosa) and differentiated the two parts of the LF in T. bütschlii. The LF consists of only one part in E. pectinis, and A. acuta. The kinetids of the LF are double in T. mucicola and A. acuta. The kineties of the LF in T. mucicola, T. baltica, C. cratera, T. subacuta, and S. steini are long, in C. scalaroides, E. pectinis, F. panamensis and A. acuta are shorter, and in P. simplex and Salpingacantha sp. are very short.

The PK, located posterior to the LF, was found in every species examined except A. acuta and Salpingacantha sp. The PK, composed of 5-29 kinetids, may begin anteriorly near the posterior end of the VK as in T. mucicola or P. simplex or may begin closer to the DK as in E. pectinis, C. scalaroides, S. steini, T. subacuta, C. cratera, and T. baltica. The kinetids of the PK are single in C. cratera, F. panamensis, C. scalaroides, E. pectinis, and P. simplex, and double in T. baltica, T. subacuta, S. steini, and T. mucicola. Associated with the PK of C. scalaroides are many nonkinetosomal staining granules of unknown composition and function. These ciliation patterns are unique to the tintinnids but at the anterior surface of the cell body in F. panamensis, C. cratera, T. baltica, T. subacuta, and S. steini the tight packing of kineties is reminiscent of heterotrichs. The widely spaced and very short kineties of Salpingacantha sp. are more oligotrich-like in character.

BUCCAL MORPHOLOGY. In A. acuta and Salpingacantha sp. the AZM is compressed laterally, lengthened along its long axis, mostly ventral in position, and very shallow in depth. The arrangement of the AZM in the other species examined agrees with the model tintinnid, with an anteriorly located circular oral opening and a deep infundibulum, and varies only in the number of membranelles whose proximal ends begin and end in the infundibulum. In T. mucicola, only one membranelle begins in the infundibulum while in S. steini there are 6-7 membranelles in this position. The AZM of the oligotrich, Strobilidium gyrans is similar in construction to

the model tintinnid (Deroux 1974).

The PM of tintinnids, as in the oligotrichs, lies to the right of the AZM. The PM of oligotrichs has been examined with TEM by Grain (1972) and with silver impregnation by Grim (1974) and Deroux (1974). In most species of tintinnids the PM courses anteriorly and to the right whereas in A. acuta the PM, as in the oligotrich, Strobilidium gyrans (Deroux 1974), courses to the left and lies just to the right and parallel to the AZM. The kinetosomal arrangement of the base of the PM ranges from a single linear row of kinetosomes to a membranellar arrangement, as in F. panamensis, with two long rows and one short one. Laval (1972) reported that the PM of Petalotricha ampulla consisted of a single row of kinetosomes. The heterotrich ciliates show a diversity in the construction of the PM from a single row of kinetosomes in Fabrea salina to the complex pattern in Bursaria truncatella (Tuffrau 1967b). Heterotrichs have the PM both on the far right (i.e., Blepharisma and Condylostoma magnum) and along the left side just to the right of the AZM (i.e., Spirostomum) (Tuffrau 1967b).

The tentaculoids and accessory combs, termed by Entz (1909) as the "Deckplättchen" and "Begleitkämme," respectively, are found exclusively in tintinnids. Tentaculoids were observed by Campbell (1926) to be contractile. Only one specimen out of over twenty stained specimens of T. subacuta possessed tentaculoids, suggesting that the tentaculoids may have been contracted in the other specimens. Accessory combs are cytoplasmic crests which often contain capsules. The crests were not seen with protargol but the capsules were often

conspicuous between the membranelles. The tentaculoids and accessory combs, if contracted and without capsules, may have gone unnoticed in some species.

NUCLEAR STRUCTURE. The nuclei vary in size, shape, and number in tintinnids but often consists of two macronuclei and two micronuclei as in, C. scalaroides, S. steini, C. cratera, and T. baltica. In some tintinnids, T. subacuta, E. pectinis, and A. acuta, the macronuclei are paired or have connections between them. Reorganization bands and condensation of the macronuclei occur during division.

The number of macronuclei may be important in specific and generic distinctions of some groups of tintinnids. Certain genera, i.e., Codonella, Dictyocysta, and Petalotricha, have multiple (over 50 in some species) macronuclei (Entz 1909).

Phylogenetic Trends within the Tintinnina

Tintinnids, existing within a lorica, face certain selective pressures other free swimming ciliates do not. Since only the oral membranelles and anterior portions of the cell body of tintinnids can extend beyond the lorica, the somatic cilia would no longer function in swimming. Therefore, it is expected that somatic ciliation, especially in the posterior portion of the cell body, would be reduced or become specialized for some other purpose. Other functions, induced by the presence of the lorica, for which the somatic cilia might be used are the removal of waste products from the lorica, lorica formation and maintenance, and positioning of the ciliate within the lorica. There would also be selection for stronger or

more efficient oral structures for swimming and feeding.

Based on the above selective pressures it is expected that the most primitive tintinnid would have many kineties per body area (high kinetal density index value), long kineties extended for the length of the body, and no or little specialization of the somatic cilia into fields or specialized kineties.

The prostomial ciliates which are more radially symmetrical with their mouth at the anterior end are generally considered primitive in relation to ciliates with ventrally placed mouths. If the same reasoning is applied to the mouth types of tintinnids then those tintinnids with the most prostomial (anteriorly located) mouths would be considered most primitive.

The species examined in this paper can be separated into four groups based on the number of kineties per area (the kinetal density index), the length of the kineties, and the position and construction of the mouth. The first and possibly most primitive of the tintinnids examined is T. mucicola with long kineties, little specialization of somatic cilia, and the most prostomial mouth. A less primitive characteristic of T. mucicola is its low kinetal density index value. Parfavella denticulate, examined by protargol and SEM by Hedin (1976a), has long kineties which reach the posterior end and has a low kinetal density index value.¹⁴ P. denticulata is tentatively placed in this first group, though its oral structure has not been described in detail. The next group would be comprised of

¹⁴The kinetal density value is 1.7 as calculated from an SEM photograph in the publication by Hedin (1976a).

those species with a high kinetal density index, specialized ciliation, and a mouth with slight ventralization (more membranelles beginning in the infundibulum). Included in this second group are T. baltica, C. cratera, T. subacuta, S. steini, C. scalaroides and F. panamensis. E. pectinis and P. simplex comprise the third group and have a low kinetal density index, shorter kineties which are specialized, and a prostomial mouth with slight ventralization. The last group comprised of two species, A. acuta and Salpingacantha sp. have a low kinetal density index, few short kineties, and a ventral mouth. The somatic kineties of these two species show little specialization.

The relative phylogenetic position of these species is in agreement with the phylogenetic model proposed by Kofoed and Campbell (1939) which is based on lorica morphology, except that E. pectinis belongs to the same family as A. acuta and Salpingacantha sp. The differences in buccal morphology and somatic ciliation patterns argue against this assignment to the same family. It is expected that many changes in taxonomic position will be necessary when the somatic ciliation patterns and buccal morphology, based on protargol stained specimens, are examined for other tintinnids.

Phylogenetic Position of the Tintinnina

Fauré-Fremiet (1950, 1970) suggested that the heterotrichs gave rise to the oligotrichs and that the oligotrichs in turn gave rise to the tintinnids. This relationship is unlikely in that an oligotrich with only a few cilia or kineties would have to give rise to a loricate ciliate with many rows of cilia.

This is in opposition to the hypothesis that the existence of a ciliate in a lorica has a tendency to reduce somatic ciliation. It is therefore suggested that the tintinnids did not evolve from oligotrich ancestors.

Heterotrichs, with many long rows of cilia and an AZM would be likely ancestors of tintinnids. This ancestral heterotrich would have to possess an anteriorly located mouth. Evolution within the lorica would lead to reduction of the somatic cilia, especially at the posterior end of the cell, and specialization of those cilia or kineties which remain. Since representatives of a large group of tintinnids do fit this pattern it is suggested that the tintinnids evolved from heterotrichs or from a more primitive ancestor common to both the heterotrichs and tintinnids.

Recommendations

It is suggested, in order to decrease the variability of measurements and to observe the specimens in a more natural state, that a method be developed to fix tintinnids in the expanded state and still allow staining by the protargol staining technique. Sectioning of the protargol stained cells, as Entz (1909) did with hematoxylin stained specimens, is also recommended. In addition, live observations, unfortunately few in this report, should accompany descriptions based on stained material.

The obvious importance of cytological data, as demonstrated in this report, should no longer be overlooked in studies of tintinnid taxonomy. The technique of protargol staining has

been shown to reveal many important cytological structures upon which phylogenetic relationships, within the tintinnids and between the tintinnids and other groups of ciliates, can be constructed. Morphogenesis and in particular stomatogenesis, both of phylogenetic importance, can also be studied using the protargol technique and should be examined in future studies. Further systematic studies on tintinnids should be based on both the lorica and cytosome.

APPENDIX A. A modified Bodian Protargol Technique.

The procedures given in this appendix are those that I found to work best for staining tintinnids.

Modified Bodian Protargol Staining Technique

EMBEDDING PROCEDURE

1. Add concentrated free animals to Bouins fixative for a minimum of one day.
2. Wash in tap water by centrifugation until the majority of the fixative is diluted out.
3. Dehydrate in a graded isopropyl alcohol series (15-30-50-70-85%) for 5 minutes in each change.
4. On a 22 mm square coverslip place a small drop of Mayer's egg albumum (1/2 glycerine and 1/2 egg white) and spread out with little finger.
5. Allow albumen to dry until 'sticky,' about 1-5 minutes.
6. With a micropipette add concentrated drop of animals from 85% isopropyl alcohol to albumenized coverslips.
7. Allow some of the alcohol to evaporate but not enough to permit the desiccation of the animals.
8. Put two coverslips back to back and place in a Columbian jar of 95% isopropyl alcohol for 5 minutes.
9. Place the pairs of coverslips in 100-100% isopropyl for a minimum of 5 minutes in each.
10. Place in absolute methanol for 5 minutes.
11. Dip each coverslip pair into 0.5% Parlodion and out again with a deliberate and even movement without stopping. Drain off excess Parlodion on paper toweling.
12. With fine forceps hold the coverslip pair in air until they become hazy white. Do not let air dry.
13. Place in 70% isopropyl alcohol for 3-4 minutes.
14. Run through 50-30-15% isopropyl alcohol for 5 minutes in each.

15. Wash in tap water 3 times for 30 seconds in each wash.

STAINING PROCEDURE

16. Dip coverslips into 0.5% solution of KMnO_4 for 2.5 minutes.
17. Wash in water to remove excess KMnO_4 . A single wash should suffice.
18. Dip coverslips in 5% oxalic acid solution for 5 minutes. This should remove the brown color produced by the KMnO_4 .
19. Wash several times in water. 3 to 6 washes to remove the oxalic acid which reacts precipitously with protargol.
20. Place in protargol solution placing steel-wool polished copper strips between each coverslip pair. If a Columbian staining jar is used, 5 pieces of copper cut to the size of a coverslip are quite adequate.

Protargol solution: Make a 2% solution by sprinkling the powder on to the surface of the measured volume of water. It is allowed to dissolve without stirring. The pH of the solution is then taken and adjusted to 8.6. If the pH is too high, add 0.1 N HCl to lower it; if it is too low, add .1 N NaOH to raise it.

21. Coverslips are left in protargol overnight at room temperature.
22. Remove coverslips from protargol and place in a freshly made saturated solution of hydroquinone for 5 minutes.

23. Wash in water 2-3 times.
24. Dip coverslips as fast as possible in a 1% solution of gold chloride.
25. Place coverslips in a 2% oxalic acid solution immediately after the gold chloride dip. Leave in for 2.5 minutes.
26. Wash once in water.
27. Place coverslips in a 5% sodium thiosulfate ($\text{Na}_2\text{S}_2\text{O}_3$) solution for 5 minutes.
28. Wash once in water.
29. Dehydrate in isopropyl alcohol series: 15-30-50-70-85-95-100-100%, 5 minutes for each transfer.
30. Place in xylene, two washes of 5 minutes each.
31. Mount coverslips on slides with Permount.

Appendix II. Statistical and Meristic Data

Given below are the symbols used in this appendix, the definition of the symbols, and the units of each symbol.

<u>Symbol</u>	<u>Definition</u>	<u>Units</u>
n	Sample size	
\bar{X}	Mean	μm
SD	Standard deviation	μm
SE	Standard error	μm
CV	Coefficient of variation	%
R_h	Upper limit of range	μm
R_l	Lower limit of range	μm
Med	Median	μm

Tintinnopsis baltica Brandt 1896

	n	\bar{X}	SD	SE	CV	Rh	Rl	Med
<u>Lorica</u>								
Length	19	62.3	8.00	1.84	12.9	83.4	52.6	
Oral diameter	20	37.0	1.83	0.409	4.95	41.3	33.2	
Nuchal Constriction	11	31.4	1.17	0.353	3.73	33.5	29.3	
Bowl	23	34.5	2.32	0.484	6.72	42.4	30.6	
<u>Cytology</u>								
Length	19	34.3	4.25	0.975	12.4	43.9	28.9	
Width	21	23.4	3.93	0.858	16.8	29.5	15.1	
Diameter AZM	22	19.3	1.03	0.219	5.33	21.7	17.5	
Length macronuclei	11	8.74	1.36	0.409	15.5	11.8	6.89	
Width macronuclei	11	5.63	1.14	0.345	20.3	6.70	3.40	
Diameter micronuclei	11	1.9	0.14	0.043	7.4	2.2	1.7	
Diameter capsules	10	0.86	0.057	0.018	6.7	0.92	0.73	
# Membranelles	5					17	17	17
# Kineties	11					34	30	32
# Kineties in LF	11					24	21	22
# Kineties in RF	18					9	6	7

Codonella cratera (Leidy 1877) Vorce 1881

	n	\bar{X}	SD	SE	CV	Rh	Rl	Med
<u>Lorica</u>								
Length	17	58.4	4.03	0.979	6.90	65.0	58.8	
Oral diameter	19	36.2	2.42	0.556	6.69	39.5	31.5	
Nuchal constriction	20	32.5	1.65	0.369	5.08	35.1	30.4	
Bowl	20	41.1	2.27	0.508	5.52	46.1	36.9	
Length ant. cylinder	14	25.1	6.43	1.72	25.6	36.0	12.8	
<u>Cytology</u>								
Length	17	27.1	4.80	1.16	17.1	35.9	20.3	
Width	17	27.1	3.16	0.767	11.7	31.8	19.8	
Diameter AZM	17	18.8	1.74	0.422	9.26	22.7	16.7	
Length macronuclei	22	12.1	2.69	0.575	22.3	20.0	8.9	
Width macronuclei	23	6.64	0.916	0.191	13.8	8.40	4.73	
Diameter micronuclei	12	3.4	0.64	0.18	19	4.3	2.1	
Diameter LFG	10					1.1	0.83	0.92
# Membranelles	3					16*	16*	
# Kineties	6					33	30	32
# Kineties in LF	8					23	19	22
# Kineties in RF	9					9	7	8
# Kinetosomes in DK	8					39	25	29
# Kinetosomes in PK	4					13	8	11

* no oral views - only approximate counts

Tintinnopsis subacuta Jorgensen 1899

	n	\bar{X}	SD	SE	CV	Rh	Rl	Med
<u>Lorica</u>								
Length	22	92.6	5.93	1.27	6.41	102	78.9	
Oral diameter	23	35.5	2.48	0.518	6.99	39.8	29.9	
Bowl	23	42.0	2.68	0.558	6.37	47.2	35.6	
Length ant. cylinder	14	45.2	3.59	0.958	7.94	50.0	37.4	
<u>Cytology</u>								
Length	22	48.0	6.30	1.34	13.1	58.8	35.3	
Width	22	26.7	3.33	0.711	12.5	31.8	20.0	
Diameter AZM	22	20.7	1.78	0.380	8.63	23.5	16.9	
Length giant ciliary tuft	8	71.8	24.1	8.52	33.6	99.7	29.3	
Length macronuclei	10	8.20	2.21	0.699	26.9	12.3	5.74	
Width macronuclei	10	4.69	0.680	0.215	14.5	5.65	3.90	
Diameter micronuclei	10	1.9	0.23	0.072	12	2.2	1.5	
# Membranelles	14					20*	17*	19*
# Kineties	8					40	35	38
# Kineties in LF	12					27	22	24
# Kineties in RF	12					13	10	11
# Kinetosomes in DK	10					58	28	42
# Kinetosomes in PK	11					25	18	22

* no oral views - only approximate counts

Stenosemella steini Jorgensen 1924

	n	\bar{X}	SD	SE	CV	Rh	RI	Med
<u>Lorica</u>								
Length	16	52.9	6.47	1.62	12.2	66.9	47.2	
Oral diameter	9	24.8	4.44	1.48	17.8	31.8	19.2	
Width at shoulders	16	40.0	8.37	2.09	20.9	54.0	28.4	
Bowl	21	48.7	5.60	1.22	11.5	59.3	42.3	
<u>Cytology</u>								
Length	21	30.3	6.80	1.48	21.3	42.4	23.9	
Width	24	33.4	8.99	1.84	26.9	65.4	24.8	
Diameter AZM	11	25.9	5.94	1.79	22.9	33.0	18.8	
Length macronuclei	10	10.8	2.69	0.851	24.9	14.9	6.20	
Width macronuclei	10	5.93	1.18	0.373	19.9	7.62	4.36	
Diameter micronuclei	10	2.23	0.582	0.184	26.2	2.98	1.24	
Diameter LFG	10	0.83	0.084	0.027	10	1.0	0.69	
# Membranelles	2					20	20	20
# Kineties	7					42	34	40
# Kineties in LF	8					32	22	29
# Kineties in RF	11					7	9	8
# Kinetosomes in DK	10					62	22	42

Climacocylis scalaroides Kofoid and Campbell 1929

	n	\bar{X}	SD	SE	CV	Rh	RI	Med
<u>Lorica</u>								
Length	8	112	20.9	7.39	18.6	136	77.8	
Oral diameter	8	33.0	1.97	0.693	5.95	35.5	29.1	
# Spiral turns	8					7	3	6
<u>Cytology</u>								
Length	7	39.4	6.01	2.27	15.2	45.1	31.6	
Width	7	21.1	2.12	0.802	10.0	23.5	19.6	
Diameter AZM	7	20.8	1.20	0.488	5.75	22.4	19.2	
Length macronuclei	14	7.14	1.17	0.267	16.4	8.86	5.09	
Width macronuclei	14	4.75	1.10	0.249	23.2	7.21	3.03	
Diameter micronuclei	11	1.7	0.21	0.062	12	1.9	1.4	
# Membranelles	2					19	18	19
# Kineties	4					30	28	29
# Kineties in LF	4					21	19	20
# Kineties in RF	5					7	7	7
# Kinetosomes in DK	5					31	25	30
# Kinetosomes in PK	5					16	6	10

Favella panamensis Kofoed and Campbell 1929

	M	\bar{X}	SD	SE	CV	Rh	Rl	Med
<u>Lorica</u>								
Length	22	213.	29.9	5.32	11.7	254	162	
Oral diameter	23	101.	9.54	1.99	9.40	123	85.6	
Bowl	23	80.0	10.3	2.14	12.8	105.	63.9	
Length spine	23	46.8	13.2	2.76	28.2	71.	20.9	
Distance from oral rim to annulation	19	9.31	1.26	0.29	1.19	11.3	6.77	
<u>Cytology</u>								
Length	15	80.7	30.7	7.87	37.8	168	40.2	
Width	15	65.7	8.81	2.28	13.4	79.1	39.1	
Diameter AZM	15	60.2	8.84	2.28	14.7	71.6	34.3	
Length macronuclei	10	26.8	5.22					
Width macronuclei	15	8.67	1.92	0.496	22.2	12.3	5.32	
Diameter micronuclei	9							
Diameter LFG (small)	10	1.1	0.21	0.064	19	1.5	0.73	
Diameter LFG (large)	10	1.9	0.36	0.11	19	2.4	1.3	
# Membranelles	3					17	17	17
# kineties	2					87	88	88
# kineties in RF	4					55	34	46
# kineties in LF	6					50	30	39

Tintinnidium mucicola (Claparède and Lachmann 1858) Daday 1887

	n	\bar{X}	SD	SE	CV	Rh	Rl	Med
<u>Lorica</u>								
Length	20	83.5	21.3	4.76	25.5	113	43.4	
Bowl	22	44.1	4.12	0.878	9.34	37.4	9.34	
Length ant. extension	9	41.5	14.1	4.68	33.9	61.7	21.3	
Length bowl	9	22.7	2.43	0.809	10.7	25.6	17.3	
<u>Cytology</u>								
Length	20	20.9	4.26	0.95	20.4	28.6	13.6	
Width	21	24.9	1.90	0.416	7.63	29.7	22.2	
Diameter AZM	23	22.6	1.26	0.263	5.58	26.8	20.9	
Length macronuclei	23	9.04	1.66	0.347	18.4	13.0	5.78	
Width macronuclei	23	6.45	0.852	0.178	13.2	7.85	4.54	
Diameter micronuclei	1					1.7	1.7	1.7
Diameter LFG	6	1.3	0.095	0.039	7.6	1.4	1.2	
# Membranelles	10					17	17	17
# Kineties	14					16	16	16
# Kineties in RF	14					2	2	2
# Kineties in LF	14					14	14	14

Amphorelloopsis acuta Schmidt 1901

	n	\bar{X}	SD	SE	CV	Rh	Rl
<u>cytology</u>							
Length Macronuclei	6	7.63	1.93	0.789	25.3	9.87	4.91
Width Macronuclei	6	3.84	0.672	0.274	1.75	4.82	2.98

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