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CLASSIFICATION AND PHYLOGENY IN
THE SUBORDER EUPLOTINA
(CILIOPHORA, HYPOTRICHIDA)

BRUCE FLEMING HILL

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(CILIOPHORA, HYPOTRICHIDA)

University of New Hampshire

PH.D.

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CLASSIFICATION AND PHYLOGENY IN THE SUBORDER EUPLOTINA
(CILIOPHORA, HYPOTRICHIDA)

BY

BRUCE F. HILL

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M. S. , The George Washington University, 1973

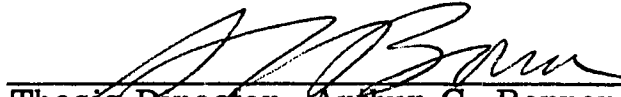
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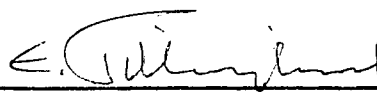
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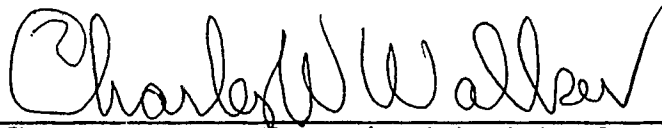
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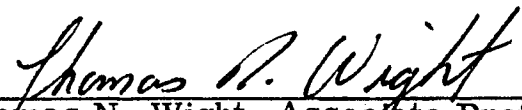
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To My Parents

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ABSTRACT

Eleven genera of hypotrichs were placed in the family Euplotidae by Borror and, with his description of Cytharoides, Tuffrau added a twelfth genus. Corliss' recent review of ciliate taxonomy has placed these 12 genera into 3 families (Aspidiscidae, Euplotidae and Gastrocirrhidae). Five of the 12 genera (Euplotes, Aspidisca, Diophrys, Euplotaspis and Uronychia) were studied for an understanding of their cortical structure and process of cortical morphogenesis during cell division. The results were compared to the division process in other genera, other morphogenetic processes occurring during conjugation, encystment-excystment and regeneration. This investigation, which combined light microscopy of living and stained (Protargol, Chatton-Lwoff) specimens and scanning electron microscopy of preserved specimens, has provided information which leads to certain taxonomic decisions and speculation on the evolution of these hypotrichs.

A number of major taxonomic revisions are proposed: eleven genera are removed from the suborder Sporadotrichina and placed in a new suborder, Euplotina, within the order Hypotrichida. Unifying morphogenetic and cortical characteristics of the new suborder include (1) the opisthe oral primordium developing de novo just posterior to the parental adoral zone of membranelles with continuing development occurring in a subsurface pouch, (2) the oral primordium not donating

kinetosomes to any developing cirral primordia, (3) the cirral primordia for frontoventral and transverse cirri forming separately and apart from any other primordia or parental structures, (4) the left marginal cirral primordia developing lateral to the parental left marginal row, (5) the parental AZM becoming the proter AZM, (6) a well-developed argyrome system, (7) no right marginal cirri, (8) pair formation during conjugation is ventral-surface-to-ventral-surface and (9) cysts covered by two layers form without all the kinetosomes being resorbed. Frontoventral and transverse cirral primordia developing in association with oral primordium in Discocephalus (according to Wicklow) causes this genus to remain in the sub-order Sporadotrichina. However, its division process shows a possible evolutionary step in the line toward euplotine hypotrichs.

The suborder Euplotina is divided into four families:

Aspidiscidae, Euplotidae, Gastrocirrhidae and Uronychidae.

Aspidiscidae: flat, disk-shaped animals with reduced paroral and endoral membranes, AZM entirely on the ventral surface, no left marginals or caudal cirri (rudimentary caudals in Euplotaspis) and long frontoventral and transverse cirral primordia, which include the genera Aspidisca, Euplotaspis and, tentatively, Paraeuplotes (until more is known about its division process).

Euplotidae: presence of both left marginals and caudal cirri

with a large ventrally opening buccal cavity; includes the genera Diophrys, Certesia and the 51 species which are included in the genus Euplotes.

The genus Euplotes is divided into 5 separate genera: (1) Euplotiscus: 10 frontoventral cirri, single dorsal argyrome with all six species being marine; (2) Euplotes: 10 frontoventral cirri, double dorsal argyrome with most of the 17 species being marine, (3) Euplotopsis: 9 frontoventral cirri in pattern I, double to complex dorsal argyrome with most of the 15 species being marine: (4) Euplotoides: 9 frontoventral cirri in pattern II, double dorsal argyrome with all 7 being freshwater species; (5) Euplotaleos: 9 frontoventral cirri, dorsal argyrome with long, longitudinal polygons between a double system, with a single marine species.

Gastrocirrhidae: no left marginal or caudal cirri (rudimentary left marginal cirrus in Euplotidium) with a large anteriorly opening buccal cavity; includes the genera Gastrocirrhus, Cytharoides, Euplotidium and, tentatively, Swedmarkia (until more is known about its division process).

An additional new family, Uronychidae, is formed to contain the single genus Uronychia. Morphogenetic and cortical characteristics of the new family include (1) development during division of a proter and opisthe oral primordium; (2) presence of large, left marginal cirri;

(3) presence of large, ventral caudal cirri; and (4) a well-developed two-part buccal membrane.

It is suggested that the main line of evolution within the sub-order Euplotina has been through the family Euplotidae (Diophrys — Certesia — Euplotiscus — Euplotes — Euplotopsis — Euplotoides — Euplotaleos). The family Uronychidae (Uronychia) branches early from an ancestor of the entire sub-order. The family Aspidiscidae (Euplotaspis — Aspidisca) branches from a Euplotiscus-like organism while the family Gastrocirrhidae (Euplotidium — Cytharoides — Gastrocirrhus) branches from a Euplotes-like organism.

INTRODUCTION

Some 7,200 species have been described in the phylum Ciliophora of which nearly 500 are found in the order Hypotrichida. Representing the pinnacle of ciliary differentiation, the hypotrichs are among the most easily recognized of the free-living protozoa due to the striking nature of these ciliary morphological features. Today, they are becoming popular experimental organisms (over 800 references in the genus Euplotes alone (Hill, 1980a)). These highly evolved ciliated protozoa are known to be important members of the still incompletely explored benthic communities of estuarine and tidal marshes (Borror, 1965b, 1968a, 1972a, 1975; Brown, 1973; Dragesco, 1962; Fenchel, 1967, 1968A, 1968b, 1969; Johannes, 1965; Kirby, 1934; Tietjen, 1969; Webb, 1956). There they exert a significant influence on these communities by their large numbers. In areas rich in bacterial growth, such as fine sands and tidal marshes, the ciliates range from 10^6 to 4×10^7 individuals per m^2 and therefore are 10 - 100 times more numerous than the total number of metazoa (Fenchel, 1967). Their biomass ($0.03 - 2.3g$ wet wt./ m^2) can be on the same order and often larger than the biomass of micrometazoa.

The large populations of ciliates which inhabit the salt marshes and sandy habitats of the open coast are made up of many different species. These diverse communities of microorganisms which are

interwoven in time and space have become well-recognized as links in the transformation of macrophyte structural materials into compounds usable by larger carnivorous and omnivorous animals (Barlocker & Kendrick, 1973, 1975a, 1975b; Barsdale et al., 1974; Fenchel, 1968a, 1969, 1970, 1971, 1975; Lee et al., 1976). Ciliates may account for up to 25% or more of the total animal respiration of sub-littoral sands (Fenchel, 1969) which is comparable to values established in Spartina flats (Weiser & Kanwisher, 1961). Studies on aufwuchs protozoa have indicated that most species have high reproductive rates over wide physiological conditions (Fenchel, 1968b; Lee et al., 1970, 1976; Persoone & Deplaecie, 1972), but relatively specialized dietary requirements (Persoone et al., 1975). Present evidence suggests that herbivore food specialization coupled with high reproductive rates underlies the dynamic changes in community structure and the high rates of mineralization and nutrient turnover characteristics of these communities (Muller & Lee, 1977). One can imagine that the present highly diverse community structure is finely tuned, the result of rapid co-evolution of the small herbivores and the larger carnivores and omnivores. A difficult problem in understanding the biology of these communities by physiological ecology, nutritional studies or any other type of investigation is the discernment of taxonomic and evolutionary relationships of the marine ciliates.

A number of reasons have contributed to our lack of understand-

ing, but now there is intense interest in the systematics of marine ciliates. Within the past 10 years, new methods have disclosed how widespread and important ciliates are in the marine community. As new niches are found and studied, many new species have been discovered. New methods of cultivation, fixation and staining allow detailed investigation of many different species spawning new hypotheses of evolution and classification of different groups of ciliates.

A detailed review of hypotrich systematics has provided the impetus for a more modern investigation of hypotrich systematics thru the use of cortical morphogenetic patterns during cell division. The process of cortical morphogenesis, whether during binary fission, reorganization, conjugation or excystment, has been known in a few ciliates for a long time (Trembley, 1744). With the advent of silver impregnation methods in the late 1920's and 1930's, details of both buccal and somatic infraciliary organelles could be revealed allowing the morphogenetic patterns of dividing cells to be studied. Starting with the pioneering work of Chatton, Lwoff and Fauré-Fremiet, well designed studies have shown that differences in morphogenetic patterns during ontogeny can provide data of significance in determining an organism's phylogenetic affinities. Only in the past 20 years however, with the description of cortical morphogenesis during fission in a number of different species, have these processes become important in the study of ciliate phylogeny and evolution. The possible phylogenetic relation-

ship between (1) astomes and the thigmotrichs (de Puytorac, 1954, 1959, 1963, 1972) (2) chonotrichs and the cyrtophorine gymnostomes (Faure-Fremiet, 1950; Guilcher, 1951) (3) suctorians and holotrichs (Canella, 1957; Faure-Fremiet, 1950a; Guilcher, 1951) and (4) peritrichs and the hymenostomes (Faure-Fremiet, 1950, 1965; Lom, 1964) have all been strengthened by detailed studies of the morphogenetic sequence of patterns during binary fission. Much of this work has been oriented toward the lower taxa (Corliss, 1974; Dragesco et al. 1977; Evans & Thompson, 1964; Hatzidimitriou & Berger, 1977; Jankowski, 1968; de Puytorac, 1972; Raabe, 1970), but other more diverse groups of ciliates (Batisse, 1975; Jankowski, 1973; Lom, 1964; Wicklow & Borrer, 1977) have also been studied. Previous descriptive analyses of cortical morphogenesis of cell division of the members of the order Hypotrichida have proved helpful in determining phylogenetic relationships among the members of the order (Borrer, 1972b, 1979a, b; Borrer & Evans, 1979; Deroux & Tuffrau, 1965; Diller, 1975; Grimes, 1972; Grimes & L'Hernault, 1978; Jerka-Dziadosz & Frankel, 1969; Tuffrau, 1964; Walker & Grim, 1973; Wicklow, 1978, 1979).

Although considerable significance has been placed on descriptive analysis of cortical morphogenetic events in the study of ciliate systematics and evolution, other methods also have been developing. One of the most promising areas of study is through the

use of multivariate analysis to characterize the ciliates highly differentiated cortical regions. This method, which studies variations in form and function as partitioned among subpopulations of genetically related organisms, provides the tools for assessing the evolutionary process as it applies to any particular group of organisms. The procedure is to choose a large series of derived discriminatory characteristics and to measure them (developing sample means, standard errors, ranges, coefficients of variation and estimates of variability) using large samples ($n=100$) from diverse geographic sources and then to analyse them using large appropriate uni- and/or multivariate techniques (Berger, 1977; 1978; 1979). Among the hypotrichs, the procedure has shown that the genus Euplotes can be divided into six evolutionary different groups (Gates, 1977; 1978a, b, c; 1979). However, with many species, this method has two inherent problems: (1) the actualization of large samples from many different geographic sources of species which have only been found several times and which never have been cultivated in the laboratory (e. g. Euplotaspis, Discocephalus); (2) the morphometric inseparability of what are known to be separate species (Gates & Berger, 1976) coupled with our limited knowledge of sibling species in the multipolar mating type syngens commonly seen in the hypotrichs (Heckmann, 1963; Katashima, 1959; Kosaka, 1973; Luporini & Dini, 1977; Luporini & Nobili, 1967; Nobili, 1966). Even though this method may present problems in separation of specific closely-related species (e. g. Paramecium,

Euplotes), it should prove invaluable at the beta level (higher-order classification) and gamma level (evolutionary studies) of taxonomy.

A second approach is the use of electrophoretic migration of specific isozymes to separate closely-related species. Electrophoresis is used to separate different isozymes which can be distinguished and characterized by their sign and relative magnitude of their net charge under specific standard conditions. To taxonomically distinguish the 14 species in the Paramecium aurelia complex (Allen & Gibson, 1971; Allen et. al. , 1971; 1973; Sonneborn, 1975; Tait, 1970), the number can be used. The procedure has also been very useful in identifying different strains within the breeding syngens of Tetrahymena pyriformis (Borden et. al. , 1973a, b; Borden et. al. , 1973; Nanney & McCoy, 1976). Unfortunately, this method also has the inherent problems that require fairly large samples to perform the needed electrophoretic tests and, as with the morphometric method, in some cases, closely-related species cannot be separated (Allen & Gibson, 1975). However, this method has proved useful in separating commonly used species and in understanding the evolutionary structure of complexes of sibling species (Adams & Allen, 1975; Borden et. al. , 1973c).

These methods have shown that the structural organization of a cell has considerable homeostatic capacity. Patterns of organellar

associations tend to be perpetuated for an extremely long time (Nanney, 1968, 1977). Even though any type of cortical morphogenetic process is a dynamic one, a considerable amount of evidence has shown that patterns of stomatogenetic and somatic morphogenesis show less diversity than that seen in the cortical architecture of the same cell (Corliss, 1967; Nanney, 1977). Because of this stability, considerable significance has been placed on descriptive analysis of cortical morphogenetic events in the study of systematics and evolution of the ciliates, but usually at the family level or above. It now seems appropriate to review the different cortical morphogenetic events which occur within a single family to see if a similar significance concerning systematics and evolution can be placed at the generic level. A lot is known about the specific events that occur during cortical morphogenesis in the family Euplotidae during different aspects of their life cycle; conjugation, excystment and reorganization.

As a contribution toward understanding the systematics and evolution of the family Euplotidae, I have investigated the following :

1. patterns of cortical morphogenesis during division of five members of the family Euplotidae: Euplotes, Aspidisca, Diophrys, Euplotaspis and Uronychia;
2. literature on morphogenetic events occurring during conjugation, excystment and reorganization;
3. different patterns as seen in the family Euplotidae with the cortical morphogenetic patterns seen in other hypotrichs during division;

4. general evolutionary trends within the family Euplotidae using cortical morphogenetic data along with the general cortical structure of each organism.

MATERIAL AND METHODS

Collection Data:

Euplotes trisulcatus Kahl, 1932, as redescribed by Tuffrau (1960) and Dragesco (1963), was collected from an algal mat of a tidal pool located near Route 1A at Odiorne's Point, Rye, New Hampshire, (43° 02' 22" N. Lat., 70° 42' 57" W. Long.) and was maintained in filtered seawater (32⁰/oo) with rice grains at 20⁰C.

Aspidisca costata (Dujardin, 1841) as redescribed by Diller (1975), was collected from Kenilworth Aquatic Gardens, Washington, D. C., (38° 55' 30' N. Lat., 76° 58' 10" W. Long.) and maintained in Pringsheim solution with rice grains at 20⁰C. A. aculeata Ehrenberg, 1838 was collected from a tidal marsh pool located near Route 1A at Odiorne's Point, Rye, New Hampshire; and A. baltica Kahl, 1932 was collected with an alga (Ulva lactuca) from a sample taken from Great Bay near Adams' Point, Durham, New Hampshire, (43° 05' 45" N. Lat., 70° 52' 10" W. Long.). Both marine species were maintained in filtered seawater (32⁰/oo) with rice grains at 20⁰C.

Diophrys scutum (Dujardin, 1841) was collected from seawater trays at the Jackson Estuarine Laboratory, Durham, New Hampshire; D. oligothrix Borrer, 1965 was collected from a tidal marsh pool located near Route 1A at Odiorne's Point, Rye, New Hampshire. Both species were maintained at 22⁰C. in F/2-enriched seawater

media (Guillard & Ryther, 1962) made with milipore filtered seawater (28⁰/oo) and fed on the diatom Phaeodactylum tricornutum as described by Luporini (1967). D. appendiculatus (Ehrenberg, 1838) was collected from a tidal marsh pond at Adams' Point, Durham, New Hampshire, and maintained in filtered seawater (28⁰/oo) with rice grains at 20⁰C.

Euplotaspis cionaecola Chatton & Seguela 1936, an inhabitant of the bronchial cavity of Ciona intestinalis was found in this ascidian from specimens obtained from the Marine Biological Laboratory at Woods Hole, Massachusetts.

Uronychia transfuga (Müller, 1786) was collected from seawater trays at the Jackson Estuarine Laboratory, Durham, New Hampshire, and a tidal marsh pool located near Route 1A at Odiorne's Point, Rye, New Hampshire. They were maintained at 22⁰C. in milipore filtered seawater (28⁰/oo) and fed on small flagellates and ciliates (Holosticha diademata, Uronema marinum) which fed on rice grains.

Listed in appendix I are the 24 different species of Euplotes that have been cultivated in the laboratory during the past five years.

Fixation and Staining Techniques:

Permanent slides for light microscopic observation of cortical morphogenesis of cells were stained by the following modified protargol method (Deroux & Tuffrau, 1967; Grimes, 1972; Jerka-Dziadosz &

Frankel, 1969; Tuffrau, 1967; Hammersmith (personal communication)

1. Concentrate animals by centrifugation and cool to 5°C.
2. Add cool (5°C.) Perenyi's fluid (chromic acid 1% (w/v), 3 ml.; nitric acid 10% (v/v), 8 ml.; ethanol 95% (v/v) 6 ml.; distilled water 3 ml.; mixed just before using) to concentrated animals for 3 min.
3. Using centrifugation wash fixed cells twice (5 min.) in 70% isopropyl alcohol.
4. Place in 95% isopropyl alcohol for 10 min.
5. On a 22 mm square coverslip place a small drop of Meyer's egg albumen and spread out very thin with your finger.
6. Allow albumen to dry until tacky; about 10 min.
7. Using a micropipette add a small drop of concentrated animals from the 95% isopropyl alcohol to the albumenized coverslip.
8. Allow some of the alcohol to evaporate, but not enough to cause the dessication of the animals.
9. Slowly pipette 2-3 drops of formal alcohol (10% aqueous formaldehyde, 3 parts; 95% ethyl alcohol, 1 part) onto coverslip for 3-4 min.
10. Place two coverslips back-to-back into a Columbia jar of formal alcohol for 30 min.
11. Place paired coverslips consecutively in 95%; 100%; 100% isopropyl alcohol for 5 min. each.
12. Place in absolute methanol for 10 min.
13. Dip each coverslip pair into collodian (25% flexible Parlodoin; 75% absolute methanol) and out again with a deliberate and even movement

without stopping and drain off excess on paper toweling.

14. With forceps hold the coverslip pair until the collodian is just dry.
15. Place in 95% isopropyl alcohol for 5 min.
16. Hydrate cells by passing through a series (70%, 50%, 30%, 15%) of isopropyl alcohol for 5 min. each.
17. Wash 3 times in distilled water for 2 min. each wash.
18. Place in 0.5% (w/v) potassium permanganate for 10 min.
19. Wash 2 times in distilled water for 5 min. each wash.
20. Place in 5% oxalic acid for 10 min.
21. Wash 2 times in distilled water for 5 min. each wash.
22. Put 10 ml. distilled water (pH 5.3) in Columbia jar and add 0.2 gm. Roque protargol powder. Do not mix, but let powder float undisturbed on surface of water until completely dissolved by heating to 70°C.
23. Add paired coverslips just after protargol powder has dissolved for 30 min. at 70°C.
24. Wash in distilled water for 2 min.
25. Place paired coverslips into solution of 1% hydroquinone (w/v); 5% sodium sulfite (w/v) — disregard time and observe with dissecting scope until animal's AZM becomes dark brown.
26. Wash 3 times in distilled water for 30 sec. each wash.
27. Place in 2.0% (w/v) oxalic acid for 10 min.

28. Wash 2 times in distilled water for 5 min. each wash.
29. Place in 5.0% (w/v) sodium thiosulfate for 10 min.
30. Wash 2 times in distilled water for 5 min. each wash.
31. Dehydrate cells by passing through a series (15%, 30%, 50%, 70%, 95%, 100%) isopropyl alcohol for 5 min. each.
32. Place in absolute methanol for 10 min.
33. Place in absolute isopropyl for 5 min.
34. Place in two changes of absolute xylene for a minimum of 10 min. each.
35. Mount coverslip on slide.

The above protargol method was modified when working with thigmotatic species (e. g. Aspidisca). The modification involved fixation and adhesion of specimens to coverslips. Clean 22 mm square coverslips were lowered onto the scum of stock cultures, lifted with a minimum of culture fluid, and placed scum-side up on paper toweling. A drop of the following (chromic acid 1%, 3 ml. ; nitric acid 10%, 8 ml. ; ethanol 95%, 0.5 ml. ; t-butanol, 5.5 ml. ; distilled water, 3 ml. ; mixed just before using) was pipetted onto the coverslip from a height of 2-3 cm. After 5 sec. , the coverslip was flooded with additional drops of fixative; and 1 min. later excess fixative was drained off and the coverslip placed in formal alcohol. The normal protargol procedure was followed from this point.

A second method for observing the processes of cortical morphogenesis was by Corliss' (1953) modification of the Chatton-Lwoff (1936) technic of silver impregnation.

1. Concentrate animals by centrifugation and cool to 5⁰C.
2. Add cold Champy's fluid with DaFano's solution (cobalt nitrate 1g, sodium chloride 1g; formalin 10 ml; distilled water 90 ml)
4. Change the DaFano's solution three more times until all the Champy's fluid is removed.
5. Leave organisms in clean DaFano's solution overnight.
6. Wash cells with distilled water 3 times until all the DaFano's solution is removed.
7. Place a small, concentrated drop of organisms on a clean, grease-free, pre-warmed (35⁰ - 40⁰C) slide.
8. Add a small drop of warm (35⁰ - 40⁰C) salinated gelatin (powdered gelatin, 10g; sodium chloride 0.05g; distilled water 100 ml; dissolve gelatin slowly and completely, cool to room temperature and store in refrigerator)
9. Mix drop of organisms and gelatin with a clean, warmed glass needle.
10. Immediately start to withdraw the gelatin-water fluid until organisms are left in a film that causes the organisms to dimple the surface of the gelatin.
11. Transfer slide immediately from warm stage to a cold chamber (5⁰C) and leave until gelatin has gelled, approximately 5 min.
12. Place preparation in cold (5⁰ - 10⁰C) 3% silver nitrate (w/v) solution in the dark for 45 min.

13. Flush slide thoroughly with cold distilled water and submerge to a depth of 1-4 cm in cold (5^o - 10^oC) distilled water in a white-bottomed dish under a source of ultraviolet light. Use a 2530 nm lamp at a distance of 20-30 cm.
14. Remove preparation and flush thoroughly with cold, distilled water.
15. Dehydrate cells by passing through series (70%, 85%, 95%, 100%, 100%) of ethyl alcohol for 5 min. each.
16. Place in 2 changes of absolute xylene for a minimum of 10 min. each.
17. Mount using #0 or #1 coverslips

General cortical structures were also observed by using nigrosin staining methods (Borrer, 1968b; 1969).

Nigrosin-Mercuric Chloride-formalin Method (NMF)

1. Concentrate animals by centrifugation
2. Pipette a small, concentrated drop of organisms onto a clean, grease-free slide.
3. Drop fresh NMF (mercuric chloride (saturated), 10 ml; glacial acetic acid, 2 ml; formalin, 1 ml; t-butanol; 10 ml) from a height of 2-3 cm onto the drop of organisms.
4. Drain off excess fixative and stain and place slide into 70% ethol alcohol for 5 min.
5. Dehydrate cells by passing through a series (70%, 95%, 100%, 100%) of ethyl alcohol for 5 min. each.
6. Place in 2 changes of absolute xylene for a minimum of 10 min. each.

7. Mount using #0 or #1 coverslips.

The fixation and adhesion of specimens to coverslips was modified (Borrer & Evans, 1979) when staining Aspidisca and Euplotaspis. The animals were concentrated by centrifugation and then fixed with Champy's fluid for 15 min. A small drop of fixed organisms was pipetted into a lightly albuminized slide and from a height of 5 cm a drop of acetic-nigrosin-butanol (nigrosin 0.5% (w/v), 3 ml; t-butanol, 3 ml; 1 drop of glacial acetic acid) was pipetted onto the fixed organisms. Additional drops of stain are added until the slide is flooded. Drain off excess stain and place slide into 70% ethal alcohol for 5 min. The normal NMF procedure was followed from this point.

Cells were prepared for scanning electron microscopy (SEM) by a method modified from the methods of Grimes & Adler, 1976, Grimes & L'Hernault, 1978 and Ruffolo, 1974.

1. A small drop of animals concentrated by light centrifugation were placed in a depression slide and cooled for 6-8 min. at 4°C.
2. The cells were pre-fixed by adding an equal volume of cold 2.0% (w/v) OsO₄ in 28°/oo boiled and milipore filtered seawater for 3 min.
3. Washed in 28°/oo boiled and milipore filtered seawater.
4. Fixed in 3.0% (v/v) glutaraldehyde in 28°/oo

boiled and milipore filtered seawater for 30 min.

5. Post-fixed in the same solution as the pre-fix for 30 min.
6. Cells were dehydrated and critical-point dried in a chamber made from a BEEM capsule. The pointed end of a capsule was cut off and the ends covered with #10 Nitex (20 um pore size) held in place by rings made from BEEM capsule tops. See Fig. 1. After fixation the cells were transferred by micropipet to a chamber covered at one end by the Nitex and dehydrated (15%, 30%, 50%, 70%, 85%, 95%, 100%, 100%) ethyl alcohol for 15 min. each, the other end was covered by Nitex and the cells critical-point dried with CO₂.
7. The ciliates were sprinkled onto an adhesive tape-coated stub, followed by coating with carbon and gold-palladium (60:40) and then viewed with an AMR 1,000 S. E. M.

Drawings of organisms and sequences of fission morphogenesis from protargol and Chatton-Lwoff stained specimens were prepared with the use of a Nikon drawing instrument. Photographs were made using a Nikon automatic photomicroscope employing high contrast copy film.

FIG. I. BEEM capsule chamber for critical point drying

An exploded pictorial assembly drawing. Key: A, ring cut from a BEEM capsule cap; B, #10 Nitex cloth, 250 mm (20 um pore size); C, chamber cut from a BEEM capsule.

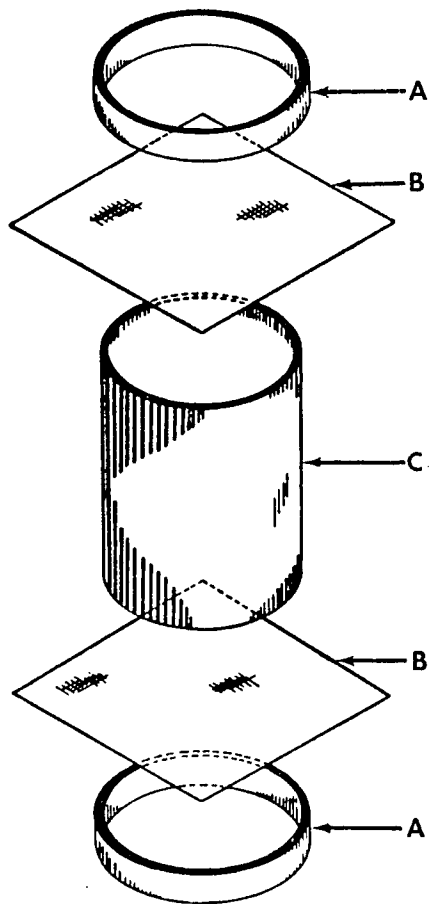


Figure I.

MORPHOGENESIS OF CELL DIVISION

Terminology of the ventral ciliature is based on topographic and developmental characteristics as previously outlined (Bakawska & Jerka-Dziadosz, 1978; Borrer, 1979b; Borrer & Evans, 1979; Grimes, 1972). When describing relative positions on the cell, the terms "right" and "left" are employed from the organism's "point of view", thus the viewer's right is the organism's left. Ciliary components of the ventral surface consist of the ciliary membranelles which lie next to the buccal cavity and four groups of somatic cirri (See Fig. II). The adoral zone of membranelles (AZM) extends along the left side of the buccal cavity and, in some cases, at the anterior end of the organism, arches around to the dorsal surface. The AZM is composed of both anterior "collar" and buccal "lapel" membranelles. To the right of the buccal cavity are 2 undulating membranes or ciliary structures morphogenetically related to them. The one immediately to the right of the AZM is the endoral membrane and usually is composed of a single longitudinal row of ciliated kinetosomes. The outer paroral membrane usually is composed of 4 rows of ciliated kinetosomes (Bakawska & Jerka-Dziadosz, 1978). These membranes extend from the cytosome anteriorly along the edge of the right buccal overture in Diophrys, but are reduced in Euplotes to a small patch of kinetosomes (endoral apparatus) and are reduced further in Aspidisca to a short row of non-ciliated kinetosomes. The buccal and somatic

ciliature to the right of the buccal cavity arises from an orderly series of 7 different ciliary primordia labeled with Roman numerals from the ciliate's left to right (modified from the Wallengren system (Wallengren, 1901) . The endoral membrane develops from row I, the paroral membrane and paroral cirrus (Tuffrau & Fryd-Versavel, 1977) from row II and the other frontal and transverse cirri from rows III - VII. Posterior to the transverse cirri are caudal cirri (C) and along the left ventral side of the organism are the left marginal cirri (LM). Often a dorsolateral row (kinety) of cilia is found on the ventral surface while other rows are on the dorsal surface. Each ciliary organelle has a complex ultrastructure which appears to be quite regular in structure even though there is some variability in the number of ciliary structures (Bakowska & Jerka-Dziadosz, 1978; Grimes, 1972; Ruffolo, 1976a).

Euplotes

The process of asexual reproduction by binary fission was first observed in Euplotes by Stein (1859) who noted that there was complete resorption of the parental cirri and replacement by two complete new sets in the daughter cells. Others (Möbius, 1887; Schuberg, 1900) investigated division in Euplotes, but it was not until Wallengren (1901) that a detailed description of cirral development was presented. Later it was pointed out (Griffin, 1910; Yocum, 1918) that the parental AZM remains apparently unchanged as the AZM of the proter. Turner (1933)

and Hammond (1937) described the neuromotor system, now known to be the microtubules and microfibrils associated with ciliary organelles, and its replacement during division. The division process of the dorsal silver line system and its associated kinetal cilia was first described by Gelei (1934) and further elaborated on by Hammond (1937); Chatton (1942) and Chatton & Séquéla (1940).

Morphogenesis of the micronucleus and macronucleus was first studied by Griffin (1910) and details further refined by studies of Turner (1930) and Yocom (1918). However, it was not until the advent of electron microscopy showing the fine structure (Faure-Fremiet et al., 1957; Kluss, 1962; Murti, 1976; Ringertz et al., 1967; Roth, 1957; Ruffolo, 1978; Saito, 1967) and radioautographic studies showing metabolic activity (Ammermann, 1971; Gall, 1959; Prescott & Kimball, 1961) that structure and morphogenesis was beginning to be understood (Prescott & Murti, 1974). Wise (1965) divided the process of cortical morphogenesis during cell division into seven stages as it relates to changes occurring in the macronucleus and to the cell cycle. Recent studies have added to our overall knowledge of the different morphogenetic processes which occur simultaneously during binary fission (Ruffolo, 1976) and to specific aspects of these processes; contractile vacuole formation (Diller, 1974) and caudal cirri development (Hufnagel & Torch, 1967). The present study examines the structure and events of prefission cortical morphogenesis in a species of

Euplotes with 10 frontoventral cirri and compares it with other species of Euplotes and other euplotids.

E. trisulcatus is a relatively small marine Euplotes with non-dividing cells being 28-50 μm (mean 37.5 μm ; $n=50$) long and 25 - 40 μm (mean 30.5 μm ; $n=50$) wide. The elongated ellipsoidal body has at the anterior end a prominent shoulder on the right side while the posterior end is narrowed. The peristomial cavity is narrow with the right buccal overture formed by a single lip which extends posteriorly from the anterior-most frontoventral cirrus and ends beside the left-most transverse cirrus. In the mid-region of the lip is a prominent depression. Figure II illustrates ciliary components of the ventral surface. The AZM extends from the cytosome along 2/3 of the left side, then, at the anterior end, arches around to the dorsal surface. The AZM is composed of both anterior and buccal membranelles. In the recess under the right buccal overture a small patch of cilia; the endoral apparatus, develops from row I. Cirri make up the remaining ventral ciliature with paroral cirrus II/1 the only ciliary structure developing from row II. The other 9 frontoventral cirri (III/2, III/3, IV/2, IV/3, V/2, V/3, VI/2, VI/3, and VII/2) and 5 transverse cirri (III/1, IV/1, V/1, VI/1 and VII/1) develop from rows III - VII. There are 1 to 2 caudal cirri (numbered C1 and C2) and 2 left marginal cirri (LM1 and LM2). The number of cirri within each group appear to be constant both in number and arrangement except

for the caudal cirri. The first dorsolateral row (kinety) of cilia is on the left side of the ventral surface whereas the other rows are on the dorsal surface. E. trisulcatus from the New Hampshire seacoast had seven kineties, however, variation has been reported (Dragesco, 1963); the number of rows varies from 7 to 9.

Onset of cortical morphogenesis in E. trisulcatus is the initial development of the oral primordium. Kinetosomes appear beneath the ventral cell surface to the left and posterior of the parental AZM (Figs. IIIa, IVa). The oral primordium increases in size by proliferation of kinetosomes while along the right side this kinetosomal patch begins to submerge below the surface forming a subsurface pouch where the new opisthe AZM will develop (Figs. IIIb, IVb). In the right anterior corner of the pouch differentiation of the AZM begins and proceeds to the left and posteriorly. New membranelles are aligned just anterior to the region of kinetosome proliferation. Two rows of kinetosomes align first in formation of new membranelles with a third row being added later to the more anterior membranelles. The third row forms anteriorly to the original rows and begins along the right margin of the AZM (Ruffolo, 1976b). The oral primordium expands until it lies beneath the parental AZM and buccal cavity (Fig. IIIc). The subsurface pouch begins to open with a longitudinal cleavage along its left side. The entire process continues until just before the cell completes division. The kinetosomes formed in the oral primordium

field are not contributed to any other cirral primordia.

Five cirral primordia for the frontal and transverse cirri form to the right of the buccal cavity and anterior to the parental transverse cirri. The first kinetosome(s) of each cirral primordia (which do not appear to be formed in conjunction with any parental ciliary structures) appears as a single linear array of paired kinetosomes just beneath the ventral cell surface. As streak development continues kinetosomes proliferate laterally near the middle and posterior end of each cirral primordium and then progress toward the anterior ends. Proter and opisthe cirral primordia form as each cirral primordium divides in half just below the area of kinetosome proliferation (Fig. III d).

As ciliary buds begin to erupt through the cell surface, the two sets of cirral primordia enlarge and begin to form lobes which break apart and form distinct cirri (Figs. III e, IV c). Each field consists of five transverse cirri (III/1 - VII/1) and 9 frontoventral cirri (III/2, III/3, IV/2, IV/3, V/2, V/3, VI/2, VI/3 and VII/2) (Fig. III f).

The formation of distinct cirri by ciliary outgrowth from ciliary buds proceeds in a posterior-to-anterior and left-to-right developmental gradient within each cirrus primordium with a similar developmental gradient across each cirrus field. Cirri continue to grow by addition of kinetosomes while the cirral fields expand as new membrane develops between individual cirri. The cirral bases begin to show the

characteristic geometrical shape as they move to their final positions.

After frontoventral and transverse cirri from streaks III-VII are well developed, primordia for the paroral cirri (II/1) move from row II (Figs. IIIg, IVd). In the proter the paroral cirral primordium forms along the inside right edge of the buccal cavity. In the opisthe the primordium forms within the subsurface pouch so that paroral cirrus does not become part of the ventral ciliature until the pouch opens to form the buccal cavity. The endoral apparatus which forms from row I develops in the opisthe near the region of kinetosome proliferation for the AZM (Fig. Va). In most cases the proter endoral apparatus comes from the parental organism apparently unchanged, however, in a few cases some reorganization occurs. Whether some kinetosomes are completely resorbed during dedifferentiation and new ones formed during reorganization could not be determined. The parental AZM becomes the AZM of the proter, apparently unchanged. After the cirri to the right of the buccal cavity start migrating to their final positions, two left marginal primordia develop on the ventral surface between the proter and opisthe AZMs and the cell's left margin. Initially, small streaks are formed, but, by kinetosome proliferation, two lobes develop which separate as new membrane is formed developing two left marginal cirri (LM1 and LM2) in each daughter cell (Figs. IIIh, Vb). Kinetosomes from parental left marginals are not contributed to the daughter cell's left marginals.

New dorsal cilia develop within each of the original kineties starting near the prospective fission line (Fig. Vd). Paired kinetosomes form just posterior to parental bristles at both the anterior and posterior ends of each row until a linear array of closely spaced pairs develops. New caudal cirri (C1 and C2) form in conjunction with the morphogenetic process occurring in the two dorsal right-hand kineties. Proter caudal primordia develop anterior to the fission line whereas, in the opisthe, they develop at the posterior end of the cell. After cirral development by lateral proliferation of kinetosomes within each developing caudal primordia, they migrate to the ventral surface during final stages of division.

As ciliary structures continue to develop in the new daughter cells, some parental ciliary structures start to be resorbed. Beginning with cirrus VI/1 there is a sequential resorption of old cirri as new cirri approach with the process continuing until well after cytokinesis. Grimes (1972) and Ruffolo (1976b) report that cirri are resorbed with the axonemes being retracted into the cytoplasm in a non-autophagic process.

In E. trisulcatus two new contractile vacuole systems develop in close association with ciliary primordium VII. They appear to develop de novo because of the distance from the parental contractile vacuole pore; however, it could not be determined if the old vacuole

system or developing ciliary structures aided in the formation of new vacuole systems. Once the contractile vacuole system is developed and, as the cirri move toward their permanent sites and the dorsal bristles begin to move apart, a cleavage furrow forms in the mid-region of the cell. The subsurface pouch begins to open rapidly with the AZM following the constriction furrow around the anterior portion of the developing opisthe (Figs. IIIi, Vc). The cleavage furrow continues to deepen until cytokinesis is complete. However, cortical morphogenesis is not finished until the remaining parental cirri (IV/2, V/3, VI/1 and VI/3) are resorbed, the buccal cavity matures and the caudal cirri migrate to their permanent position on the ventral surface.

The process of cellular morphogenesis in E. trisulcatus resembles that described in E. raikovi, E. eurystomus, and E. aediculatus except in the number of cirri formed and the pattern of formation of the frontoventral cirri (Washburn & Borrer, 1972; Ruffolo, 1976; Wise, 1965a).

Aspidisca

Müller, in 1773, was the first to describe an Aspidisca-like protozoan; calling it Trichoda lynceus. Ehrenberg (1832) erected the genus Aspidisca where over 50 nominal species have been transferred or added. Of 25 recognizable species, most are found in the marine environment. The general nomenclature in the genus is in taxonomic

confusion and has been reviewed recently (Brown, 1968; Curds, 1977; Diller, 1975; Wu & Curds, 1979). Borrer (1972b) used as his main support the morphogenetic patterns that develop during cell division to eliminate the family Aspidiscidae (Ehrenberg, 1838) and to place its contained genera, including Aspidisca, into the Euplotidae. However, Corliss (1979), in his review of ciliate taxonomy, retained the family Aspidiscidae.

The morphogenetic process of asexual reproduction by binary fission has been described in Aspidisca. Behavior of the horseshoe-shaped macronucleus during division has been studied (Summers, 1935; Diller, 1975). Both accounts agree that replication of the macronucleus begins with the separation of a small amount of chromatin material from the apex of the macronucleus and to the right of the single micronucleus. This chromatin body increases in size, a clear zone surrounding it, and pushes across the macronucleus until it reaches the inner margin. It then expands laterally dividing into two replication bands which subsequently move to the ends of the macronucleus. Among the accounts of cortical morphogenesis during cell division, however, there are differences in interpretation of the origin of several ciliary structures. According to Tuffrau (1964) and Deroux & Tuffrau (1965), the developing "anterior membranelles" of the opisthe differentiate from the developing AZM; but, Diller (1975) described the same structure, called the "tooth", as developing from

streak I (Wallengren system) of the frontoventral transverse system. These differences cause corresponding differences in the origin of other ventral cirri such as the left antero-most cirrus, described as developing from streak II (Diller, 1975) and streak I (Deroux & Tuffrau, 1965). The number and arrangement of the cirri on the ventral surface along with their morphogenetic patterns during division are being used as stable diagnostic features useful in clarifying taxonomic relationships and nomenclatural problems. Therefore, it is important to understand the precise ontogeny of the ventral ciliary organelles during cell division in Aspidisca.

A. costata, considered a junior synonym of A. cicada Müller, 1786 by Wu & Curds (1979) is a small fresh water species. The non-dividing organisms are variable in size ranging in length 28 - 35 μm (mean 27.5 μm ; n=50) and width 16 - 35 μm (mean 25.5 μm ; n=50). The smooth body outline approximates an oval which is slightly convex along the left posterior side. The dorsal surface is arched with 6 to 7 prominent longitudinal ridges. Diller (1975) states that, depending upon culture conditions, the ridges can vary in both size and number (3 to 10).

Ciliary components of the ventral surface are seen in Fig. VI. The AZM is divided into two parts with the 3 anterior membranelles which appear superficially being cirrus-like in structure and located

in the antero-left sector of the organism. The buccal membranelles are located along the left side of the buccal cavity which is partially enclosed by a ventral plate. Along the right side of the buccal cavity is an argentophilic area which is a rudimentary endoral structure. The paroral cirrus (II/1), 6 frontoventral cirri (III/2, III/3, IV/2, IV/3, V/2, VI/2) and 5 transverse cirri (III/1, IV/1, V/1, VI/1 and VII/1) make up the remaining ventral ciliature which are in a "lynceus-arrangement" (Wu & Curds, 1979). A ridge between cirrus IV/1 and cirrus V/1 divides the transverse cirri into two groups. There are five dorsal kineties.

A. aculeata is a small (length 35 - 46 μm (mean 40.6 μm ; $n=50$), width 27 - 31 μm (mean 29.5 μm ; $n=50$)) species found in the marine environment. The body is oval, slightly more convex along the right side and has a smooth outline. The dorsal surface is arched with 3 or 4 longitudinal ridges. Most descriptions include the dorsal ridges, however, both Ehrenberg (1838) and Mansfeld (1923) describe a dorsal thorn which was not seen in the New Hampshire variety. The ventral surface is also sculptured with cirri arising from depressions. As described by Borrer (1965b) the posterior edge of a two-part buccal cavity is a highly refractile Y-shaped ridge. The ventral ciliary components are very similar to those of A. costata, however, there are 4 anterior membranelles and 6 transverse cirri caused by the splitting of cirrus III/1. The ventral ciliature is in a "polystyla-

arrangement" (Wu & Curds, 1979). There are four dorsal kineties.

A. baltica, considered a junior synonym of A. pulcherrima Kahl, 1932 by Wu & Curds (1979), is a medium sized (length 49 - 70 μm (mean 61.5 μm ; n = 50), width 35 - 41 μm (mean 38.0 μm ; n = 50)) marine species. The body is oval, slightly more convex along the right side and has a jagged body outline caused by two small projections along the left anterior border and a prominent peristomial spur followed by three-four dentations along the left posterior border. The arched dorsal surface has four low longitudinal ridges. The ventral surface is sculptured by a two-part buccal cavity with base depressions around each cirrus. The ventral ciliature, which is in a "polystyla-arrangement", is similar to that of A. costata with differences being an additional frontoventral cirrus, VII/2, 6 or 7 anterior membranelles, and 7 transverse cirri caused by the splitting of cirrus III/1. There are four dorsal kineties.

Cortical morphogenesis begins in Aspidisca with the subcortical appearance of the oral primordium kinetosomes (Fig. VIIIa). This anlage forms to the left and posterior of the parental AZM. There is rapid proliferation of kinetosomes as the anlage recedes below the surface forming a pouch where the new opisthe AZM will develop (Fig. VIIa). In the posterior end of the pouch is the region of kinetosomal proliferation with new membranelles being aligned just

anterior to this area (Fig. VIIb). As the anterior end of the developing opisthe AZM migrates to the surface, membrane, developing posterior to the first few membranelles (3 in A. costata, 4 in A. aculeata and 7 in A. baltica), creates a developing separation into anterior and buccal membranelles (Fig. VIIe). The former migrate attaining the characteristic geometric pattern of cirri, to form "anterior membranelles" (Deroux & Tuffrau, 1968) or "tooth" (Diller, 1975) (Fig. VIIf). Anterior membranelles of the AZM arise by a separation of several ciliary units from the anterior end of the developing opisthe AZM as occurs in other genera of Euplotidae (e. g. Uronychia (Borror, 1972b; Hill, 1978b)) thus, bear no direct ontogenetic relationship with the frontal ciliature developing to the right of the buccal cavity as interpreted by Diller (1975). Both anterior and buccal membranelles of the parental AZM become the corresponding part in the AZM of the proter.

Simultaneous to development of the new opisthe AZM, 3 ciliary primordia (III - V) to the left (Fig. VIIb) and later 2 ciliary primordia (VI - VII) to the right of cirrus VI/2 (Fig. VIIc) appear. In A. baltica these streaks are considerably longer than in A. costata or A. aculeata, extend beyond the cytosome, and are found on both sides of cirri VI/2 and VII/2 (Fig. VIIIb). As a result of kinetosome proliferation the streaks within this single latitudinal zone of proliferation enlarge and each cirral primordium divides forming the proter and opisthe cirral

primordial fields (Fig. VIIId). Within each field, kinetosome proliferation continues until each streak develops numerous lobes which coalesce forming distinct fields of cirri for both proter and opisthe (Figs. VIIe, f, VIIIe). Each field usually consists of 5 transverse cirri (III/1 - VII/1) and 6 frontoventral cirri (III/2, III/3, IV/2, IV/3, V/2 and VI/2). An additional seventh frontoventral cirrus can develop from row VII as in A. baltica (VII/2) (Fig. VIIIb) and A. lyncaster (VII/2) (Tuffrau, 1964) or from row VI as in A. orthopogon (VI/3) (Deroux & Tuffrau, 1965). The number of transverse cirri also can vary, but the number of streaks that contribute cirri to the transverse cirri system is apparently always five. In A. baltica cirrus III/1 divides into 3 separate cirri (Fig. VIIIe) and A. aculeata 2 separate cirri and in A. polystyla (15 cirri) all the transverse cirri divide into several parts (Tuffrau, 1964). As the cirri begin to assume their characteristic geometric shape a new cirral primordium (streak II) forms in the proter to the right of the buccal cavity and in the opisthe to the right of the developing AZM. These streaks form cirrus II/1, the paroral cirrus (Figs. VIIe, f, g, VIIIc, d) and is not cirrus II/2 of the Wallengren system as interpreted by Diller (1975). Appearing near the posterior end of the proter AZM and developing opisthe AZM is an argyromophilic area which quite possibly is the equivalent of the endoral apparatus seen in other genera of Euplotidae (e. g. Euplotes (Ruffolo, 1976b; Tuffrau, et. al. 1976), Diophrys (Hill, 1978a) and

Euplotaspis (Hill, 1979b)). As parental cirri begin to dedifferentiate and are resorbed, an equatorial cleavage furrow forms that will complete the cytokinesis of division (Figs. VIIIh, i).

Diophrys

Several species of Diophrys have often been reported in ecological (Faure'-Fremiet, 1950b, 1951; Hartwig, 1973b; Nobili, 1957; Raikov, 1962) and taxonomic-morphological (Borrer, 1965a; Dragesco, 1963; Hartwig, 1973a) studies as members of an important genus of benthic communities of estuarine and tidal marshes. Only recently have other aspects of their biology been studied; for example, ultrastructure (Nobili & Rosati Raffaelli, 1968, 1971; Torch & Hufnagel, 1961; Walker, et. al., 1976), conjugation (Ito, 1963; Luporini, 1967) and cell cycle (Dini et. al., 1975). Several accounts of macronuclear changes during cell division agree that single replication bands appear at the proximal ends of each macronucleus, proceed centrally, disappearing as the two nuclei fuse. A constriction forms in the mid-region with secondary constrictions appearing in each half causing the nucleus to divide simultaneously into four parts at cytokinesis (Ganapati & Rao, 1956; Summers, 1935). The three incomplete observations on pre-division morphogenesis of the cortex do not offer complete understanding of ventral ciliary organelle development (Borrer, 1972b; Dembowska, 1926; Faure'-Fremiet, 1964). Because ciliary organellar ontogeny is important in understanding taxonomic

relationships in the order Hypotrichida, this study on Diophrys was undertaken.

The lengths of the three Diophrys species used in this study are as follows: D. scutum non-dividing cells 89 - 195 um (mean 123 um; n=50), D. oligothrix non-dividing cells 65 - 101 um (mean 58 um; n=50) and D. appendiculata non-dividing cells 38-58 um (mean 47 um; n=50). The oval body has little sculpturing except on the ventral surface where the frontoventral cirri and left marginal cirri are set down in grooves and the transverse cirri are set in individual pockets. Ciliary components of the ventral surface are seen in Fig. IX. The AZM extends from the cytostome along 2/3 of the left side, then, at the anterior end it arches around to the dorsal surface and back toward the ventral surface extending about 1/4 of the way down the right side of the cell. The AZM is composed of both anterior and buccal membranelles. To the right of the AZM are 2 undulating membranes. The one topographically nearest the AZM is the endoral membrane, the other the paroral membrane (Fig. XIa). These membranes extend from the cytostome anteriorly along the edge of the right buccal overture. The endoral membrane develops from row I, the paroral membrane and a paroral cirrus (II/1) from row II. Cirri make up the remaining ventral ciliature with 6 frontoventral cirri (III/2, III/3, IV/2, VI/2, and VI/3) and 5 transverse cirri (III/1, IV/1, V/1, VI/1 and VII/1) developing from rows III - VII. There are 3 caudal cirri numbered C1, C2, and

C3 and 2 left marginal cirri numbered LM1 and LM2. The number of cirri is variable (frontoventrals 7 - 9, transverse 5 - 6, caudal 3 - 4 and left marginals 1 - 3). The first dorsolateral row (kinety) of cilia is on the right side of the ventral surface while the other rows are on the dorsal surface. There are usually 5 kineties in D. scutum, 5 in D. appendiculata and 4 in D. oligothrix, however, this number is variable with an additional 1 or more rows. Thus, the cortical surface of Diophrys shows some variability in number of ciliary structures.

The process of precession cortical morphogenesis begins in Diophrys scutum by the apparent de novo development of a small patch of kinetosomes beneath the ventral surface, to the left and posterior of the parental AZM, the oral primordium (Fig. XIIc). After initial formation of the oral primordium rapid proliferation of kinetosomes develop a pouch where growth continues. As the pouch enlarges, kinetosomes align into membranelles of the new opisthe AZM. Alignment begins along the right side at the anterior end and proceeds to the left and posteriorly. Young membranelles align first to form two rows of kinetosomes with a third row being added later to the more anterior membranelles. This third row begins along the right margin of the AZM and anterior to the original rows with development proceeding to the left. At the posterior end of the pouch is the region of kinetosome proliferation with new membranelles being aligned just anterior to this area. The entire process of AZM development is not complete until

just before the cell completes division. Kinetosomes which are formed in the oral primordium are not contributed to any other cirral primordia.

As the new opisthe AZM is developing, there appear the cirral primordia of frontoventral and transverse cirri. Five streaks form to the right of the buccal cavity and anterior to the parental transverse cirri (Fig. Xa, XIIId). Three cirral primordia (III - V) form to the left and 2 additional (VI - VIII) to the right of parental cirrus VII/2. Each streak is a single linear array of paired kinetosomes just beneath the surface which appear not to be formed in conjunction with any parental structure (Fig. XIb). As each cirral primordium lengthens, kinetosomes laterally proliferate, first near the middle and posterior end of each streak, and then progressively toward the anterior end. Each streak divides in half just below the central area of kinetosome proliferation forming the proter and opisthe cirral primordium fields (Figs. Xb, XIIIa). As the kinetosomes continue to proliferate rapidly, the two sets of primordia enlarge and begin to form lobes which break apart and develop distinct cirri (Figs. Xc, XIc). Each field usually consists of 5 transverse cirri (III/1 - VII/1) and 6 frontoventral cirri (III/2, III/3, IV/2, V/2, and VI/3). Anterior-to-posterior and right-to-left developmental gradient within each cirrus primordium (as seen by ciliary outgrowth) and development across the cirrus field (as seen by the degree of cirrus formation) occurs. Cirri continue to grow laterally by addition of kinetosomes while the cirral fields expand as

new membrane develops between individual cirri. As the frontoventral and transverse continue to develop, a proter paroral primordium develops to the right of the posterior end of the proter AZM (Figs. Xd, XIIIb). The proter primordium of the opisthe forms later and posterior to the proter paroral primordium (Figs. Xe, XIId). These primordia elongate and widen anteriorly through proliferation of kinetosomes. The anterior end forms the paroral cirrus (II/1) while the posterior part, the paroral membrane, continues to lengthen along the right buccal overture (Fig. Xf). The proter endoral primordium develops to the left of the paroral primordium in close proximity to the posterior end of the AZM. In the opisthe the endoral primordium develops in the region of kinetosome proliferation of the AZM. Each endoral primordium elongates through kinetosome proliferation into a membrane along the inside edge of the right buccal overture.

On the ventral surface between proter and opisthe AZMs and the cell's left margin two left marginal primordia develop (Figs. Xf, XIIIc). Kinetosomes rapidly proliferate into two lobes (usually) which separate as new membrane is formed, developing two left marginal cirri in each daughter cell. Unlike Oxytricha fallax, parental left marginals do not contribute kinetosomes to the formation of the left marginal cirri. Dorsally, new cilia develop within each original kinetal row, starting near the mid-region of the cell. Newly paired kinetosomes form just posterior to the parental kinetal cilia as in Euplotes (Ruffolo, 1976a,

1976b). Kinetosomes are added to both anterior and posterior ends of each row until there is a linear array of closely spaced pairs on both sides of the prospective fission line. New kinetosomal pairs are not formed next to all parental kinetal cilia; this is particularly true of those located at the anterior and posterior ends of the parental organism. Caudal cirri develop within the two right-hand kinetal rows. Proter caudal primordia develop just anterior of the fission line. Those of the opisthe develop at the posterior end of the parental cell. There is lateral proliferation of kinetosomes in the caudal primordium area as daughter kinetal cilia develop. The developing primordium in the outer-most kinetal row develops into two lobes which separate forming two caudal cirri (C2, C3), the inner row forms one (C1) (Fig. XIIa).

During the final stages of binary fission the individual fronto-ventral and transverse cirri attain their characteristic geometric shapes and separate as they migrate toward their permanent sites. Cirrus II/1 of the proter and opisthe align with other cirri in their respective fields. Endoral and paroral membranes continue to elongate anteriorly. The pouch has enlarged its opening to the surface with a considerable number of membranelles being formed (Fig. Xg). Parental cirri, starting with cirri V/1 and III/2, begin rapidly to be dedifferentiated and resorbed, especially when new cirri approach old cirri. However, kinetosomes of parental cirri are not included in

development of ciliary structures of daughter cells. The AZM of the opisthe begins to migrate around the anterior portion of the developing opisthe following the developing equatorial cleavage furrow (Figs. XIIb, XIIIId). Just before cytokinesis the dorsal kinetal cilia separate and the caudal cirri start to migrate toward their final positions. Many parental cirri are resorbed; II/1, III/1, V/2 and VI/3 (Fig. Xh).

After division, most proter cortical morphogenesis has been completed except that caudal cirri are not yet in their final location. Usually two parental cirri (III/3, IV/2) are not resorbed (Fig. Xi). In the opisthe, transverse cirri are not at their final site and some parental cirri are still to be resorbed (IV/1, VI/1, VII/1, left marginal and several caudal cirri) (Fig. Xi).

Cortical cellular morphogenesis in D. oligothrix and in D. appendiculata resembles that of D. scutum.

Euplotaspis

Since its original description, Euplotaspis cionaecola Chatton & Séquéla, 1936, a commensal found in the branchial cavity of Ciona intestinalis, has been of interest to protozoan taxonomists because of its showing a possible evolutionary link between the genus Euplotes and the genus Aspidisca. E. cionaecola is similar to the Aspidiscids with its almost oval shape, lack of left marginal cirri and with all the ciliary structures being broad and made up of short cilia. Euplotaspis

is similar to some of the Euplotes (i. e. Euplotes crassus) with the presence of a single dorsal argyrome, an AZM where the membranelles are not divided into two structures, an endoral ciliary structure and a C-shaped macronucleus. E. cionaecola is unique among the hypotrichs with its four large tufts of cilia which form a fringe along the right ventral side of the body.

Little is known about any of the morphogenetic processes of E. cionaecola because, since its original description, it has only been recorded once. Burrell (1973) found E. cionaecola in three different species of solitary ascidians (Ascidia paratropa, A. callosa, Pyura haustar) collected by dredging near the San Juan Archipelago. E. cionaecola from Ciona intestinalis collected near Woods Hole, Massachusetts allowed this study on the cortical structure and ontogeny of ciliary organelles during pre-division to be undertaken in order to help clarify several taxonomic relationships in the family Euplotidae.

In the non-dividing state, E. cionaecola is 58.5 - 85.0 μm (mean 68.7 μm ; n=50) long and 42.5 - 61.5 μm (mean 51.2 μm ; n=50) wide. The smooth body outline of E. cionaecola is oval. The dorso-ventrally flattened body has no dorsal ridges and the ventral surface is slightly convex. The living organism is filled with granular inclusions. Ciliary components of the ventral surface are seen in Figs. XIV, XVIa.

All ventral ciliary structures are broad, made up of many short cilia which are believed to assist the organism's attachment to the bronchial cavity lining. The AZM extends from the cytosome along 3/4 of the left side, then arches around the anterior end of the ventral surface. The AZM does not extend onto the dorsal surface as it does in some other euplotids (i. e. Euplotes, Diophrys and Certesias). The buccal cavity is short and shallow with the cilia of the endoral apparatus situated along the right buccal margin near the cytosome. The paroral cirrus (II/1) is located at the anterior end of the right buccal margin. The endoral apparatus develops from row I, the paroral cirrus from row II. The 9 other frontoventral cirri (III/2, III/3, IV/2, IV/3, V/2, V/3, VI/2, VI/3 and VII/2) and the 5 transverse cirri (III/1, IV/1, V/1, VI/1 and VII/1) develop from rows III - VII. Four tufts of cilia form a fringe along the right ventral side of the body. There are 2 to 3 small caudal cirri (3-5 kinetosomes) numbered C1, C2, C3. The first dorsolateral row (kinety) of cilia is on the right side of the ventral surface while the other 6 to 7 rows are on the dorsal surface. The dorsal interkinetal argyrome pattern is composed of longitudinal kineties with simple transverse connections forming a single row of polygons between kineties (as in Euplotes crassus). Thus, the structure of the interphase organism is similar to the original description, however, the number of kineties, transverse and caudal cirri varied.

Cortical morphogenesis during cell division begins in E. cionaecola with development of the opisthe oral primordium by the apokinetal appearance of a patch of kinetosomes beneath the ventral surface, posterior of the parental AZM (Fig. XVa). After initial formation of the oral primordium there is rapid proliferation of kinetosomes with the formation of subsurface pouch where the new AZM will develop. As the pouch enlarges, membranelles of the AZM align starting in the right anterior corner of the pouch and proceeding to the left and posteriorly (Figs. XVb, XVIb). In the posterior end of the pouch is the region of kinetosome development. Just anterior to the area of kinetosome proliferation the young membranelles align by forming two rows of kinetosomes, with a third row being added later to all membranelles except those near the cytosome. The subsurface pouch with its developing opisthe oral primordium continues to expand anteriorly until a portion of it lies beneath the parental AZM (Fig. XVd, e). The pouch opens with a longitudinal cleavage along its left side with the entire process of opisthe AZM formation continuing until just before the cell completes cytokinesis (Fig. XVf, g, h). The parental AZM is retained as the AZM of the developing proter. As in Aspidisca (Hill, 1979d) and other euplotids, kinetosomes formed in the oral primordium are not contributed to any other primordia.

Simultaneous with new opisthe AZM development, 5 longitudinal ciliary streaks appear to the right of the buccal cavity and anterior

of the parental transverse cirri. They will develop into frontoventral and transverse cirri of both proter and opisthe. The initial streak (VII) forms to the right of parental cirri VI/3 and VII/2 (Fig. XVb). The second streak (VI) forms to the right of parental cirrus VI/2 and, later, 3 additional cirral primordia (III - V) form to the left of cirrus VI/2 (Fig. XVc). Parental ciliary structures do not appear to contribute kinetosomes at any time during development of these primordia. At first each streak appears as a linear array of paired kinetosomes just beneath the cell surface. The primordium lengthens as kinetosomes proliferate laterally, first near the middle and posterior end of each streak and then progressively toward the anterior end. The streaks enlarge and divide into proter and opisthe cirral primordia fields (Fig. XVd). Within each field kinetosomes proliferate rapidly with the streaks within each field enlarging and forming lobes until they break apart forming distinct fields of cirri for both the proter and opisthe (Fig. XVe). Each field usually consists of 5 transverse cirri (III/1 - VII/1) and 9 frontoventral cirri (III/2, III/3, IV/2, IV/3, V/2, V/3, VI/2, VI/3 and VII/2) (Figs. XVf, XVIc). The number of transverse cirri can vary with cirrus III/1 dividing to form 2 separate cirri, thus the number of streaks that contribute cirri to the transverse cirri system is apparently always 5. There is a posterior-to-anterior and right-to-left development gradient across the cell. Individual cirri grow laterally and attain their characteristic shapes by addition of more kinetosomes. The cirrus field expands as new membrane develops

between cirri, causing them to separate and migrate toward their permanent sites. As cirri IV/3, V/3, VI/3 and VII/2 reach their permanent positions, kinetosomes within the right half of each cirrus divide to form 4 tufts of cilia that make up the ciliary fringe (Figs. XVh, XVIId).

Simultaneously with the frontoventral-transverse system development the proter paroral cirrus develops to the right of the anterior end of the buccal cavity (Fig. XVf). The paroral cirrus in the opisthe forms later along the right anterior side of the developing buccal cavity (Fig. XVg). The parental endoral apparatus is inherited apparently unchanged by the proter. In the opisthe the endoral primordium develops in the region of kinetosome proliferation of the AZM, but differentiates further along the inside edge of the right buccal overture (Figs. XVb, XVg). Near the mid-region of the cell on the dorsal surface a row of new cilia develops within each original kinety. A linear array of closely spaced pairs of kinetosomes form at the anterior and posterior ends of each developing row. Caudal cirri develop in some or all of the 3 right hand kineties. Proter caudal cirri primordia form anterior to the developing cleavage furrow while opisthe caudal cirri form at the posterior end of the parental cell. Caudal cirri differentiation occurs by the lateral proliferation of kinetosomes in the kineties.

Late in pre-fission morphogenesis, parental cirri are dedifferentiated and resorbed as new cirri approach them, starting with cirri III/2. Kinetosomes of parental cirri are not included in ciliary structures of daughter cells. As the opening of the pouch enlarges forming the buccal cavity, the opisthe AZM follows the developing equatorial cleavage furrow across the anterior end of the ventral surface (Fig. XVI). As the cleavage furrow deepens the final parental cirri are resorbed. After cytokinesis cortical morphogenesis is completed except that the opisthe AZM and the caudal cirri are still migrating to their final locations.

Uronychia

Some of the most unique ciliates in both structure and behavior are members of the genus Uronychia in the family Euplotidae.

First to describe an Uronychia-like protozoon was Müller (1786), calling it Trichoda transfuga. The genus Uronychia was erected by Stein (1859) where there are now 6 nominal species (Borror, 1972b). These common cosmopolitan species have been considered closely related to the Euplotids because of their general body shape and location of major locomotory cirri. This relationship is further strengthened by sharing a common pre-division morphogenetic plan with Euplotes (Borror, 1972b).

Uronychia, with its elaborate buccal membranes, giant posterior

cirri and rapid backward avoiding reaction (Fauré-Fremiet, 1964; Jennings, 1906) has not been studied using modern cytological techniques. However, Uronychia has proved in the past to be a useful organism in studying different morphogenetic processes. Wallengren's (1901) classical investigation of U. transfuga confirmed that ciliary organelles of the parent are resorbed during fission, while a new set emerges for the daughter cells. Knowledge of regeneration processes (Calkins, 1911; Dembowska, 1926; Young, 1922) has been summarized and extended by Taylor (1928). Only two observations of the process of pre-division morphogenesis have been made since (Borrer, 1972b; Fauré-Fremiet, 1964). Since cortical morphogenetic patterns have proved significant in clarifying taxonomic relationships among other genera assigned to the family Euplotidae, I undertook this study on cortical structure and ontogeny of ciliary organelles in Uronychia.

U. transfuga in the non-dividing state is 55 - 97.5 μm (average 73.8 μm , $n=50$) long and 30.0 - 70.0 μm (average 51.9 μm , $n=50$) wide. In some cultures, cannibal giants develop whose length is about twice the normal size (185 - 130 μm). U. transfuga is highly sculptured, oval, with a flattened ventral and rounded aboral surface. The anterior end is truncated with short spines arising along the dorsal surface. The posterior end is sculptured into three deep concavities from which arise caudal, left marginal and transverse cirri. Ciliary components of the ventral surface are seen in Figure XVII. The AZM is divided into two

parts, 11 anterior membranelles and 5 buccal membranelles. The first 6 anterior membranelles are approximately the same size and circle around the dorsal anterior surface. The next 3 are larger, extending from the dorsal surface over the left shoulder to the ventral surface. To their right on the ventral surface are 2 short membranelles. One small and four large buccal membranelles are on the left side of the cytosome. The conspicuous buccal membrane is also divided into two parts (Fig. XIXa). Part one, the right buccal membrane, follows the course of the right buccal overture starting near the cytosome. The second part, the left buccal membrane, begins anterior to the buccal membranelles and follows the course of the left buccal overture ending anterior to the right buccal membrane. A cortical flap extends from the left buccal overture and partially covers the buccal membrane on that side (Fig. XIXa). Cirri make up the remaining ventral ciliature. The paroral cirrus (II/1), to the right of the anterior end of the right buccal membrane, is formed from the second ciliary primordium. Cirri of the frontoventral-transverse system develop from primordia III - VII: 4 large (III/1, IV/1, V/1, VI/1) and 1 small (VII/1) transverse cirri, 2 small frontoventral cirri (VII/2, VII/3) along the right edge and 3 frontoventral cirri (III/2, IV/3, IV/2) located near the paroral cirrus. Three left marginal cirri (LM1 - LM3) increase in size from anterior to posterior. An even smaller fourth anterior left marginal cirrus is sometimes present.

The largest cirri are the 3 caudal cirri (C1 - C3) on the dorsal surface and are uniquely bent to the left after they pass the posterior edge of the body. Six kineties contain closely set short cilia set down in grooves. The first row is on the right side of the dorsal surface with other rows being to the left. Most rows stop at the level of caudal cirri, however row 4 extends to the posterior end. Row 5 starts anteriorly on the dorsal surface and rolls over the left edge to end on the ventral surface. Row 5 and row 6 come close together to the left of the left marginal cirri where the cilia are so close as to form a stubby membrane (Fig. XIXb). In wet silver preparations, specimens show a meshwork of small elongated polygonal areas delimited by argentophilic lines (Borrer, 1963). Thus, the cortex of U. transfuga is regular, without the variability seen in other Euplotids (Gates, 1978b; 1979; Gates & Curds, 1979).

Cortical morphogenesis of division starts with the subcortical appearance of a small patch of kinetosomes, the opisthe oral primordium on the ventral side posterior and to the right of the parental cytosome (Fig. XVIIIa). Subsequently, after this field has started, a second patch of kinetosomes, the proter oral primordium, develops to the right of the left buccal membrane just anterior to the parental buccal membranelles (Figs. XVIIIb, XXd). Origin of the initial kinetosome(s) in either primordia appears not to have been originally part of any parental ciliary structure. The opisthe oral primordium develops

by a rapid proliferation of kinetosomes within a subsurface pouch. As this anlage grows through the proliferation of basal bodies, kinetosomes align into membranelles, beginning along the anterior edge on the left side, proceeding to the right and posteriorly in the pouch (Figs. XVIIIb, c, d). The proter oral primordium also develops within a pouch; with new membranelles aligning along its left side (Fig. XVIIIb, c, d). Young membranelles align first by forming 2 rows of kinetosomes; additional rows are added later. Kinetosomes continue to proliferate at the posterior end of each pouch with new membranelles aligning just anterior of this area. In the opisthe oral primordium there develop on the bottom of the pouch from left to right 6 short, 3 long, and 2 short membranelles (anterior membranelles) and along the right side of the pocket 5 membranelles (buccal membranelles). Thus, 16 membranelles form in the opisthe AZM anlage; the same number as in the parent (Figs. XVIIIe, XIXd, XXIa). In the proter oral primordium however, only 3 long and 2 short anterior membranelles and 5 short buccal membranelles develop (Figs. XVIIIf, XXa, XXIb). Thus, in the parent, 10 membranelles are replaced and 6 parental membranelles remain to become part of the AZM of the proter. As the membranelles continue to develop, new membrane forms between the anterior and buccal membranelles, causing them to separate (Fig. XVIIIg). Subsequently, anterior membranelles migrate forward around the anterior end of the developing organisms. This is not completed until just before cytokinesis (Fig. XVIIIi).

Kinetosomes formed in either oral primordium are not contributed to any other primordia.

After the AZM begins to align, the primordium for the buccal membrane develops along the right edge of each opening pouch. First, a long row of paired kinetosomes forms with the posterior end developing in close proximity of the kinetosome proliferation area of the developing AZM's (Figs. XVIIIe, d, XIXc, XXd). Kinetosomes proliferate laterally at both ends of the anlage while the center region elongates rapidly. This elongation causes an arching out of the primordium forming the large, sweeping buccal membrane (Fig. XVIIIg). The final structure of the buccal membrane begins to form at each end while kinetosome proliferation continues centrally. The area of elongation and kinetosome production continues to move anteriorly until it is just posterior of the anterior membranelles of the AZM (Fig. XVIIIh). Before completion of division, the buccal membrane divides and overlaps at the anterior end, forming the right and left buccal membranes.

Concomitant with AZM and buccal membrane development, 4 separate cirral primordia (III - VI) appear to the right of the parental right buccal membrane and anterior to the transverse cirri. At first these streaks appear as single linear arrays of paired kinetosomes (Fig. XVIIIb). The rows become quite long before lateral proliferation

begins near the middle and posterior ends of the streaks (Figs. XVIIIc, XXc). A fifth primordium (VII) forms to the right of other streaks just before they all divide, just below the central area of kinetosome proliferation, to form proter and opisthe cirral primordium fields (Fig. XVIIIId). Cirral primordia in each field enlarge and begin to form lobes which break apart and form distinct cirri. Each field consists of 5 transverse cirri (III/1 - VII/1) and 8 frontoventral cirri (III/2, III/3, IV/2, IV/3, V/2, VI/2, VII/2 and VII/3) (Figs. XVIIIf, XXIc). Near the central region of kinetosome proliferation in each buccal membrane anlage the primordium for the paroral cirrus develops (II/1) (Figs. XVIIIf, g, XXIc). As the frontoventral cirri (III/2, III/3 and IV/3) migrate anteriorly, they line up the paroral cirrus to the right of the anterior membranelles of the AZM (Fig. XXa). The two small cirri from row VII migrate to the right margin of the cell, where they resemble right marginal cirri. Other frontoventral cirri (IV/2, V/2 and VI/2) are resorbed as the other cirri migrate to their final positions.

On the ventral surface between the parental buccal membranelles of the AZM and the cell's left margin and between the opisthe oral primordium and the parental left marginal cirri the primordia for the left marginal cirri develop. During rapid kinetosome proliferation four lobes develop within each anlage which separate as new membrane forms between them (Fig. XXIId). In most cases, the antero-most

developing left marginal is resorbed as the other cirri migrate to their final positions. Dorsally, new cilia develop within each of the 6 original kineties, starting near the mid region of the cell. Kinetosomes are added to both ends of a developing linear array of closely packed basal bodies. The kinetosomes become evenly spaced within each kinety during final stages of division. The unique caudal cirri of Uronychia form as they do in Diophrys with development occurring in the two right-hand kinetal rows. The primordium in the outer-most kinety row develops into two lobes, forming two caudal cirri (C2, C3). The inner row forms one caudal cirrus (C1) (Fig. XXb).

As new ciliary structures of the daughter cells migrate to their final positions, parental ciliary structures (5 anterior and all buccal membranelles of the AZM; frontoventral, transverse, caudal and left marginal cirri; and right and left buccal membrane) dedifferentiate and are resorbed (Fig. XXa). The kinetosomes of these parental structures are not included in development of ciliary structures of the daughter cells. An equatorial cleavage furrow constricts, dividing the cell into two daughter cells. With most of the cortical morphogenesis complete, the two parts of the buccal membrane, anterior membranelles of the AZM and caudal cirri finish migrating to their final positions and the buccal cavity is shaped.

FIG. II Diagram of Euplotes cortical structures and features

Key: A - AZM, anterior membranelles of AZM; B - AZM, buccal membranelles of AZM; PC, paroral cirrus or cirrus II/1; EA, endoral apparatus; III/1, IV/1, V/1, VI/1, VII/1 transverse cirri; III/2, III/3, IV/2, IV/3, V/2, V/3, VI/2, VI/3, VII/2 frontoventral cirri; C1, C2 caudal cirri; LM1, LM2 left marginal cirri.

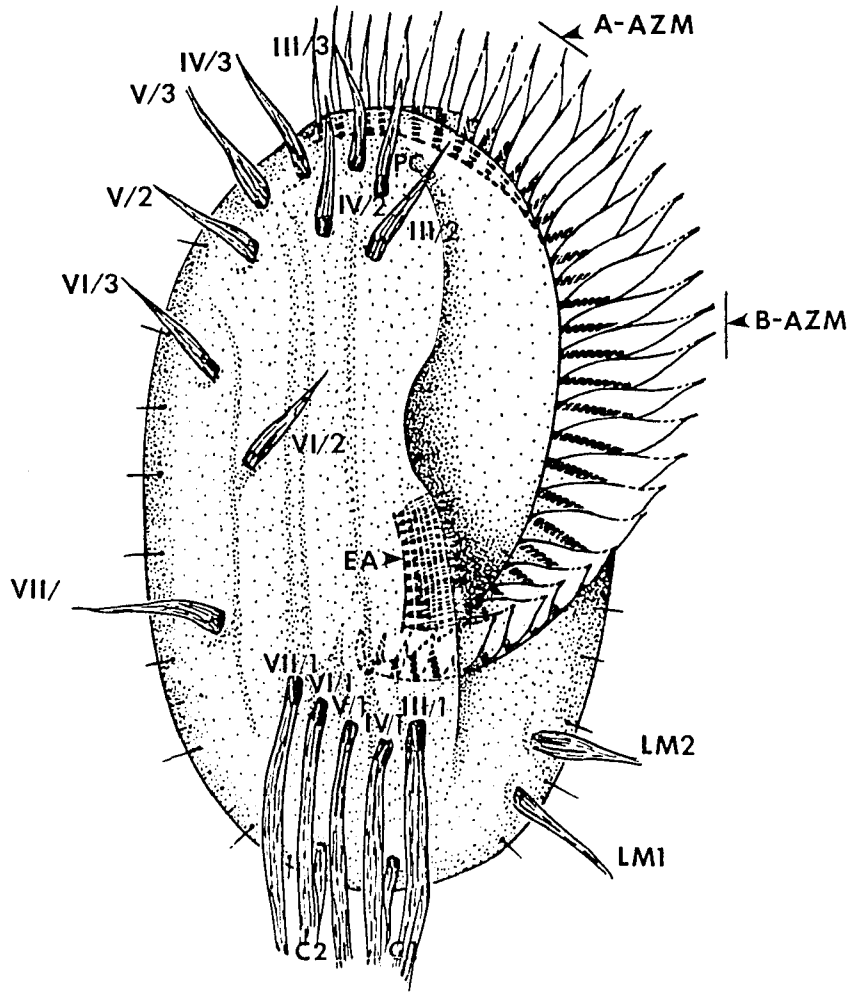


Figure II.

FIG. III. Diagram of Euplotes division stages

- a. Beginning of opisthe oral primordium
- b. Alignment of membranelles in opisthe oral primordium
- c. Opisthe oral primordium expanding beneath parental AZM
- d. Formation of proter and opisthe cirral primordia fields
- e. Formation of distinct cirri; formation of anlage for opisthe endoral apparatus; opening of subsurface pouch
- f. Formation of anlage for proter paroral cirrus; proter and opisthe cirral fields showing 5 transverse and 9 frontoventral cirri
- g. Formation of opisthe paroral cirral and left marginal cirral primordia; resorption of parental cirrus VI/2
- h. Migration of cirri toward their final positions; formation of equatorial cleavage furrow; continued resorption of parental cirri
- i. Migration of opisthe AZM to its final position; resorption of the final parental cirri before daughter cell separation

Scale 20 μ m

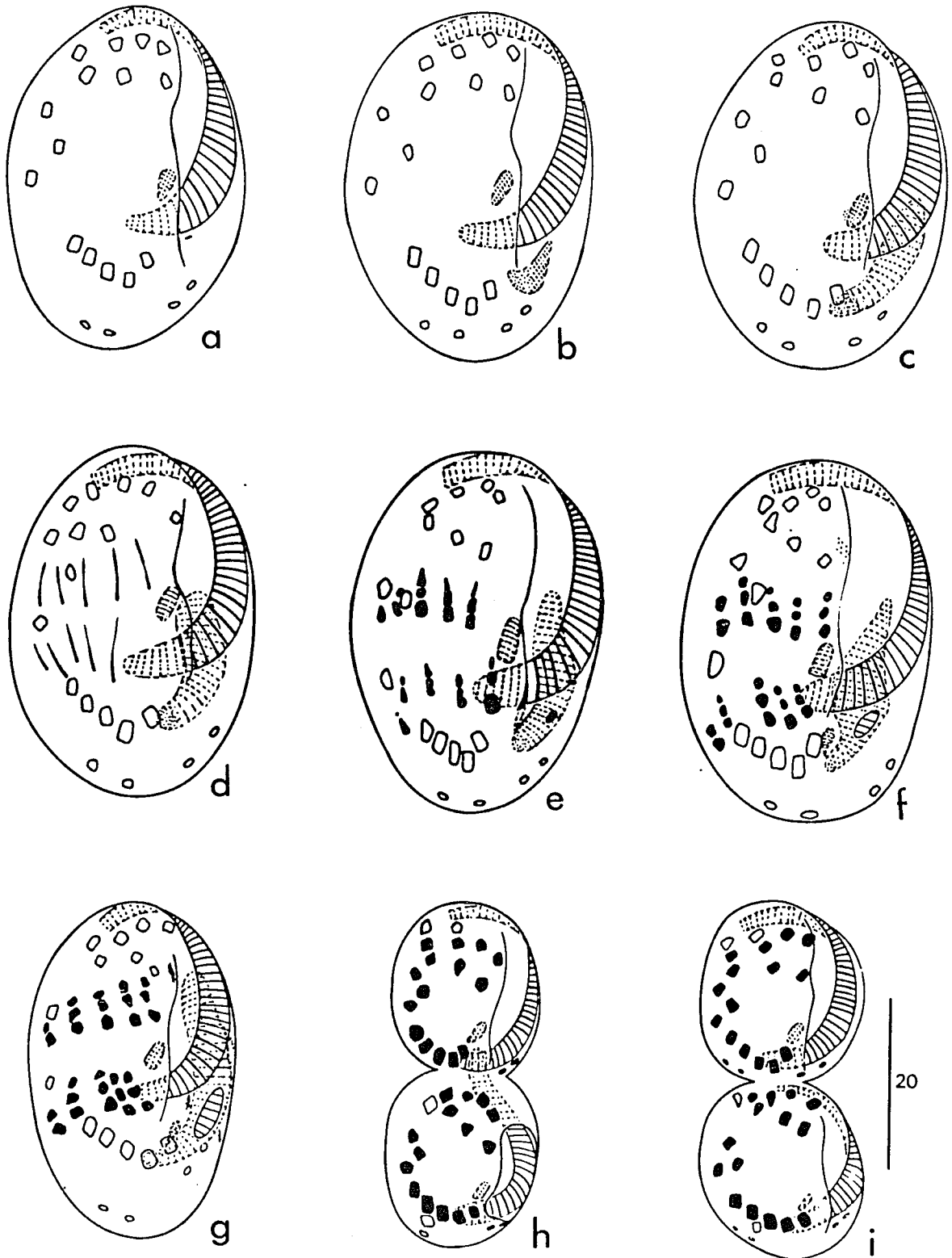


Figure III.

FIG. IV. Photomicrographs of Euplotes division

- a. Early oral anlage formation; Arrow, opisthe oral primordium; 3050x
- b. Later stage of oral anlage formation; 1540x
- c. Early stage of division showing cirral primordia breaking apart to form distinct cirri; 2980x
- d. Later stage of cirrus formation; Arrow 1, proter paroral cirrus; Arrow 2, opisthe paroral cirrus; 1550x



a



b



c



d

Figure IV.

FIG. V. Photomicrographs of Euplotes division

- a. Endoral apparatus formation; Arrow, opisthe endoral apparatus anlage; 3060x
- b. Left cirral primordia; Arrow 1, proter and opisthe left cirri; Arrow 2, parental left cirri; 4590x
- c. Late stage of division showing proter and opisthe cirral fields; 1530x
- d. Dorsal surface showing kinetal division; Arrow 1, new paired kinetosomes; Arrow 2, parental dorsal bristle; 1520x

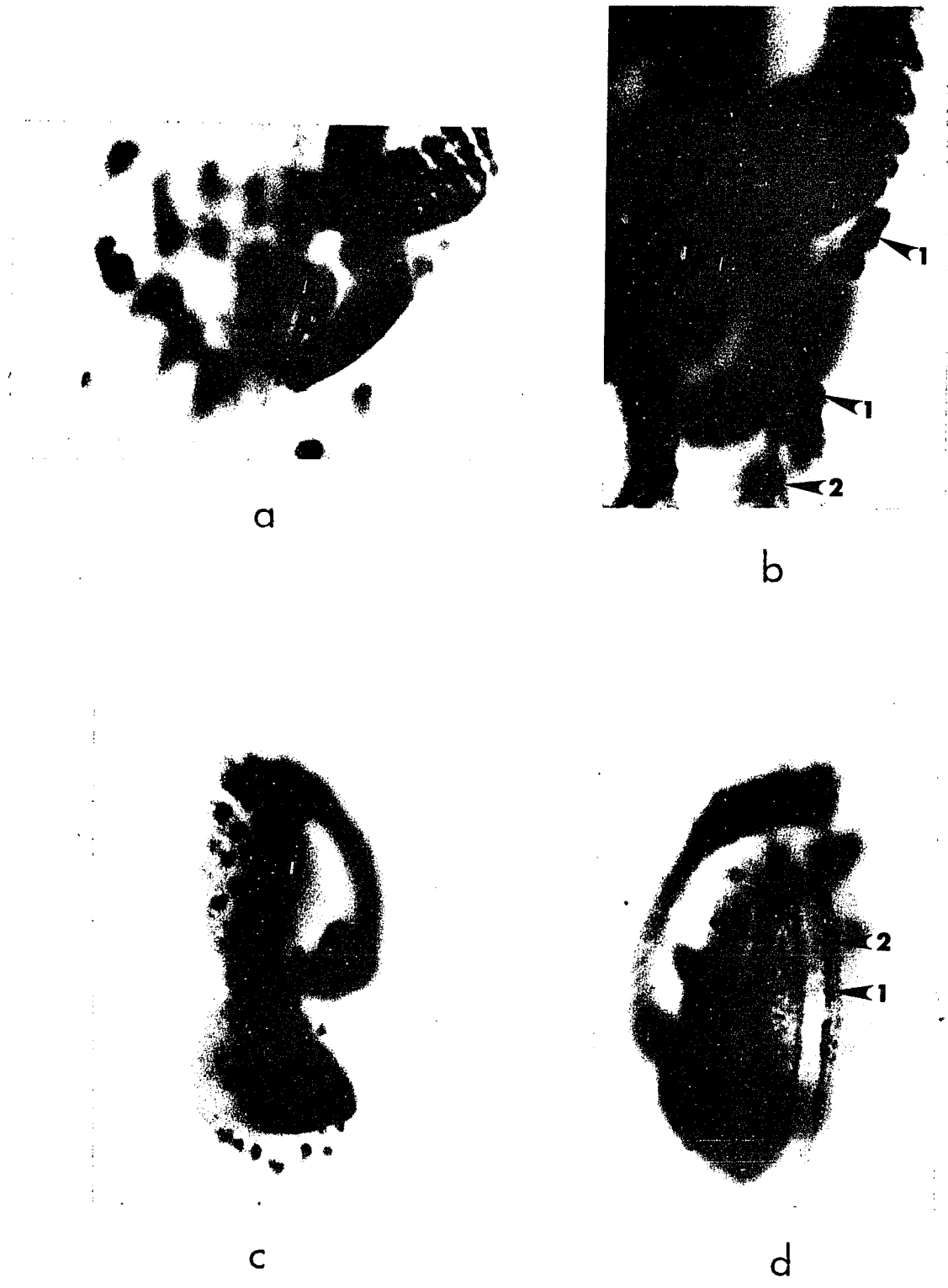


Figure V.

FIG. VI. Diagram of Aspidisca cortical structure and features

Key: A - AZM, anterior membranelles of AZM; B - AZM, buccal membranelles of AZM; PC, paroral cirrus or cirrus II/1; EA, endoral apparatus; III/1, IV/1, V/1, VI/1, VII/1 transverse cirri; III/2, III/3, IV/2, IV/3, V/2, VI/2 frontoventral cirri. Cirri; III/2, III/3, IV/2, IV/3, V/2, VI/2 frontoventral cirri.

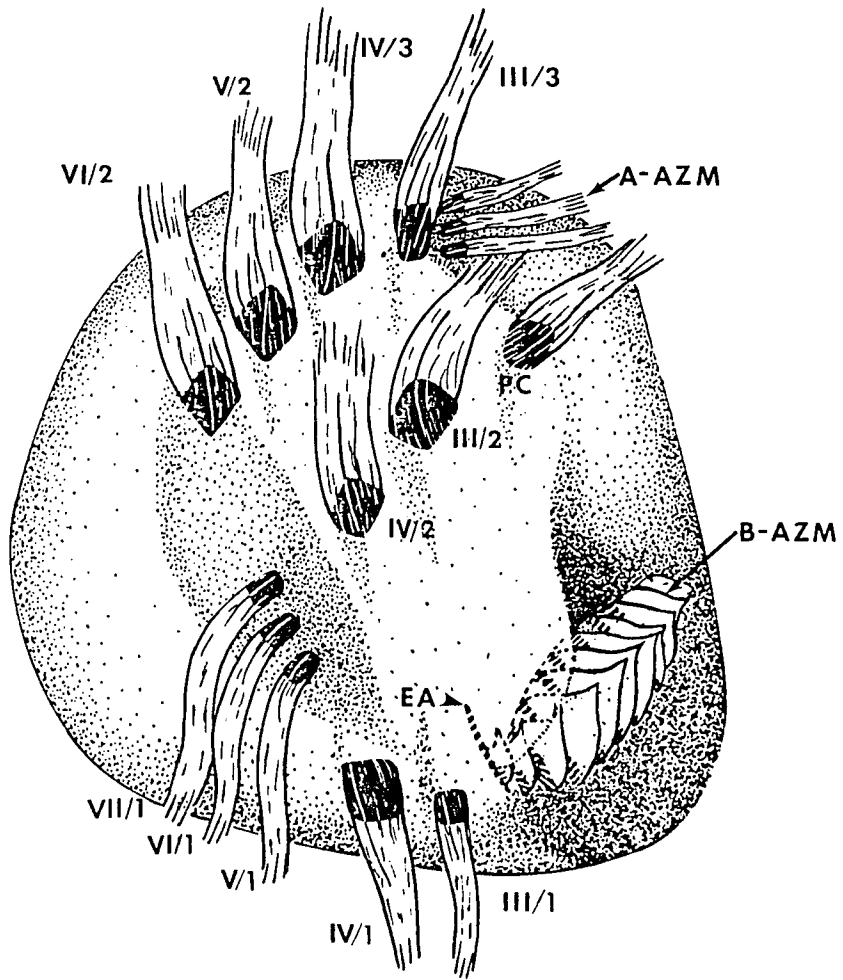


Figure VI.

FIG. VII. Diagram of Aspidisca division stages.

- a. Beginning of opisthe oral primordium and cirral primordia III, IV of frontoventral and transverse cirri.
- b. Migration of opisthe AZM to the ventral surface and formation cirral primordia V of frontoventral and transverse cirri.
- c. Formation of cirral primordia VI, VII of frontoventral and transverse cirri.
- d. Breaking away of anterior membranelles of the AZM from the developing opisthe AZM; formation of proter and opisthe cirri primordia fields; resorption of parental cirrus VI/2.
- e. Formation of anlag for proter paroral cirrus.
- f. Proter and opisthe cirral fields showing 5 transverse and 6 frontoventral cirri; formation of anlaga for opisthe paroral cirrus, resorption of parental cirrus V/2.
- g. Migration of cirri toward their final position and formation of argentophilic areas at the posterior end of the AZM's; continued resorption of parental cirri.
- h. Migration of opisthe anterior membranelles of the AZM to their final position; formation of equatorial cleavage furrow; continued resorption of parental cirri.
- i. Daughter cell separate; resorption of the final parental cirri.

Scale 10 μ m

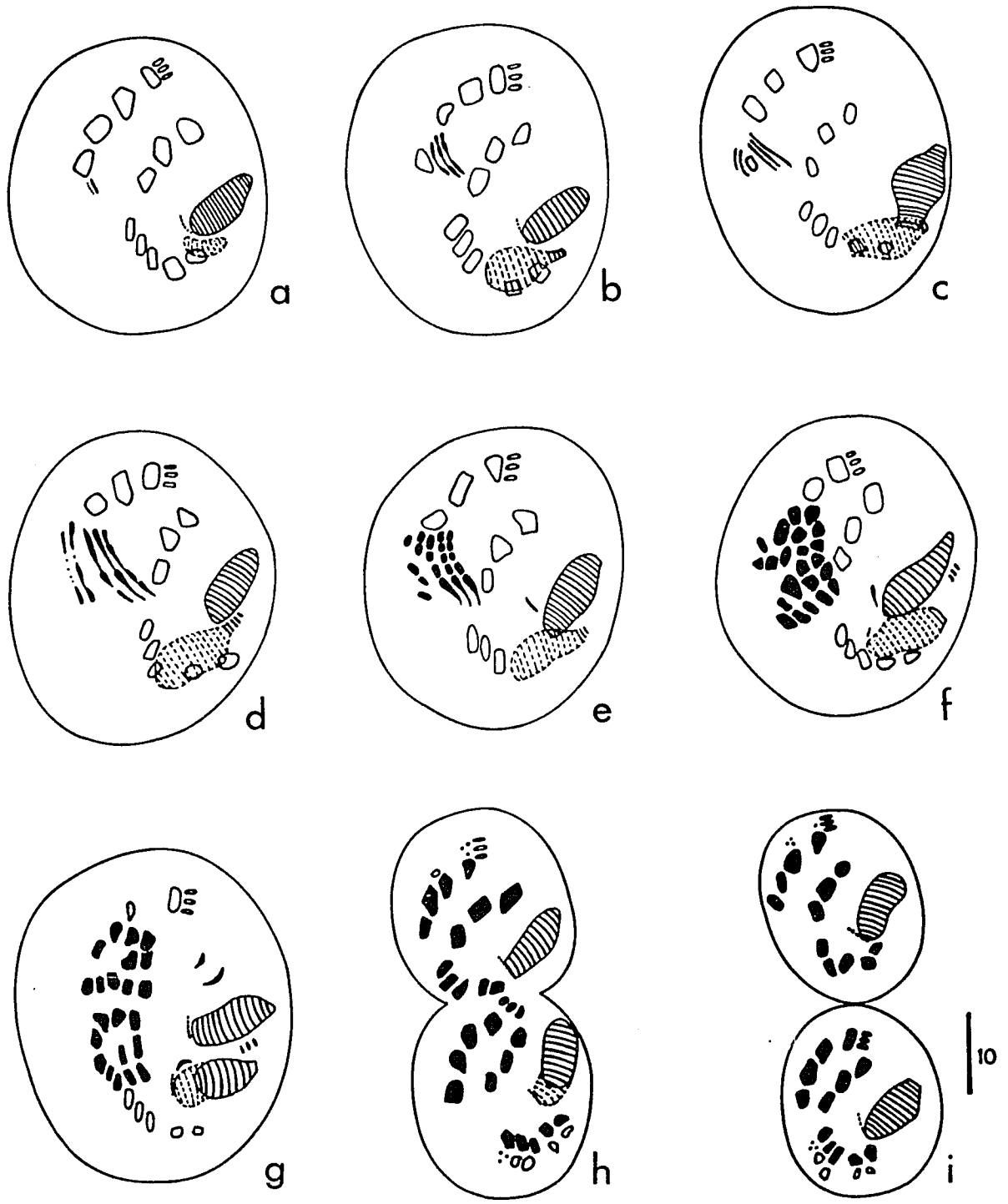


Figure VII.

FIG. VIII. Photomicrographs of Aspidisca division

- a. A. costata; early oral anlaga formation; Arrow, opisthe oral primordium; 3010x
- b. A. baltica; early stage of division showing long frontoventral, transverse streaks (III - VII) on both sides of cirri VI/2 and VII/2; 2860x
- c. A. baltica; later stage of division; Arrow 1, anlaga of proter paroral cirrus; Arrow 2, three portions of transverse cirrus III/1; 1365x
- d. A. costata; late stage of division showing proter and opisthe cirral fields; Arrow 1, anlaga of proter and opisthe paroral cirri; Arrow 2, developing anterior membranelles of opisthe AZM; 1680x



a



b



c



d

Figure VIII.

FIG. IX. Diagram of Diophrys cortical structures and features .

Key: A - AZM, anterior membranelles of AZM; B - AZM, buccal membranelles of AZM; EM, endoral membrane; PM, paroral membrane; PC, paroral cirrus or cirrus II/1; III/1, IV/1, VI, VII/1 transverse cirri; III/2, III/3, IV/2, VI/2, VI/3 frontoventral cirri; C1, C2, C3 caudal cirri; LM1, LM2 left marginal cirri.

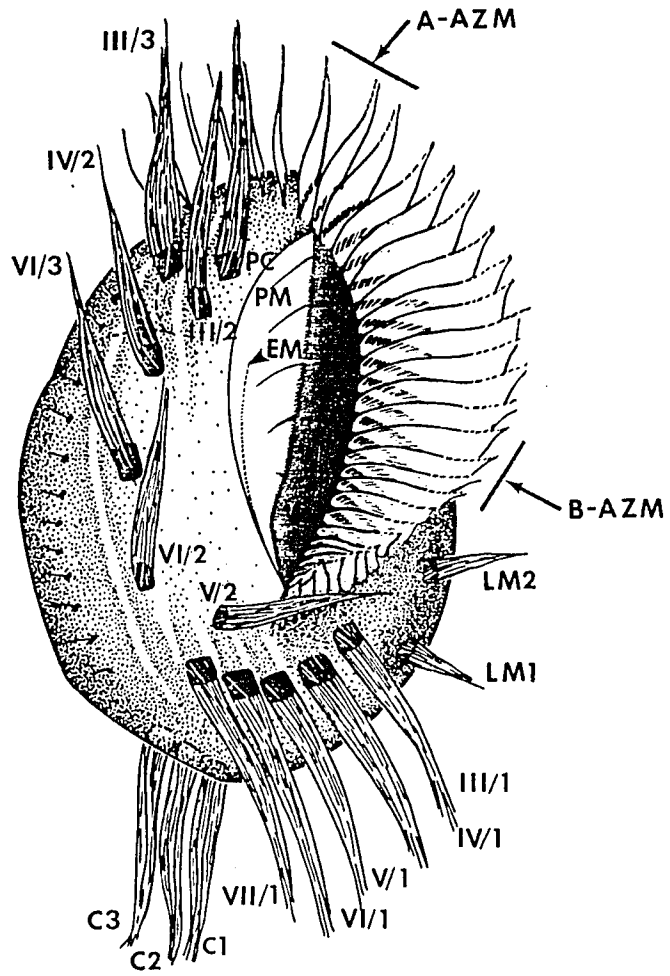


Figure IX.

FIG. X. Diagram of Diophrys division stages.

- a. Beginning of opisthe oral primordium and cirral primordia of frontoventral and transverse cirri.
- b. Formation of proter and opisthe cirral primordia fields.
- c. Formation of distinct cirri; resorption of parental endoral and paroral membranes.
- d. Formation of anlage for proter paroral membrane and cirrus; migration of opisthe AZM to the ventral surface.
- e. Proter and opisthe cirral fields showing 5 transverse and 6 frontoventral cirri; formation of anlage for opisthe paroral membrane and cirrus; formation of distinct proter paroral cirrus.
- f. Formation of distinct opisthe paroral cirrus; formation of proter and opisthe endoral and left marginal primordia.
- g. Migration of cirri toward their final position; beginning of parental cirri resorption.
- h. Formation of equatorial cleavage furrow; continued resorption of parental cirri.
- i. Daughter cell separate; resorption of the final parental cirri.

Scale 20 μm

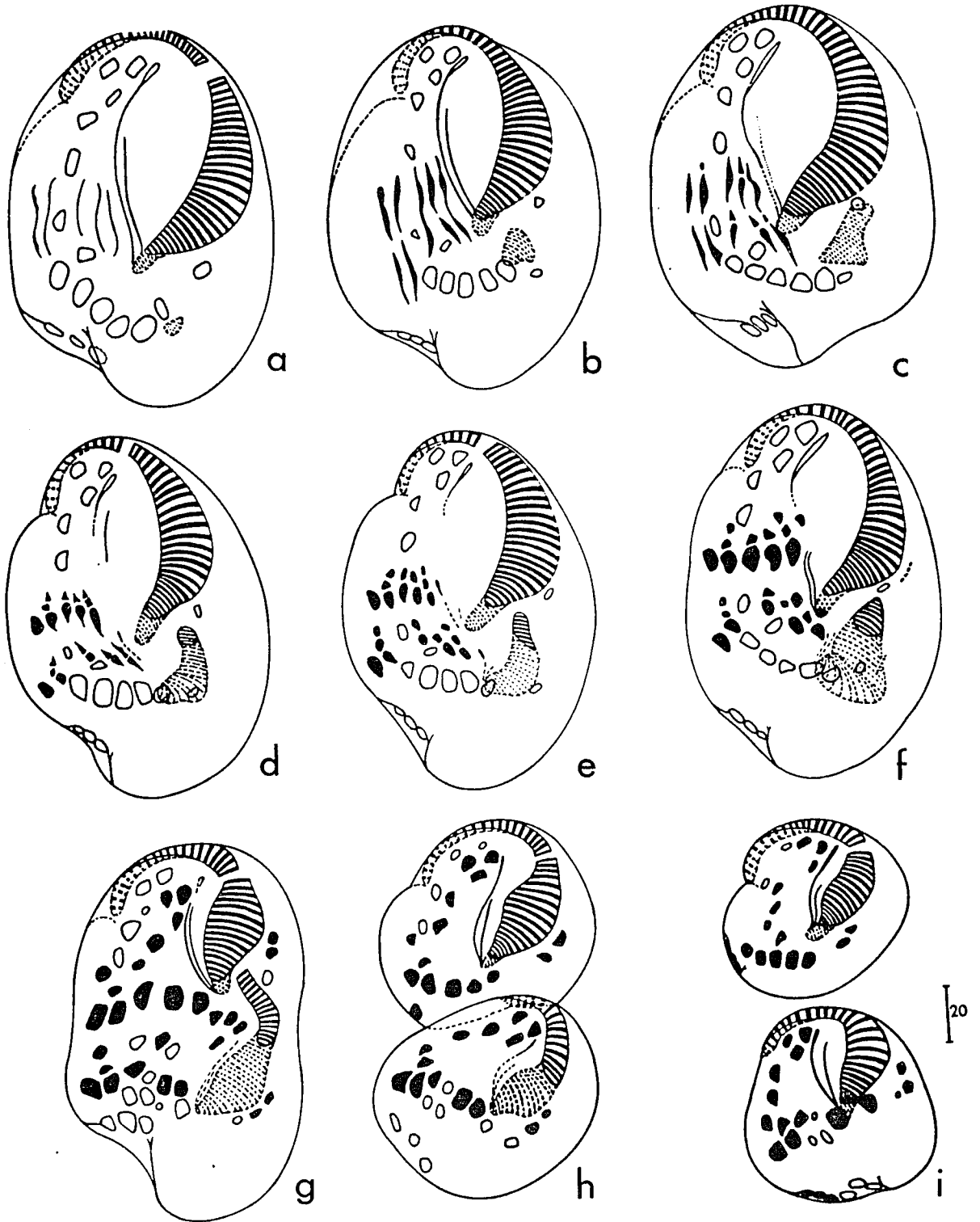


Figure X.

FIG. XI Scanning electron micrographs of Diophrys division

- a. Ventral surface of Diophrys; Arrow, endoral membrane; 510x
- b. Frontoventral-transverse cirral primordia VII; Arrows, indicate pairs of kinetosomes; Asterisk, cirrus VI/3; 6100x
- c. Opisthe cirral development; Arrow, cilium buds. 4580x
- d. Membranelles of developing opisthe AZM; Arrow, paroral primordium 4520x



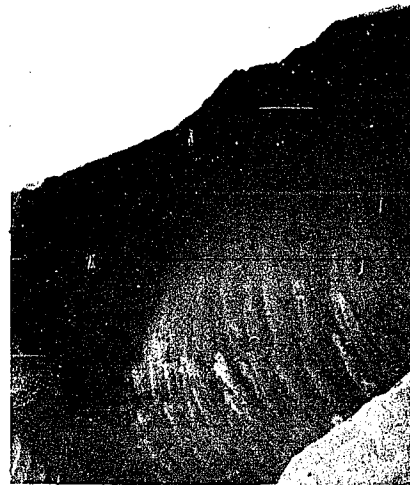
a



b



c

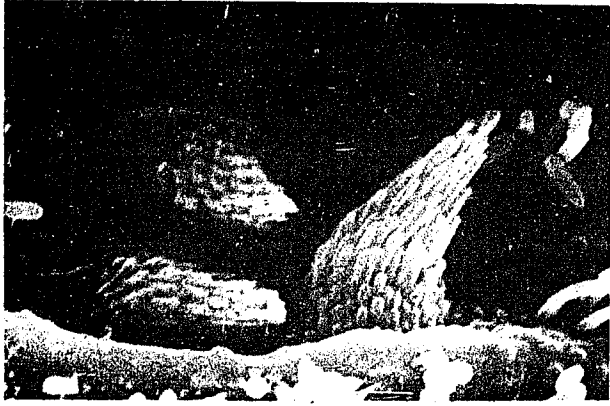


d

Figure XI.

FIG. XII. Scanning electron micrographs and photomicrographs of Diophrys division

- a. Development of caudal cirri on dorsal surface; Arrow, cilium buds. 4510x
- b. Cell with development of cleavage furrow; 520x
- c. Early oral anlage formation; Arrow, opisthe oral primordium; 550x
- d. Early stage of division showing streak formation; Arrow 1, streak III; Arrow 2, parental paroral membrane; 1110x



a



b



c



d

Figure XII

FIG. XIII. Photomicrographs of Diophrys division

- a. Cirral primordia enlarging to form cirrus lobes; Arrow 1, proter transverse cirrus III/1; Arrow II, opisthe transverse cirrus VII/1; 920x
- b. Proter cirral field; Arrow 1, proter paroral cirrus; Arrow 2, proter paroral membrane; 2120x
- c. Left marginal cirral primordia; Arrow 1, parental left marginal cirrus LM2; 2110x
- d. Cell with development of cleavage furrow; 510x



a



b



c



d

Figure XIII.

FIG. XIV. Diagram of Euplotaspis cortical structures and features

Key: AZM adoral zone of membranelles; PC, paroral cirrus or cirrus II/1; EA, endoral apparatus; III/1, IV/1, V/1, VI/1, VII/1 transverse cirri; III/2, III/3, IV/2, IV/3, V/3, V/2, VI/2, VI/3, VII/2 frontoventral cirri; C1, C2, C3 caudal cirri; TC, tufts of cilia forming a row of fringe; K, kiny number 1

Figure XIV.

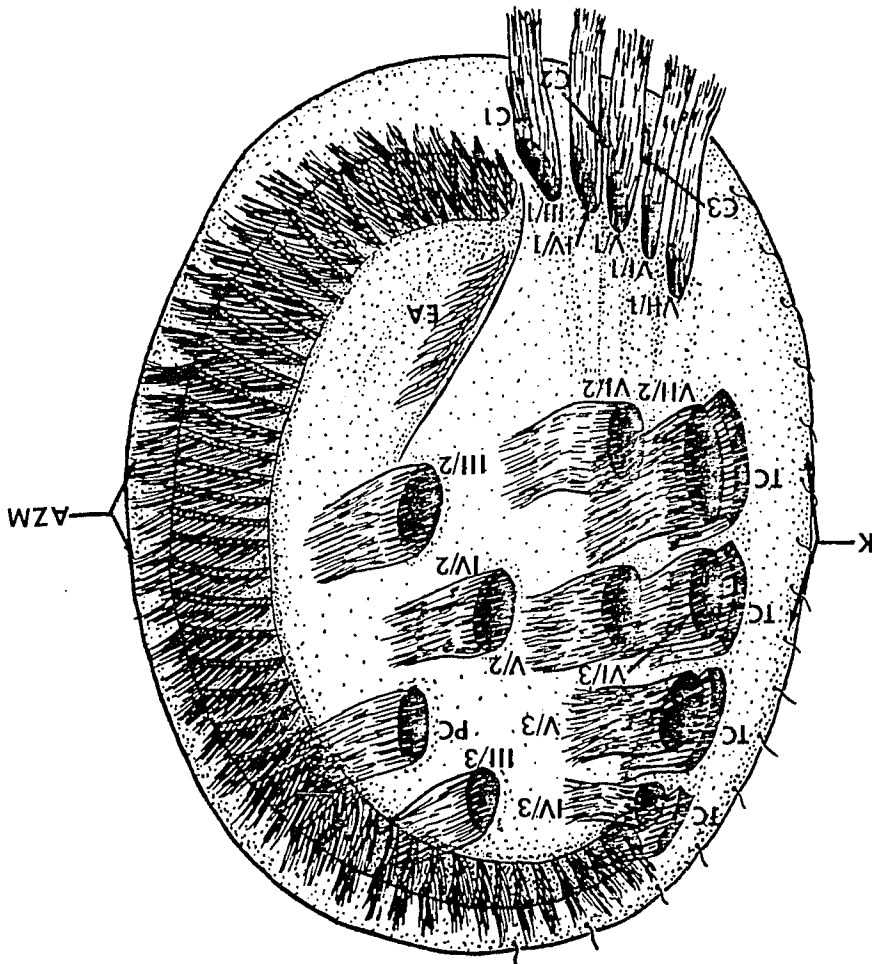


FIG. XV. Diagram of Euplotaspis division

- a. Beginning of opisthe oral primordium
- b. Alignment of membranelles in opisthe ora; primordium and beginning of cirral primordia VI, VII of frontoventral and transverse cirri and formation of endoral apparatus anlaga
- c. Opisthe oral primordium expanding beneath parental AZM and beginning of cirral primordia III, IV, and V
- d. Formation of proter and opisthe cirral primordia field
- e. Formation of distinct cirri from cirral primordia VII
- f. Formation of anlage for proter and opisthe paroral cirri; proter and opisthe cirral fields showing 5 transverse and 9 frontoventral cirri; opening of subsurface pouch
- g. Resorption of parental frontoventral cirri starting with cirrus III/2.
- h. Migration of cirri toward their final positions; formation of equatorial cleavage furrow; formation of cilia fringe from frontoventral cirri starting with cirrus VII/2; continued resorption of parental cirri
- i. Migration of opisthe AZM to its final position; resorption of the final parental cirri before daughter cell separation

Scale 30 μ m

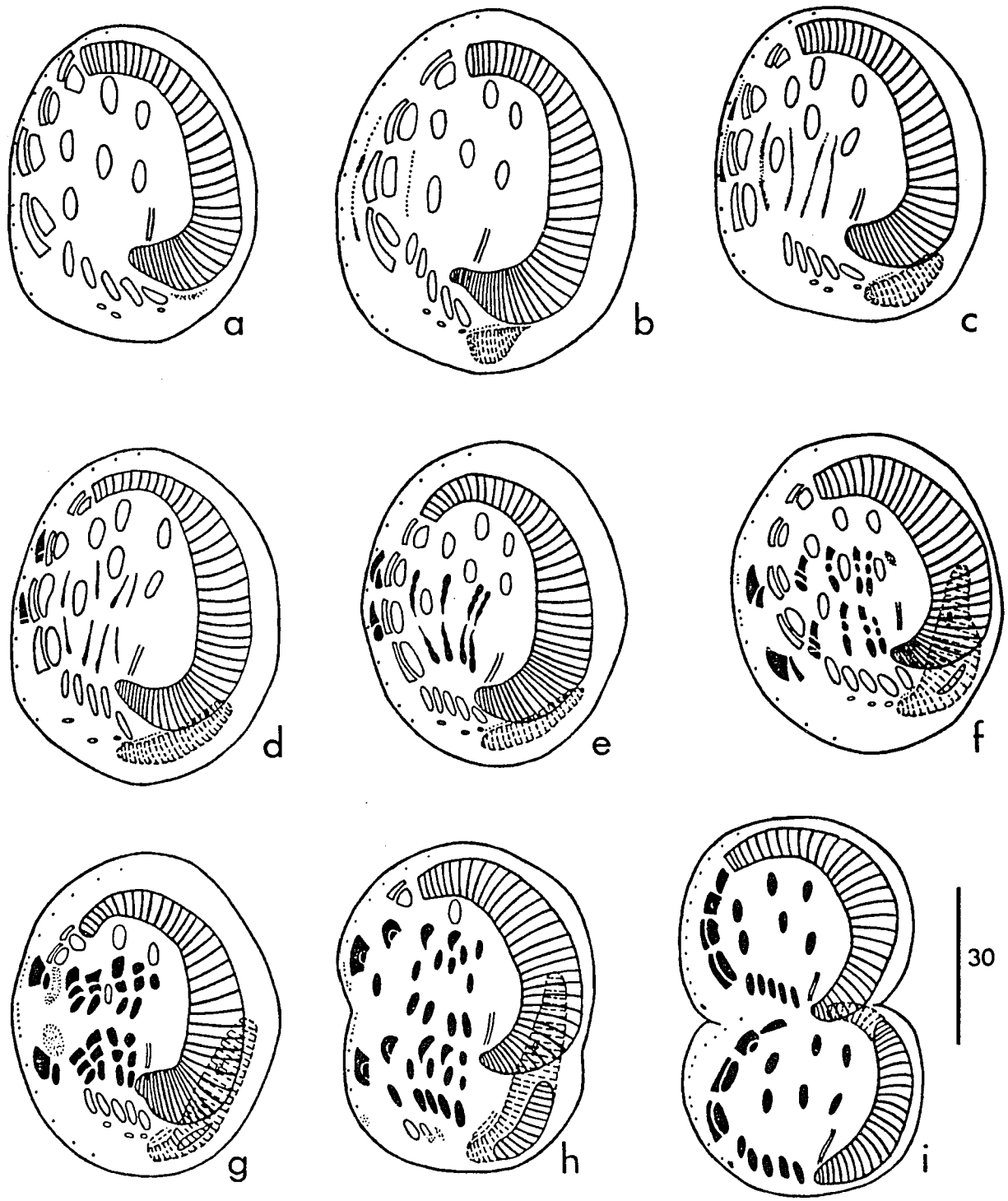


Figure XV.

FIG. XVI. Photomicrographs of Euplotaspis division

- a. Protargol stained Euplotaspis cionaecola; Arrow 1, endoral apparatus; Arrow 2, tufts of cilia which form the fringe of cilia along the right ventral surface; Arrow 3, caudal cirri; 875x
- b. Early oral anlage formation; Arrow, opisthe oral primordium; 960x
- c. Late stage of division showing proter and opisthe cirral fields; Arrow 1, anlage of proter paroral cirrus; Arrow 2, parental endoral apparatus; 825x
- d. Formation of the cilia for the fringe; Arrow 1, proter frontoventral cirrus VII/2; Arrow 2, opisthe frontoventral cirrus VII/2; Arrow 3, basal bodies from cirrus VII/2 which form the cilia fringe; 2915x



a



b



c



d

Figure XVI.

FIG. XVII. Diagram of Uronychia cortical structures and features

Key: A - AZM, anterior membranelles of AZM; B - AZM, buccal membranelles of AZM; LBM, left buccal membrane; RBM, right buccal membrane; PC, paroral cirrus or cirrus II/1; III/1, IV/1, V/1, VI/1, VII/1 transverse cirri; III/2, III/3, IV/3, VII/2, VII/3 frontoventral cirri; C1, C2, C3 caudal cirri; LM1, LM2, LM3 left marginal cirri; K, kinty number 6.

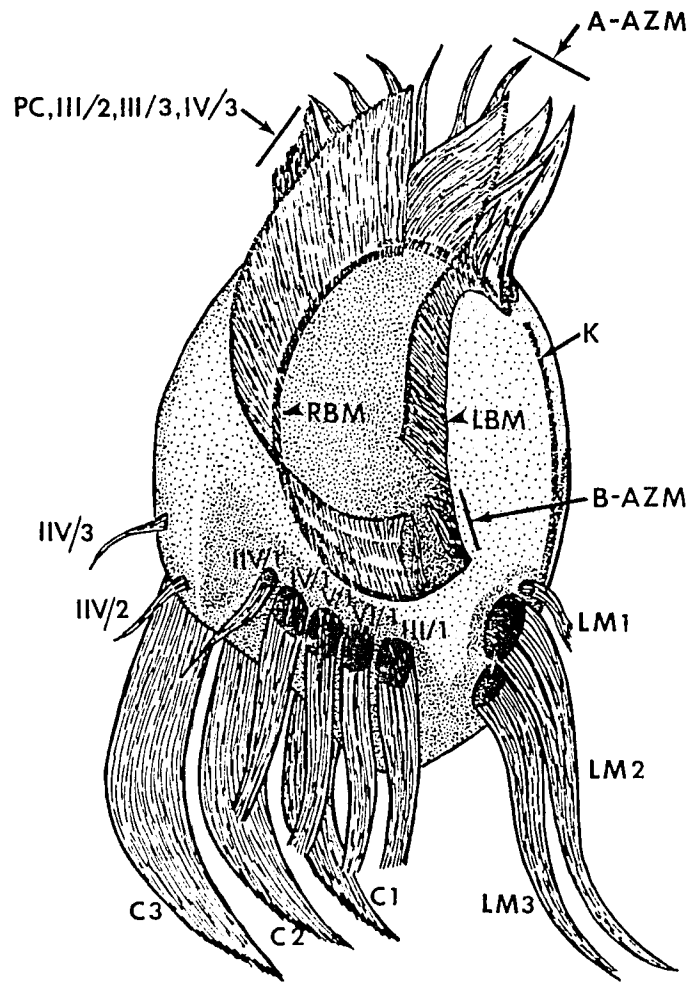


Figure XVII.

FIG. XVIII. Diagram of Uronychia division

- a. Formation of opisthe oral primordium
- b. Formation of proter oral primordium and cirral primordia III VI for frontoventral and transverse cirri; alignment of membranelles in both oral primordia
- c. Formation of cirral primordium VII and left marginal cirral primordia; migration of proter and opisthe AZM's to ventral surface; formation of proter and opisthe cirral primordia fields
- d. Formation of distinct cirri and alignment of 10 proter and 16 opisthe AZM membranelles
- e. Formation of proter and opisthe buccal membrane; proter and opisthe cirral fields showing 5 transverse and 8 frontoventral cirri
- f. Formation of proter paroral cirrus
- g. Formation of opisthe paroral cirrus; beginning of parental cirri, buccal membrane and AZM resorption
- h. Beginning of cirri and buccal membrane migration toward their final positions; continued resorption of parental ciliary structures
- i. Formation of an equatorial cleavage furrow; continued migration of ciliary structures to their final positions

Scale 30 μm

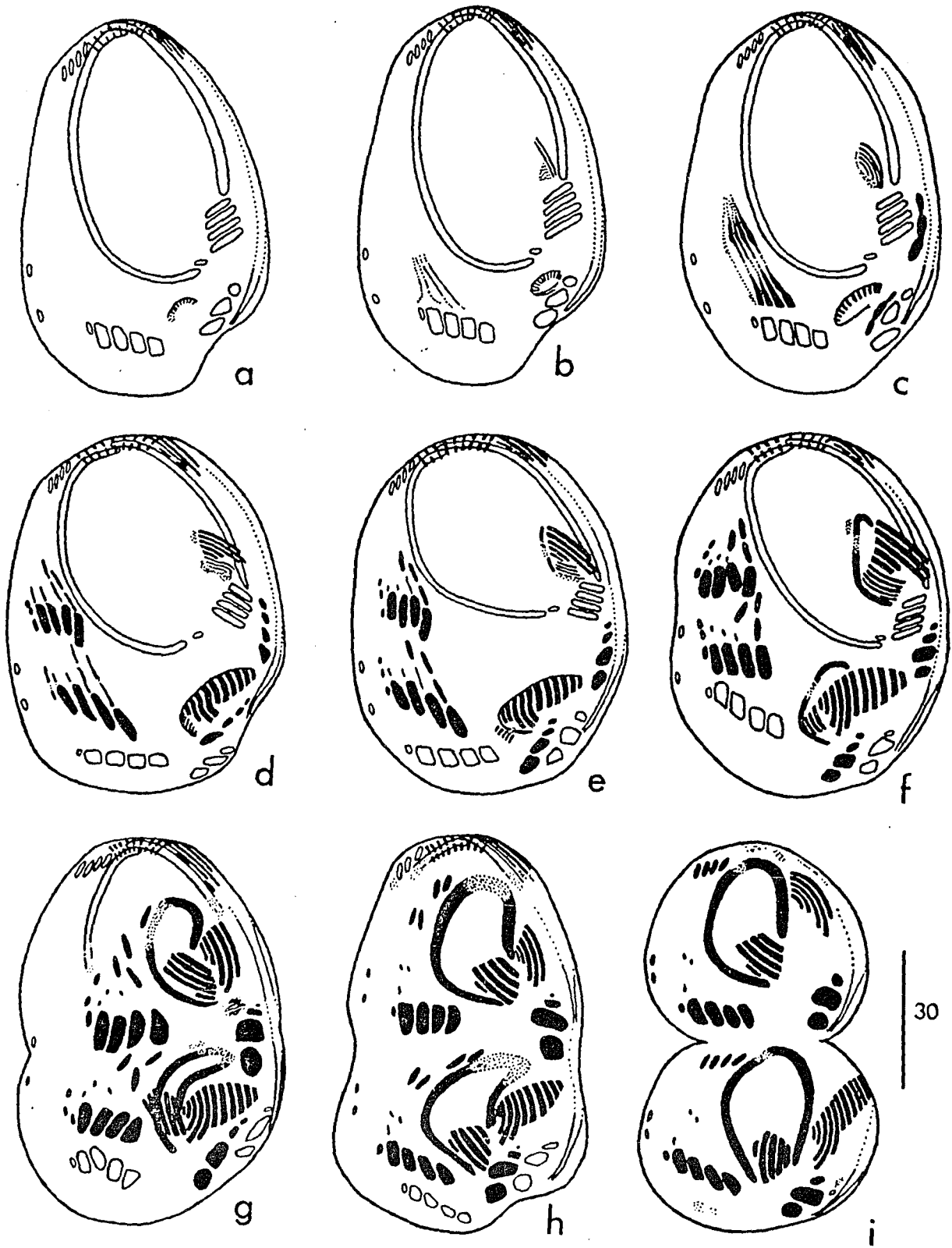


Figure XVIII.

FIG. XIX. Scanning electron micrographs of Uronychia cortical structures and features

- a. Structure of buccal membrane and cortical flap; Arrow 1, right buccal membrane; Arrow 2, left buccal membrane; Asterix, cortical flap; 2125x
- c. Kinetal rows V and VI; Arrow 1, cilium in kinetal row VI; Asterix, left marginal cirrus (LM2); 4575x
- c. Opisthe oral primordium formation; Arrow 1, membranelles of AZM; Arrow 2, buccal membrane primordium ; 2220x
- d. Formation of opisthe cortical structures; Asterix, opisthe cirral primordium field; Arrow 1, buccal membrane; Arrow 2, anterior membranelles of AZM; Arrow 3, left marginal primordium of opisthe ;2200x



a



b



c

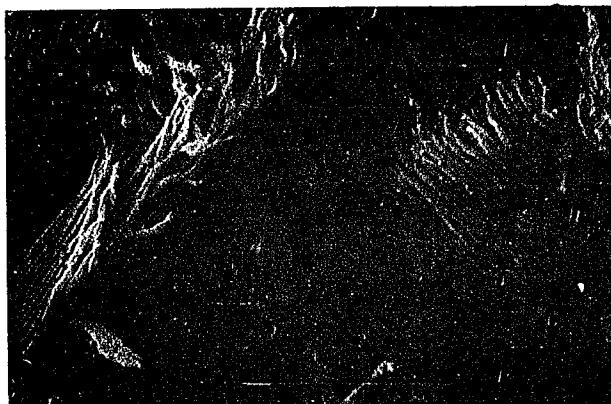


d

Figure XIX.

FIG. XX. Scanning electron micrographs and photomicrographs of Uronychia division

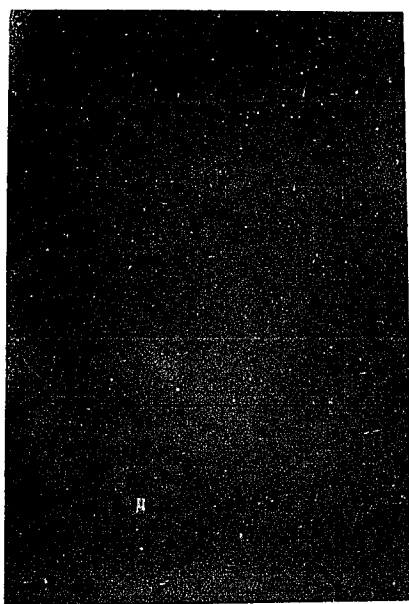
- a. Formation of proter cortical structures; Arrow 1, anterior membranelles of AZM; Arrow 2, buccal membrane; Arrow 3, proter frontoventral cirri; Arrow 4, dedifferentiating parental buccal membrane; 2065x
- b. Caudal cirri formation; Arrow 1, proter caudal cirrus (C1); 1470x
- c. Proter and opisthe cirral primordia fields III - VI; Arrow 1, parental buccal membrane; 985x
- d. Proter oral primordia formation; Arrow 1, proter buccal membrane; Arrow 2, anterior membranelles of AZM; 1215x



a



b



c



d

Figure XX.

FIG. XXI. Photomicrographs of Uronychia division

- a. Opisthe oral primordium formation; Arrow 1, 16 anterior membranelles of AZM; Arrow 2, 5 buccal membranelles of AZM; Arrow 3, buccal membrane; 1270x
- b. Proter oral primordium formation; Arrow 1, 5 anterior membranelles of AZM; Arrow 2, 5 membranelles of AZM; Arrow 3, proter buccal membrane; 1630x
- c. Proter frontoventral and transverse cirri; Asterix, transverse cirri; Arrow 1, cirri III/2 and III/3; Arrow 2, cirrus IV/3; Arrow 3, cirri VII/2 and VII/3; Arrow 4, proter paroral cirrus; 1090x
- d. Opisthe left marginal primordium; Arrow 1, anterior-most left marginal cirrus; 1260x



a



b



c



d

Figure XXI.

OTHER MORPHOGENETIC PROCESSES

The cortex of the ciliate is subject to different types of morphogenetic processes. Most often studied has been the preffission cortical changes occuring during asexual reproduction, however, other processes could prove useful in understanding the biology of ciliates. Other types of cortical morphogenesis occur at different times during the life cycle of a ciliate. The most notable is the replacement of ciliary structure following conjugation or autogamy. The dedifferentiation of ciliary structures during encystment and redifferentiation of these same ciliary structures during excystment has been described in a few ciliates. Less common are the morphogenetic processes during endogenous bud formation (Curds, 1966). Physiological reorganization, defined as the morphogenetic process reestablishing a set of ciliary structures, is commonly observed in ciliates as a response to an altered nutritional state. Through this process of reorganization, cells can develop into giants, cannibal giants or dwarfs depending upon the physiological conditions. Regeneration, which is caused by cortical trauma, is defined as the morphogenetic process resulting in the usual replacement of ciliary structures in a deficient cell. Many of these morphogenetic processes have also been studied using doublets or monster cells.

Among the Euplotids common morphogenetic processes studied

so far have been conjugation, excystment and regeneration.

Conjugation

The process of post conjugant reorganization has been described several times (Diller, 1966, 1975; Katashima, 1959a; Maupas, 1889; Tuffrau et. al. 1975; Turner, 1930). Several contradictory observations recently have been clarified (Tuffrau, et. al., 1976). In all cases observed (Euplotes, Aspidisca, Certesias, Diophrys and Uronychia) conjugation among the euplotids is unique when compared to other hypotrichs because of the ventral surface to ventral surface pairing.

Tuffrau et. al. (1976) and Kloetzel (1975) describe the process of conjugation morphogenesis in Euplotes beginning with pairing of individuals at the mid-level of the peristome. Conjugating individuals are first held together by coalescence of the buccal membranelles. As the adhesion area expands, membranes fuse, the cytosome closes, and the endoral apparatus and AZM are absorbed. Absorption of the AZM begins at the posterior end and moves anteriorly leaving about 10 of the most anterior membranelles. During absorption of ciliary structures, the first stage of cortical development begins with five cirral kinetosomal streaks forming to the right of the buccal cavity and anterior of the transverse cirri. Lateral proliferation of kinetosomes within the streaks cause lobes to form which break apart forming 5 transverse and 9 frontoventral cirri. A paroral cirrus (II/1) does not

develop. A small patch of kinetosomes develops to the left of the cirral primordia near the location of the former cytosome. This oral primordium increases in size developing into an AZM similar to the procedure of opisthe primordium development during binary fission. This new AZM has only 20 - 23 membranelles. Left marginal cirri develop as in binary fission from a primordium along the left edge of the organism. As old cirri and former AZM are resorbed, new cirri migrate toward their permanent sites and the members of the pair separate. Post-conjugants differ from pre-conjugants in lacking a cytosome, a paroral cirrus, II/2, and endoral apparatus, as well as having a greatly reduced AZM.

Shortly after this ciliature is complete, a new, stage two, oral primordium develops as in the preceding stage. This primordium develops as the opisthe oral primordium during binary fission with the membranelles emerging and migrating forward to align with the AZM that developed during the first stage. To the right of the posterior end of the new oral primordium the endoral primordium, row I, forms. Later and anterior to the endoral primordium the kinetosomes for the paroral cirrus (II/1) begin to develop in row II. As in the first stage, five cirral primordia (rows III - VII) for new frontoventral and transverse cirri form to the right of the other developing ciliary structures. All these different developing ciliary structures continue to form with a rapid proliferation of kinetosomes with the cirral primordia forming

lobes which break apart to form distinct cirri. Again, as in stage one, left marginal cirri develop from a primordium along the left edge of the cell. Five transverse (III/1 - VII/1), 9 frontoventral (III/2, III/3, IV/2, IV/3, V/2, V/3, VI/2, VI/3, VII/2) and 2 left marginal (LM1, LM2) develop as usual along with the formation of the paroral cirrus (II/1) and the endoral apparatus. As these new ciliary structures, including the new posterior end of the AZM, migrate to their permanent sites, the frontoventral, transverse and left marginal cirri from the first stage are resorbed. The completed second stage post-conjugant cell is similar to the pre-conjugant cell, but represents a composite of two stages of reorganization. The anterior portion of the AZM comes from stage one while the posterior half develops during the second stage of reorganization. The frontoventral, transverse and left marginal cirri are completely replaced during both stages whereas the paroral cirrus and endoral apparatus only develop during the second stage. The caudal cirri come from the pre-conjugant cell.

Encystment - Excystment

The process of cyst formation has been known to occur in euplotids since it was briefly described in E. charon by Schneider (1854). Stein (1859) also saw cysts of E. charon, but the process of encystment and excystment was not described until Möbius (1888) elucidated the process in E. harpa which was further clarified by Schewiakoff (1928). Encystment has also been observed in E. longipes (Strolp, 1924) believed to be

E. vannus (Borror, 1972b); E. taylori (Garnjobst, 1928) believed to be E. crassus (Borror, 1972b); E. inkystans (Chatton in Fauré-Fremiet et. al. , 1954); E. muscicola (Fauré-Fremiet et. al. , 1954) and E. elegans (Tuffrau, 1960). Among other euplotids, encystment has been observed in Diophrys (Garnjobst, 1928), Certesias (personal communication, B. Wicklow) and Ivanic (1931) described encystment in what is now believed to be a species; Aspidisca.

Cyst formation among euplotids appears to serve a protective function in response to environmental conditions (Fauré-Fremiet et. al. , 1954; Garnjobst, 1937; Melant, 1922) even though they are not viable after complete drying. As conditions worsen, encystment begins with a decrease of mobility as the organism creeps along the substratum. After extrusion of food material the organism becomes circular. Ciliary structures begin to break down into individual cilia and become sticky, affixing the organism to the substratum. With dedifferentiation of many ciliary structures, the ventral surface invaginates with a complex folding of the dorsal surface to form a rounded cyst. Upon release of material that forms the two concentric layers of the cyst's wall (endocyst, ectocyst) the process is complete. Silver impregnated cysts show that the dorsal argyrome has not been dedifferentiated. The ventral surface has been modified by dedifferentiation of many ciliary structures, but several ventral cirri and membranelles of the AZM are retained. Retention of some kinetosomes

within the euplotid cyst is different from other hypotrichs where all kinetosomes are resorbed (Grimes, 1973; Tuffrau & Fryd-Versavel, 1977).

Little is known about excystment. Much redevelopment occurs within the cyst, with a well-developed organism leaving the cyst by way of an emergence pore.

Regeneration

The morphogenetic process of regeneration has been studied in three species of euplotids (Euplotes, Diophrys, Uronychia) by causing cortical trauma by either microsurgery or ultraviolet microbeam irradiation. I have also observed the same process during reorganization in E. harpa. The most complete studies using microsurgery have been done using Euplotes (Dembowska, 1926; Taylor, 1928; Yow, 1958). It was reported that when any single cirrus or combination of cirri and AZM are removed, the resulting fragment will regenerate if the micronucleus and a portion of the macronucleus are present. Healing is accomplished immediately after surgery by fusion of the cell membrane. When only cirri have been removed, five primordia (III - VII) for the frontal and transverse cirri form in the usual place. After a rapid increase in size by kinetosome proliferation, these streaks divide in half forming the equivalent of proter and opisthe cirral fields. In the proter streak development continues with the primordia enlarging,

forming lobes which eventually break apart to form distinct cirri, while the opisthe cirral primordia are resorbed. The new cirral field consists of five transverse cirri and either 9 (E. vannus) or 8 (E. plumipes) frontoventral cirri. The primordium for the paroral cirrus develops along the right edge of the buccal cavity. A single primordium develops along the left margin of the cell which will divide forming the two left marginal cirri. New caudal cirri are formed at the posterior end of the right-hand kinetal rows. As the cirri continue to develop and move toward their permanent sites, there is a sequential resorption of all the old cirri. Exactly what happens to the AZM when surgically injured in Euplotes has not been described, however a regeneration of the injured parts probably occurs as in other euplotids (Uronychia) or as in other hypotrichs (Grimes & Adler, 1978; Hashimoto, 1961; Jerka-Dziadosz & Frankel, 1969). The disposition of the endoral apparatus during regeneration has also not been described, however, during reorganization, E. harpa's endoral apparatus is replaced (personal observation).

Wise (1965) has shown that cirral damage by ultraviolet micro-beam irradiation causes the entire ciliary organelle to disappear. Losing a cirrus, however, will not cause the cell to undergo a regeneration cycle. Rather the cirrus is replaced during the next morphogenetic cycle during pre-division. Damage by ultraviolet irradiation to the AZM will persist through many succeeding generations

of proters (11 generations tested). When either mature or primordial ciliary organelles of early dividers are damaged there is a temporary delay of normal pre-division morphogenesis which includes resorption of all primordial structures. However, in later stages of pre-division, there is only a delay of the morphogenetic process with primordial structures not being resorbed. Any developing ciliary structures which are damaged will not be replaced until the next generation.

A number of studies on regeneration have been done using Uronychia where the trauma was induced by microsurgery (Calkins, 1911; Dembowska, 1926; Young, 1922; Taylor, 1928). To study the different stages of cortical regeneration either single cirri were removed or different types of cell fragments were produced. When a portion of the macronucleus and micronucleus are retained, all locomotor ciliary organelles are resorbed, followed by formation of a complete new set of cirri. Both right and left buccal membranes are also replaced. When a portion of the AZM is lost, an oral primordium develops along the left edge of the buccal cavity, replacing the buccal membranelles and at least some of the anterior membranelles. The exact sequence of the regenerative process has not been described, but the development resembles very closely that described in Euplotes.

Regeneration has also been described in Diophrys by

Dembowska (1926). The process resembles that in other euplotids except that the entire AZM is replaced whenever there is replacement of other ciliary organelles. Also, the actual regeneration of ciliary structures begins much sooner in Diophrys (2-3 hours after surgery) as compared to other euplotids (Uronychia, 5-6 hours; Euplotes, 6-8 hours).

DISCUSSION - SPECIFIC

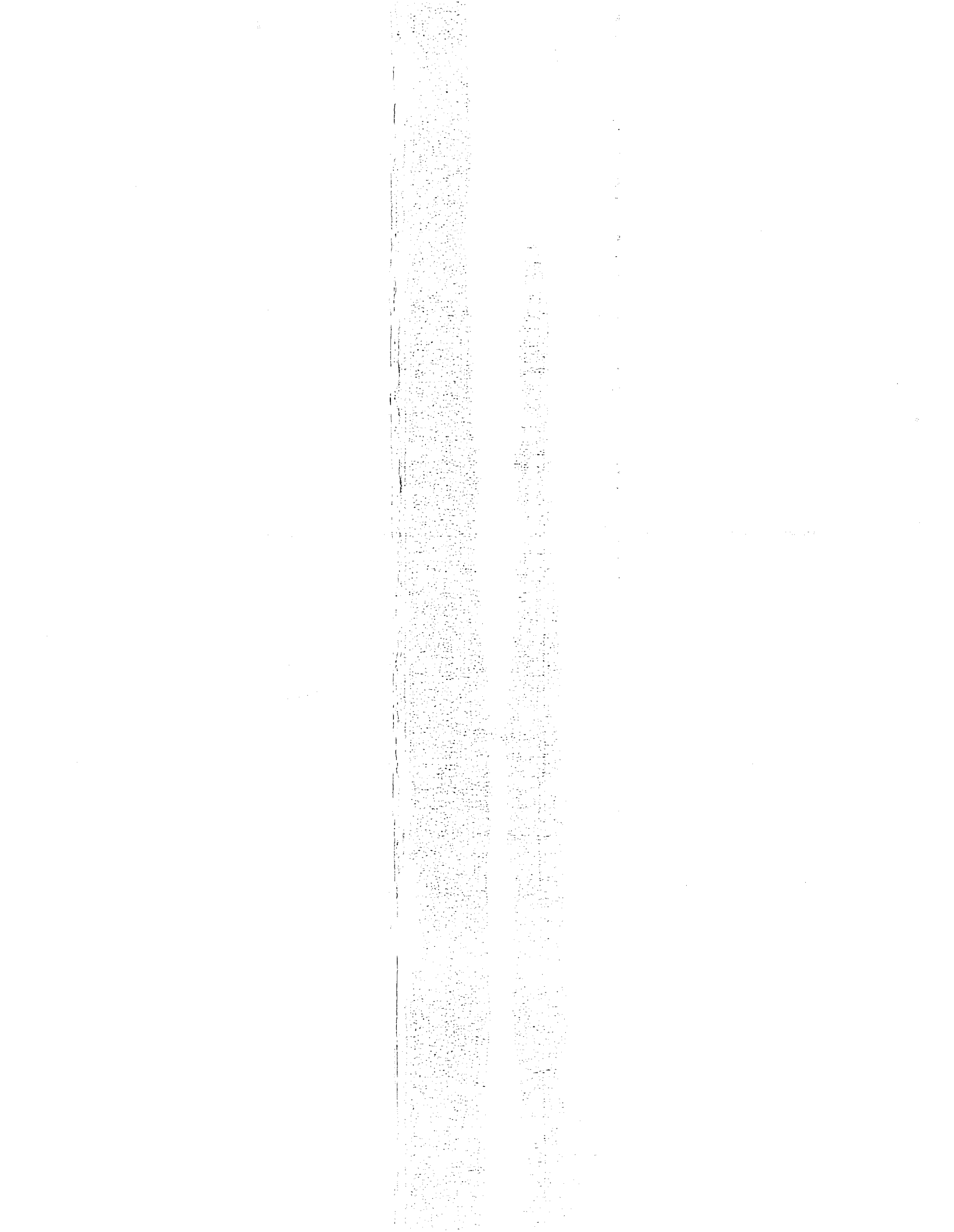
Euplotes

Members of the genus Euplotes have been known for a long time beginning with Müller's (1773) original description of Trichoda charon, now considered E. charon, the type species of the genus. Ehrenberg (1830) formed a new genus Euploea which was later changed by Ehrenberg (1831) to Euplotes because the original name was already being occupied by a genus of butterflies. Three species, E. charon, E. patella, and E. turritus were included in Ehrenberg's monograph of 1832 and, by 1838, he described 9 species to the genus, several of which are now included in the genus Aspidisca. Many species now considered to be in the genus Euplotes either have been placed in another genus when first described or have been moved back and forth between several genera in different taxonomic schemes (i. e. Ploesconia, Himantophorus, Kerona, Coccludina, and Himantopus). It was not until Kahl's monograph (1932) that the first synopsis of the genus was undertaken including 22 species and 10 varieties. During the last 40 years a number of new methods and criteria have been developed which have aided in a better understanding of the separation and identification of species. Particularly applicable methods in the study of systematics are the "wet-silver" methods which differentiate the silverline system and ciliature; protargol method which stains cilia and intracellular fibrillar system; nigrosin-HgCl₂-formalin method which elucidates

cortical sculpturing; and nuclear stains. Criteria which are now considered useful in separation of species are (1) general morphological features of body shape, sculpturing of right buccal overture and sculpturing of peristomal plate; (2) number, distribution, and spatial arrangement of ventral cirri; (3) configuration of the ventral and dorsal interkinetal network; (4) shape of AZM; (5) shape of interphase macronucleus; (6) cortical sculpturing and (7) ecological features.

Over 80 species and varieties of Euplotes have been described in the last 200 years, many of which are now considered junior synonyms. Borror (1972b) recognized 43 valid species of Euplotes in his revision of the order Hypotrichida. Several new species have been described in the last few years. Fenchel & Lee (1972) described E. antarcticus and Carter (1972) characterized E. indentatus, E. magnicirratus, E. octocarinatus and E. polycarinatus. Curds (1974) described E. parkei and Curds et. al. (1974) characterized the new species E. rariseta. Because of the addition of 7 new species listed above and of E. latus Agamaliyev (1967) listed as a true species (considered a variety of E. patella by Borror (1972b)), Curds (1975), in his guide to the genus Euplotes listed 51 different species.

Appendix I lists the 51 species, with references to the original descriptions, which I consider valid species using the criteria listed above. The list of valid species varies from Curds (1975) in



several respects: (1) one new species has come to light; E. nana Jones & Owen 1974. (2) E. octocarinatus is considered a junior synonym of E. patella because the two appear in all respects similar except that the number of dorsolateral kineties vary which is known to be different in several species (Berger, 1965; Bonner, 1954; Carter, 1972; Frankel, 1975; Heckmann, 1963; Hill & Reilly, 1976; Tuffrau, 1960) and stocks containing both 8 and 9 dorsolateral kineties have been found (personal observation). (3) E. plumipes is considered a valid species due to the shape of the macronucleus as described by Stokes (1884) and Carter (1972) (personal observation and personal communication Dr. Heckmann). (4) E. terricola Penard 1922 is no longer considered a member of the genus Euplotes because of the spatial arrangement of frontoventral and transverse cirri and presence of many left marginal cirri.

The genus Euplotes contains more species than any other genus in the order Hypotrichida and, in fact, of the 1,125 genera of ciliates less than 2% contain as many species. Now, however, based on different habitats, cirral patterns and configuration of dorsal argyrome, this genus should be divided into several smaller genera.

Corliss (1975) has presented a strong case that supports the view that the first ciliates arose in a marine environment. Within the order Hypotrichida many species are found in the marine habitat and within

the family Euplotidae only 14 species of Euplotes and several species of Aspidisca among the 12 genera are found in freshwater habitats. It cannot be determined whether the genus Euplotes arose in the marine environment given their highly complicated biology; however, Hennig (1966) suggests that the habitat with most species from a single genus represents that genus' ancestral environment. Of the 51 species listed in appendix I, 33 are from the marine environment, 3 are euryhaline and 14 are from freshwater habitats. Thus, the genus Euplotes originally arose in the marine environment with a few lines of descent moving into freshwater habitats.

The number and position of ventral cirri (particularly frontoventral and transverse cirri) have been used for a long time in taxonomic separation of different species of Euplotes (e. g. Carter, 1972; Curds, 1975; Gates, 1978b, 1978c; Kahl, 1932; Tuffrau, 1960). Frontoventral cirri which are derived along with the transverse cirri during divisional morphogenesis from 5 cirral streaks (III - VII) were shown by Washburn & Borror (1972) to form 3 distinct patterns; one with 10 cirri, two with 9 cirri. The number and pattern of frontal and transverse cirri as a taxonomic tool in the study of speciation in the genus Euplotes has been extended by Gates (1977, 1978a, 1978b, 1978c, 1979). Gates, using multiple variant analysis, obtained measures of morphometric variation of each cirrus location in reference to the other cirri. Using this method, Gates (1978b) showed that 7 species he

studied with 10 frontoventral cirri all had the same cirral configuration regardless of where the natural population was obtained or the configuration of the dorsal argyrome (Fig. XXIIa). Gates extended this observation with the view that all species of Euplotes with 10 frontoventral cirri have a similar configuration. In a further study of Euplotes with nine frontoventral cirri Gates observed two naturally occurring cirrotypes depending on the location of the second cirrus in streak VI. The first group with a 9 cirral type pattern was shown to correspond with the 10 cirral type pattern, but lacking cirrus VI/2 (Fig. XXIIb). The second group also exhibited a pattern similar to the 10 cirral type except it was missing cirrus IV/3 (Fig. XXIIc). A third cirral type pattern is seen in E. tegulatus (personal observation) which appears to be missing cirrus V/3. Further studies have shown that Euplotes with 8 or fewer cirri also show a cirrotype similar to the 10 cirral type pattern, but with a loss of a couple of cirri. This loss appears to be an evolutionary phenomenon within the genus Euplotes. Two examples further strengthen this position. Agamaliev (1966) described a population of E. raikovi having 8 frontoventral cirri. Washburn & Borrer (1972) showed that their population of E. raikovi had 7 cirri and a argentophilic plaque at cirrus location VI/2 (Fig. XXIIId). Curds (1974) described a small euryhaline Euplotes (E. parkei) having 8 frontoventral cirri. Later, a stock of E. parkei was established in freshwater with the addition of cirrus VI/3.

Thus, it appears that within the genus Euplotes the general evolutionary trend is a reduction of cirri from a 10 cirrotype pattern.

Tuffrau (1960) introduced the wet silver impregnation method of Chatton & Lwoff (1930, 1936) to the study of taxonomy in the genus Euplotes. He showed that the geometry of the dorsal argyrome silver-line system (now known to mark boundaries between adjacent subpellicular alveoli (Ruffolo, 1976a, 1976b)) was a useful characteristic in distinguishing species. This characteristic has proven to be a most stable and important taxonomic feature (Carter, 1972; Curds, 1975; Hill & Reilly, 1976) and now most of the many different species of Euplotes have been distinguished by the method. Tuffrau (1960) classified the argyrome patterns into three distinct types ('vannus', 'eurystomus' and 'muscicola'). Curds (1975) refined the different types and separated 6 different argyrome patterns (single-vannus, double-eurystomus, right and left double-patella, multiple and complex). Later it was shown that the subclassification of the double argyrome system into three separate categories is invalid due to considerable individual variation in the uniparental inheritance of the double argyrome (Gates & Curds, 1979). Also, in several rare exceptions, the multiple or complex argyrome system has been found in populations in which the single or double systems predominates (Curds, 1974; G nermont et. al. , 1976; Stein, 1859; Tuffrau, 1960). Thus, Gates

and Curds (1974) have proposed a descriptive type classification system for the dorsal argyrome of Euplotes to be either 'single', 'double' or 'multiple'. Unfortunately, this system allows the 'multiple' category to be a catch-all for a number of species of Euplotes which, by other characteristics, show few evolutionary affinities.

I propose a classification system for the dorsal argyrome which has four different patterns; 'single', 'double', 'complex' and 'longitudinal'. Only a single row of silver staining polygons is present between 2 adjacent kineties (Fig. XXIIIa), in the single dorsal argyrome type. The double type has 2 rows of polygons between adjacent kineties while the complex type has polygons which are subdivided into irregular meshwork between kineties (Fig. XXIIIc). The longitudinal system has long, longitudinal polygons between the 2 rows of polygons as seen in the double system (Fig. XXIII d). In rare variants the argyrome in a single or double form is further subdivided into a more complex pattern suggesting the argyrome type is not variable and an evolutionary sequence from single through double to multiple systems. The longitudinal system is a variant of the double system. Thus, general evolutionary change has been for the subdivision of interkinetal space by the corresponding polymerization of the subpellicular vacuoles.

On the basis of habitat, cirral pattern of frontal cirri, and dorsal argyrome pattern, it is possible to divide the genus Euplotes into 5 groups.

I propose that these groups be given generic names as outlined below.

Euplotes (Müller, 1773) Ehrenberg 1830

The 17 species which will remain in this genus are outlined in appendix II. Members of this genus usually have 10 frontoventral cirri (Fig. XXIIa), and a double dorsal argyrome. Fourteen of the species are from the marine environment; two being commensals of stronglylocentrotid sea urchins. E. balteatus, found both in the digestive tract of sea urchins and as a free-living form, is highly variable in its structure depending upon its food source. When feeding on small ciliates, it can be as long as 150 μm and have between 70 - 80 long membranelles in its AZM. However, when feeding on bacteria, it is about 30 μm long and has between 25 - 30 short membranelles in its AZM (Tuffrau, 1964a). E. tuffraui, only found in the digestive tract of echinoids, does not vary as much in size; however, it is a highly unusual case where the frontoventral cirri vary in number from 8 - 10 (Berger, 1965). This variation in structure and size seen in E. balteatus and E. tuffraui is probably related to their unique habitat in the digestive tract of sea urchins.

E. moebiusi is the only euryhaline species in this genus and, like E. indentatus, has a dorsal argyrome pattern in which there are 3 polygons between each pair of kineties. E. crenosus and E. inkystans

are the only freshwater species; however, the marine form E. harpa has been reported from minerla pools in Utah (personal communication Dr. Evans).

Euplotiscus Hill, 1980

The six marine species in this genus have 10 frontoventral cirri and a single dorsal argyrome (Fig. XXIIIa). Most of the genetic work done on euplotid-like hypotrichs has been with members of this genus. Studies on genetics of local population have revealed a multiple mating type system genetically inherited through a polyallelic series at the mt locus wherein serial and complete dominance exists (Heckmann, 1964; Luporini & Dini, 1977). Gates (1978b) analyzed intercirral distances between frontoventral and transverse cirri of E. vannus, E. crassus, E. mutabilis and E. minuta and suggested that because they all have the same configuration, they should be regarded as syngens of E. vannus. Clones of geographically isolated samples of E. vannus, E. crassus and E. mutabilis which were indistinguishable when considering their dorsal argyrome, number of frontoventral, transverse and caudal cirri and corticotype showed E. crassus and E. vannus reproductively isolated whereas E. mutabilis and E. crassus were interfertile. Thus, the 3 "typological" species correspond to only 2 "biological" species which could not be distinguished (Génermont, Machelon, Tuffrau, 1976). Nobili (1964, 1965) reported conjugation, but infertility, among samples of E. vannus, E. crassus and E. minuta. Conjugation in a highly

multiple mating type system results in gene exchange between a vast array of partners with slightly different genotypes increasing plasticity of the species. These morphologically similar, but geographically distinct populations may belong to the same mating type while microsympatric forms with similar structures may be of different mating types.

Slight irregularities in the dorsal argyrome in E. mutabilis (Tuffrau, 1960) showed a slightly complex system in this species. This species also shows some degree of polymorphism with a size ranging from 60 - 120 μm and 10 - 14 frontoventral and 5 - 7 transverse cirri, thus showing an increase in the number of cirral primordia.

Euplotopsis Hill, 1980

Members of the genus Euplotopsis usually have 9 frontoventral cirri in pattern I where cirrus VI/2 is missing (Fig. XXIIb). All 15 species; 9 marine, 2 euryhaline, 4 freshwater, in this genus, as outlined in appendix II, have a double to complex dorsal argyrome. Several species in this genus have 8 or fewer frontoventral cirri. E. parkei, when grown in a marine environment, is missing cirrus VI/2 which is present when grown in freshwater (Curds, 1974). E. poljanskyi is missing cirrus VI/2. E. raikovi, which has 7 or 8 cirri, is always missing cirrus IV/2 and V/2, however, in some populations cirrus VI/2 is present (Agamaliev, 1966) and in others

it is absent (Washburn & Borrer, 1972). E. strelkovi has the same cirral pattern as E. raikovi except an additional streak has been added between streak IV and V. E. parkei and E. elegans are both euryhaline species while E. affinis, E. gracilis, E. muscicola and E. muscorum are all from freshwater. Gates (1978c) has suggested that other species with a complex dorsal argyrome (E. elegans, E. gracilis, and E. muscorum), because of similarity in frontoventral cirral pattern and dorsal argyrome, should be placed in synonymy with E. muscicola. Fauré-Fremiet, Gauchery, Tuffray (1954) described encystment in E. muscicola.

Euplotoides Hill, 1980

Euplotoides have 9 frontoventral cirri in pattern II where cirrus VI/3 is missing (Fig. XXIIc). All these freshwater species as outlined in appendix II have a double dorsal argyrome (Fig. XXIIIb).

Genetic information of the members of this genus (Kimball, 1942) shows that they have the same multiple type mating type system as do members of the genus Euplotiscus. The only member of this genus which is sometimes found in the marine environment, E. woodruffi, is unique by only undergoing conjugation in the marine environment and only autogamy in the freshwater environment (Kosaka, 1970, 1973). E. amieti (Dragesco, 1970) is a large species and probably represents a polymorphic form of E. eurystomus, thus should be placed in synon-

ymy with the latter.

All members of this genus have been found to contain the essential endosymbiont Omikron (personal observation and personal communication, Dr. Heckmann) which have not been found in any other euplotid-like organism.

Euplotaleos Hill, 1980

The genus Euplotaleos has a single species, E. tegulatus, which has 9 frontoventral cirri with cirrus V/3 missing and a dorsal argyrome pattern which has longitudinal polygons between 2 rows of polygons as seen in the double system (Fig. XXIIIId).

Aspidisca

The nomenclature and possible taxonomic relationships among members of this genus is in a state of confusion. Recent reviews by Borrer (1972b), Diller (1975), Wu & Curds (1979), and Hill (1979d) have helped define those taxonomic characteristics which should prove helpful in coordinating information for study of this group.

There have been over 50 nominal species described or transferred to the genus Aspidisca. This number has been considerably reduced in recent reviews to 22 by Borrer (1972) and 20 by Wu & Curds (1979). As with the genus Euplotes a number of taxonomic characteristics have been used which are now known to be variable within the same

population. Also several potential diagnostic characteristics; habitat, presence of spurs or dentation along the left border, dorsal argyrome and position of ventral ciliature have not been investigated enough to test their stability within a single population or in enough species to discern their taxonomic significance. Six species have been described from freshwater habitats, however, all except one briefly described by Kahl (1932) have also been reported from marine habitats. Thus, using their habitat as a taxonomic characteristic appears questionable.

Presence of spurs along the left border or dorsal ribs has been used as diagnostic by many workers. Hamm (1964) however has shown that the size of dorsal ribs in A. costata vary under different growth conditions and both Kahl (1932) and Borrer (1965) mentioned the dorsal thorn present on only some of the specimens of A. aculeata. Many species have been described as having peripheral serrations and spurs along the left border of the cell. The actual number of spurs and degree of development appear to be variable. However, Wu & Curds (1979) believe that presence of a "peristomial spur" is diagnostic in many species. Dorsal argyrome pattern has only been described for a few species because many investigators have encountered technical difficulties in applying silver-impregnation methods to this genus. There is some indication that distinctly different argyrome patterns are present and that they could be useful in species identification (Agamaliev, 1967, 1971; Borrer, 1963, 1965; Curds, 1977; Deroux &

Tuffrau, 1965). Agamaliev (1971) pointed out that in A. caspica the dorsal argyrome pattern is highly variable. He observed single, double and multiple rows of polygons between any two adjacent kineties similar to the variability seen by Gates & Curds (1979) in Euplotes. Therefore, before the dorsal argyrome pattern can be used as a diagnostic tool in Aspidisca identification, more information on patterns seen in different species and pattern variability must be known. The number and arrangement of the frontoventral and transverse cirri (including the paroral cirrus) of Aspidisca appear to be a stable diagnostic feature. Most species have seven frontoventral and five transverse cirri with several species having an additional eight frontoventral cirrus or a transverse cirrus that is divided into several cirri as outlined above. The frontoventral cirri appear to be arranged in two basic patterns (Wu & Curds, 1979). In the "lynceus-arrangement" (Figs. VI, VIIa) all frontoventral cirri are located within the anterior half of the ventral surface with a row of four cirri along the anterior right border and a second row of three cirri nearer the center. In the "polystyla arrangement" (Fig. VIIIb) six of the seven frontoventral cirri are located in the anterior half of the ventral surface with the remaining cirrus lying in the posterior half of the body close to the transverse cirri. These two arrangements were used by Wu & Curds (1979) to divide the genus Aspidisca into 2 groups.

Identification and classification of the members of the genus Aspidisca is just beginning to be studied. The major problem is a lack of information on many of the described species in reference to their dorsal argyrome, number and pattern of ventral cirri, habitat, and possession of cytoplasmic ridges and spurs. Secondly, a detailed clonal study of a single species needs to be made varying environmental conditions to test the limits of variability occurring within a species. Thus, as more information is obtained, further sound judgements concerning nomenclature and taxonomic relationships of the genus Aspidisca can be made.

There have been two interpretations of ventral cortical morphogenesis. Tuffrau (1964) and Deroux & Tuffrau (1965) suggested that anterior membranelles of the opisthe differentiate from the AZM; however, Diller (1975) described the same structure as developing from streak I of the frontoventral transverse system. Before any taxonomic differentiation can be considered, alleged differences in ventral morphogenesis must be addressed. In the present study, anterior membranelles of the AZM in each species studied arose by separation of several ciliary units from the anterior end of the developing opisthe AZM; they bear no direct ontogenetic relationship with frontal ciliature development to the right of the buccal cavity. Such a division of the AZM into "collar" and "lapel" occurs in other

genera of Euplotidae; for example, in Uronychia (Borrer, 1972; Hill, 1978b). The paroral cirrus (II/1) develops from a streak that forms considerably after rows III - VII have formed and is not cirrus II/2 (Wallengren system) as interpreted by Diller (1975). The usual number of cirri in Aspidisca (developing from rows III - VII) is five transverse and six frontoventral. An additional seventh frontoventral cirrus can develop from row VII, as in A. baltica and A. lyncaster (Tuffrau, 1964), or from row VI, as in A. orthopogon (Deroux & Tuffrau 1965). The number of transverse cirri also can vary, but the number of streaks that contribute cirri to the transverse cirri system is apparently always five. In A. baltica, cirrus III/1 divides into three separate cirri; in A. aculeata, into two separate cirri; and in A. polystyla, all the transverse cirri divide into several parts (Tuffrau, 1964).

Diophrys

In Borrer's taxonomic review of the Hypotrichida (6) there were eleven species in the genus Diophrys. Since then D. kasymovi, Agamaliev 1971 (1); D. multinucleatus, Hartwig 1973 (26) and D. tetramacronucleata, Kattar 1970 (28, 37) have been added.

The 14 species of Diophrys form two morphologically different groups as originally put forth by Faure-Fremiet (18) and more fully expanded by Hartwig (26, 28). The first group, represented by

D. scutum, has a "typical" shape of Diophrys; a large, unified AZM, a two-part macronucleus arranged in a C-shape and a "typical arrangement and position of the 7 frontal, 5 transverse, 2 small left marginal and 3 large dorsal caudal cirri. (The caudal cirri originally were believed to be right marginal cirri (18, 28), but developmental data shows that they should be considered caudal cirri). Included in this assemblage are D. scutum, D. appendiculatus, D. magnus, D. oligothrix and D. peloetes. Also included in this group are four species whose features differ from the above only in minor ways. D. scutioides has only 5 frontal cirri (probably missing the frontal cirri that develop from streak 3); D. kasymovi has 8 frontal and 6 transverse cirri (probably has an additional CP); D. quadricaudatus has 3 left marginal and 4 caudal cirri (both cirral groups are known to be variable) and D. tetramacronucleata has a four-part macronucleus.

In the second assemblage, represented by D. irmgard, ciliates have a disc shaped body, an AZM with a more developed collar region, two to many oval macronuclei, and a similar arrangement of the 7 frontal, 4 transverse, 3 left marginal and 3 caudal cirri (the caudal and left marginal cirri are of equal size). This group includes D. irmgard, D. kahli, and D. multinucleatus. The number of cirri in each cirral group is variable.

Although briefly described, two species; D. histrix (personal observation) and D. salina (according to Ruinen (1938) do not conform to either group.

The 8 species in the first group have been separated and assigned species status on the basis of size, number of dorsolateral rows of cilia, number of cilia per row, length of the terminal portion of the AZM on the right side of the body, and number of cirri within each cirral group, characteristics now known to be highly variable and overlapping (1, 3, 4, 26, 28). Similar variable and overlapping characteristics have been used in the past to describe 51 species in the genus Euplotes. Gates (20, 21, 22, 23), using multivariate analyses of cortical structures, characterized six different evolutionary groups within the genus Euplotes, and concluded that many characteristics previously used to describe species of Euplotes no longer could be considered valid. By logical extension, in view of the identical morphogenetic process of division in D. scutum, D. oligothrix and D. appendiculata, the members of the first group of Diophrys may represent a single evolutionary grouping of morphologically inseparable populations. There may exist different biological species within this group, but, until adequate stocks for breeding tests are established and appropriate multivariate morphometric analyses made to set the limits of each species, the assemblage should be regarded as the D. scutum complex.

Morphological accounts of different species must be accompanied by an adequate description based upon morphological criteria that comes from a knowledge of natural variation of clonal samples of geographically distant populations. The second group of Diophrys probably represents a second evolutionary grouping, but the number of observations on the group is limited.

Euplotaspis

Since the original description by Chatton & Séquéla (1936), Euplotaspis cionaecola has only been recorded one other time (Burreson, 1973); until the present study. They are commensal in tunicates and have evolved specializations that allow their firm attachment to the branchial cavity lining. Most prominent of these attachment characteristics is the development by longitudinal division of four frontoventral cirri of ciliary fields which form a ciliary fringe on the cell's right border. This, along with increased width and shortening of cirri and increased width of the entirely ventrally located AZM allows this organism to use ciliary organelles for attachment rather than swimming.

The description suggests that Euplotaspis is but a single species with the only variability seen in cortical structure appearing to be the variable number (1 - 3) or absence of several small caudal

cirri. Cortical morphogenesis during division with opisthe oral primordium forming de novo in a sub-cortical pouch, and development of five cirral streaks independent of parental or other developing cirral primordia verified its position as being closely related to the other Euplotids.

Euplotaspis appears similar to members of the genus Euplotiscus. Both genera have 10 frontoventral cirri, small endoral apparatus and a single dorsal argyrome pattern. Euplotaspis and Aspidisca share characteristics of a flat oval-shaped body, lack of left marginal cirri, reduced caudal cirri (entirely lost in Aspidisca) and wide, short cirri. Though Euplotaspis is a commensal of tunicates, it shows as an evolutionary link between these two groups.

Uronychia

Although there is little information on the biology of any of the six species in the genus Uronychia, the present study on U. transfuga points to the fact that members of this genus are unique when compared to other euplotids. Only the cortical morphogenetic features of the oral primordium developing de novo in a sub-cortical pouch and the 5 cirral streaks for frontoventral and transverse cirri show clearly their close relationship to other euplotids. The members of the genus Uronychia do exhibit a

number of primitive euplotid-like characteristics; a large well-developed buccal membrane, dorsal argyrome having small polygonal spaces, and possession of caudal and left marginal cirri. However, unique characteristics set this genus apart:

1. the development of both a proter and opisthe primordium, causing the replacement of the parental collar membranelles of the AZM during proter development;
2. a large buccal membrane divided into two parts; the right buccal membrane and the left buccal membrane;
3. caudal cirri (larger than caudal cirri seen in any other euplotid) that bend to the left, and
4. dorsal kineties made up of many short and closely set cilia.

Due to the many unique characteristics of Uronychia when compared to other euplotid-like genera, the genus Uronychia should be placed in its own separate family — Uronychidae. Unlike Diophrys, or other euplotid-like hypotrichs, Uronychia transfuga has a very stable cortical structure. This, in addition to the presence of several modified primitive characteristics,

causes me to believe the family Uronychidae diverged relatively early from the main line of euplotine evolution.

FIG. XXII. Diagram of frontoventral cirrus patterns in 4 species of Euplotes

- a. Euplotes charon ; Euplotes charon
- b. Euplotes bisulcatus ; Euplotopsis bisulcatus
- c. Euplotes aediculatus ; Euplotoides aediculatus
- d. Euplotes raikovi ; Euplotopsis raikovi

Arrow, argenophilic plaque VI/2

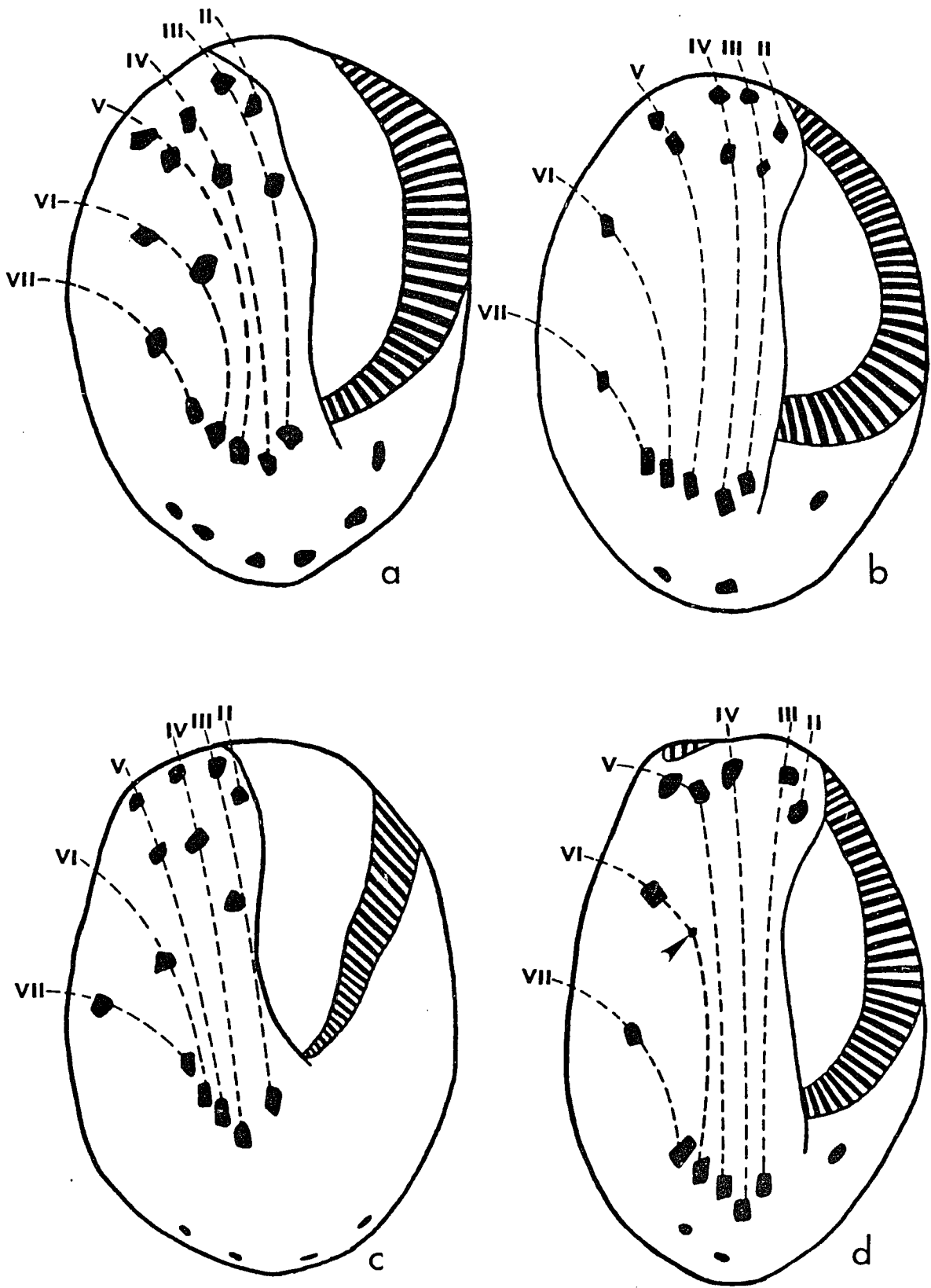


Figure XXII.

FIG. XXIII. Diagram of dorsal argyrome patterns in 4 species of Euplotes

- a. Euplotes crassus; Euplotiscus crassus
- b. Euplotes aediculatus; Euplotoides aediculatus
- c. Euplotes muscicola; Euplotopsis muscicola
- d. Euplotes tegulatus; Euplotaleos tegulatus

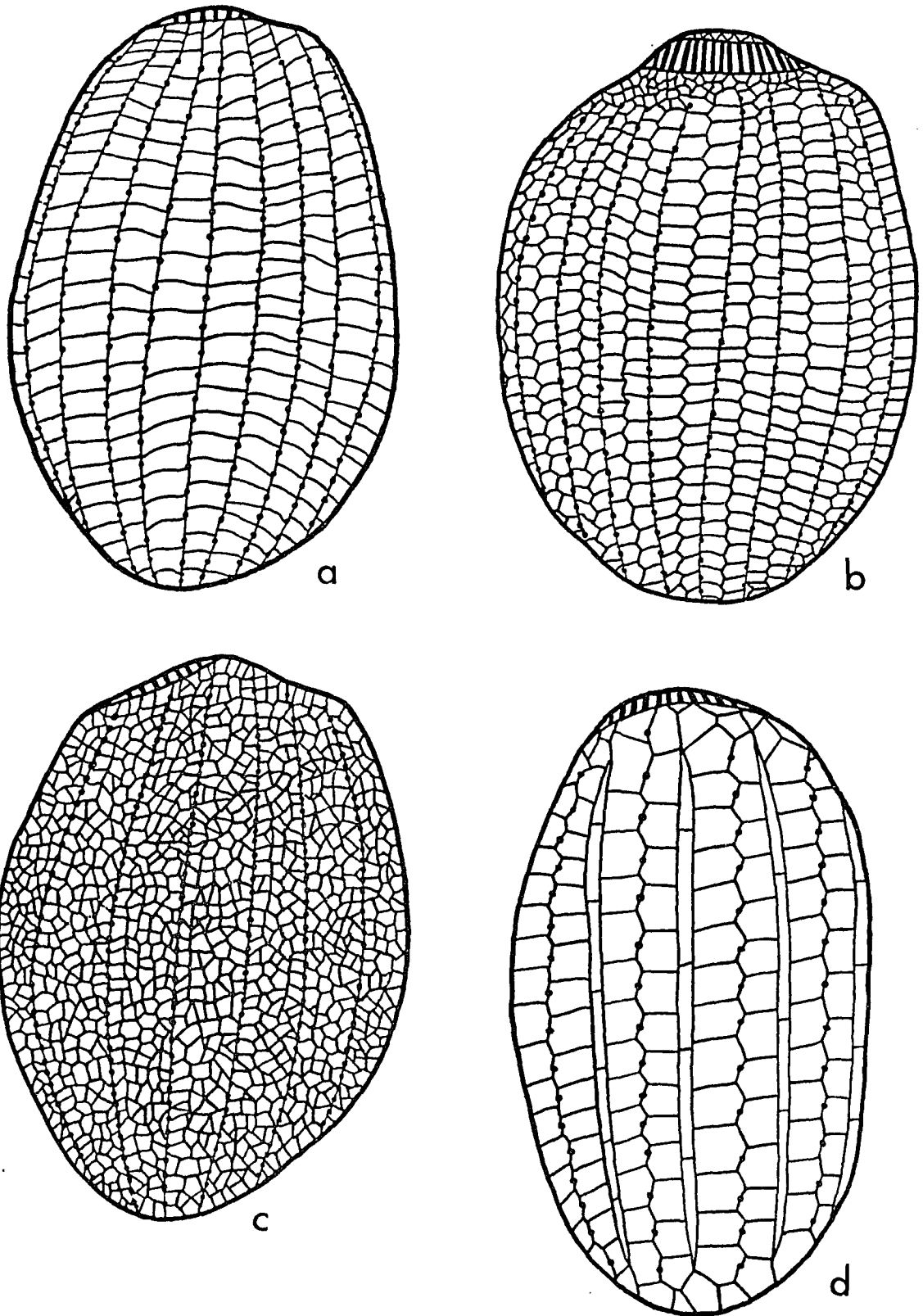


Figure XXIII.

DISCUSSION - GENERAL

In his revision of the order Hypotrichida, Borror (1972b) placed 96 species divided into 11 genera into the family Euplotidae. Since this division Tuffrau (1974) described Cytharoides, a twelfth genus, within this family. Corliss' (1979) recent review of ciliate taxonomy has placed these genera into 3 families. The present study looked at the process of cortical morphogenesis during cell division of 5 genera in the family Euplotidae to see if there was a unifying mechanism of division. The morphogenetic information was coupled with material on cortical structure, cyst formation, and conjugation in a review of the systematics and evolution of euplotids.

Recent studies of division patterns in the order Hypotrichida (Borror, 1979b; Borror & Evans, 1979; Grimes, 1976; Grimes & L'Hernault, 1978; Hill, 1978a, 1978b, 1979b, 1979d; Jerka-Dziadosz, 1972; Jerka-Dziadosz & Frankel, 1969; Ruffolo, 1976b; Tuffrau & Fryd-Versavel, 1977; Wise, 1965a) have shown that there are at least three different divisional patterns to the development of frontal and buccal ciliature.

This "Oxytricha pattern" is exemplified by Paraurostyla weissei, Fig. XXVIIa (Jerka-Dziadosz & Frankel, 1969). Division begins with formation of a longitudinal field of basal bodies developing posterior to the parental AZM and along the left side of the organism. This

field, which will develop into the opisthe buccal ciliature, continues to lengthen. Basal bodies from the right edge of the primordium develop into several longitudinal cirral primordial streaks (usually 7 in Oxytricha, fewer in Paraurostyla). The inner 2 streaks will develop into the endoral and paroral membranes of the opisthe, while the other five form the frontal ciliature of the opisthe. Some transverse cirri in P. weissei are of somatic origin. In the proter, the parental AZM is retained, but the paroral and endoral membranes differentiate. Their kinetosomes become part of the paroral and endoral membranes or frontal ciliature in the proter. The parental frontal ciliature de-differentiates to form 5 cirral primordia which develop into the frontal and some of the transverse cirri of the proter. Marginal cirri of both the proter and opisthe develop within marginal rows of the parent.

"Urostyla pattern"

This pattern is exemplified by Urostyla marina, Fig. XXVII, (Borror, 1979b). The parental AZM is resorbed, with new membranes of the proter AZM arising from a field of basal bodies that form near the posterior end of the parental buccal cavity. The parental paroral and endoral membranes differentiate with the proter membranes appearing later in the same region. The frontal ciliature for the proter organism develops from a longitudinal field of basal bodies that forms to the right of the parental paroral membrane. This field alongates and forms a longitudinal series of oblique streaks. Streaks

in the anterior portion of the field mature to form the frontal ciliature, those in the mid-region form the mid-ventral cirri, with the transverse cirri developing from the posterior end of the postero-most streak of the field. The opisthe buccal ciliature forms from a longitudinal field of basal bodies that develop posterior to the parental AZM and along the left side of the organism. Basal bodies from the right posterior side of this field form the paroral and endoral membranes. The frontal, mid-ventral and transverse cirri arise from a series of oblique streaks which develop to the right of the developing buccal ciliature. The marginal cirri of both the proter and opisthe develop within the parental marginal rows of cirri.

"Euplotes pattern"

In euplotids, the opisthe oral primordium develops de novo just posterior to the parental AZM with continuing development occurring in a sub-surface pouch, whereas among other hypotrichs, kinetosomes from parental structures may participate in the formation of the opisthe oral primordium (Grimes, 1972) which develops on the ventral surface (Jerka-Dziadosz & Frankel, 1969; Borrer, 1979b). The developing oral primordium in euplotids does not donate kinetosomes to the developing endoral, paroral or cirral primordium and the cirral primordium for the frontoventral and transverse cirri form separately and apart from the other primordia or parental structures. Also, the left marginal cirral

primordia develop lateral to parental marginal cirral rows rather than within rows as in other hypotrichs.

Besides divisional morphogenetic differences just summarized, morphogenetic processes in regeneration, encystment and conjugation are also unique in euplotids. This is particularly true in encystment. The cyst in most hypotrichs have four morphogenetically distinct layers whereas in the euplotid cyst there are only three concentric layers. Also, encystment in most hypotrichs involves resorption of kinetosomes (Grimes, 1973; Tuffrau & Fryd-Versavel, 1977). However, Faure-Fremiet, Gauchery and Tuffrau (1954) clearly described several ciliary structures in E. muscicola retained within the cyst. Diophrys cysts also contain kinetosomes (G. Walker, personal communication). The morphogenetic process of euplotid conjugation and regeneration is similar to that seen in division (e. g. opisthe oral primordium forming in a sub-cortical pouch and frontoventral transverse cirral primordium forming separately from developing primordia or cirral structures). During conjugation in many hypotrichs, pair formation occurs with the union of the anterior ends of each organism, however, in euplotids, conjugation pair formation occurs ventral surface to ventral surface.

The above morphogenetic data on division, encystment, regeneration and conjugation along with the morphological fact that all euplotids have a well-developed argyrome system and lack right

marginal cirri cause me to believe that this group of hypotrich ciliates should be separated from other members of this order in a new sub-order, Euplotina.

An evolutionary scheme for the development within the sub-order Euplotina is outlined in Fig. XXVIII. Within the new sub-order Euplotina there appear to be four main lines of evolution: (1) the Gastrocirrhidae (Gastrocirrhus (Fig. XXIVc), Cytharoides (Fig. XXIVb), Euplotidium (Figs. XXVa, XXVb): animals with an anteriorly pointing buccal cavity, reduced paroral and endoral membranes and loss of left marginal and caudal cirri; (2) the Aspidiscidae (Aspidisca, Euplotaspis, Paraeuplotes) (Fig. XXVIa): flat, disc-shaped animals with reduced paroral and endoral membranes, loss of left marginal and caudal cirri; (3) the Uronychidae (Uronychia): animals unique among euplotids in having a proter oral primordium develop during the cortical morphogenetic process of division, large caudal and left marginal cirri, a buccal membrane divided into two separate portions; (4) the Euplotidae (Diophrys, Certesia (Fig. XXIVa), Euplotiscus, Euplotes, Euplotopsis, Euplotoides, Euplotaleos): oval-shaped animals with a large ventrally opening buccal cavity, left marginal and caudal cirri present. Morphologically, Diophrys is more like other hypotrichs with highly developed paroral and endoral membranes, thus this genus appears to be the most primitive member of the sub-order.

Borrer (1972b) included the genera Discocephalus and Swedmarkia in Euplotidae. They have not been included in the general evolutionary diagram of the sub-order Euplotina due to uncertainty in their taxonomic relationship to other genera in the sub-order. In the case of Discocephalus, the cortical morphogenetic pattern (Wicklów, 1978) is unique compared to other euplotids. In the case of Swedmarkia, with its unique cortical structure and total lack of morphogenetic data, this genera is provisionally placed in the sub-order Euplotina pending further investigation.

FIG. XXIV. Diagram of Certesias, Cytharoides and Gastrocirrhus

- a. Certesias quadrinucleata Fabre-Domergue, 1885
(redrawn from Fabre-Domergue, 1885 and Wicklow, 1979)
- b. Cytharoides balechi Tuffrau, 1974
(redrawn from Tuffrau, 1974)
- c. Gastrocirrhus adhaerens Faure-Fremiet, 1954
(redrawn from Faure-Fremiet, 1954)

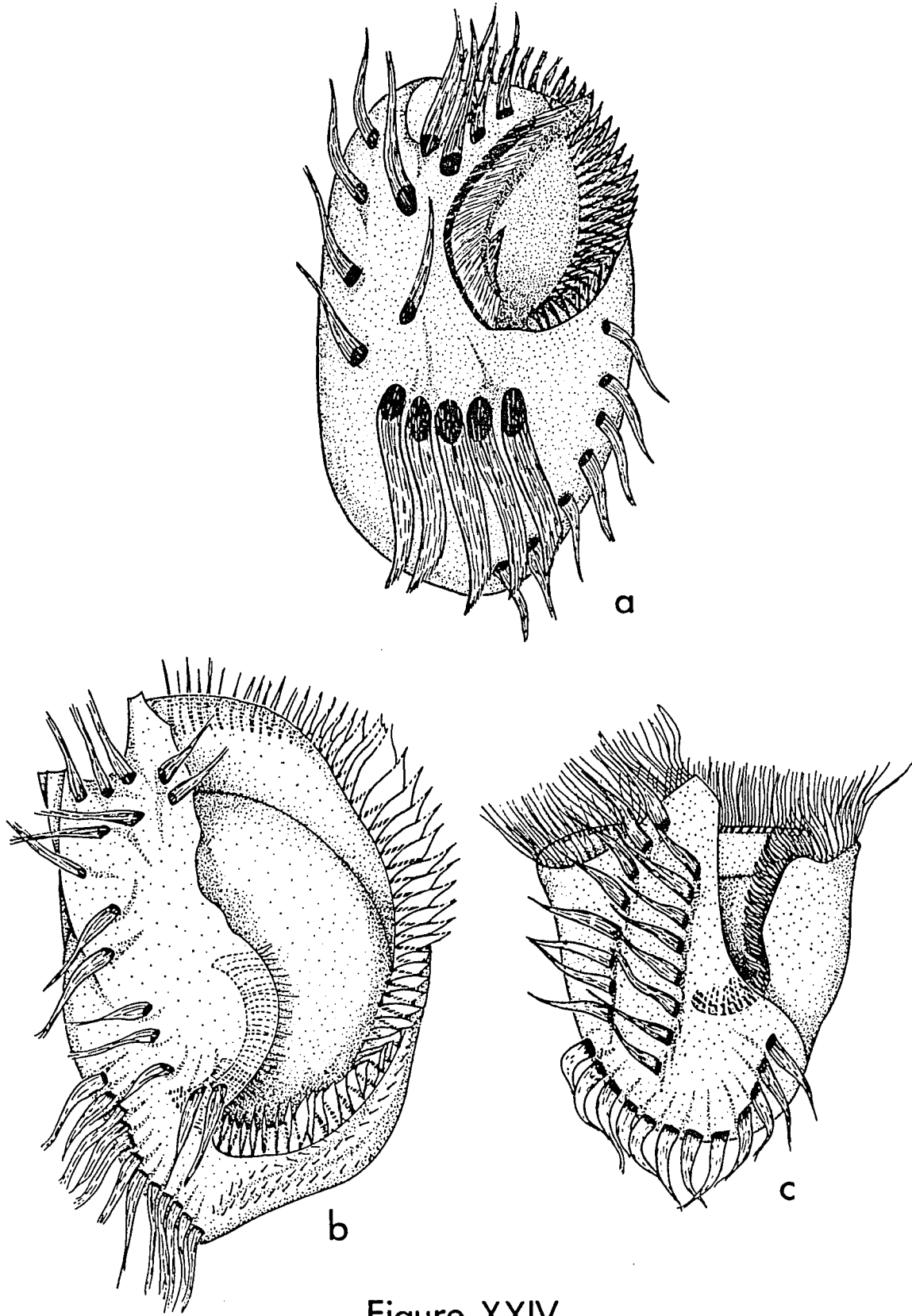


Figure XXIV.

FIG. XXV. Diagram of Euplotidium agitatum and Euplotidium arenarium

- a. Euplotidium agitatum Noland, 1937
- b. Euplotidium arenarium Magagnini & Nobili, 1964
(redrawn from Magagnini & Nobili, 1964)

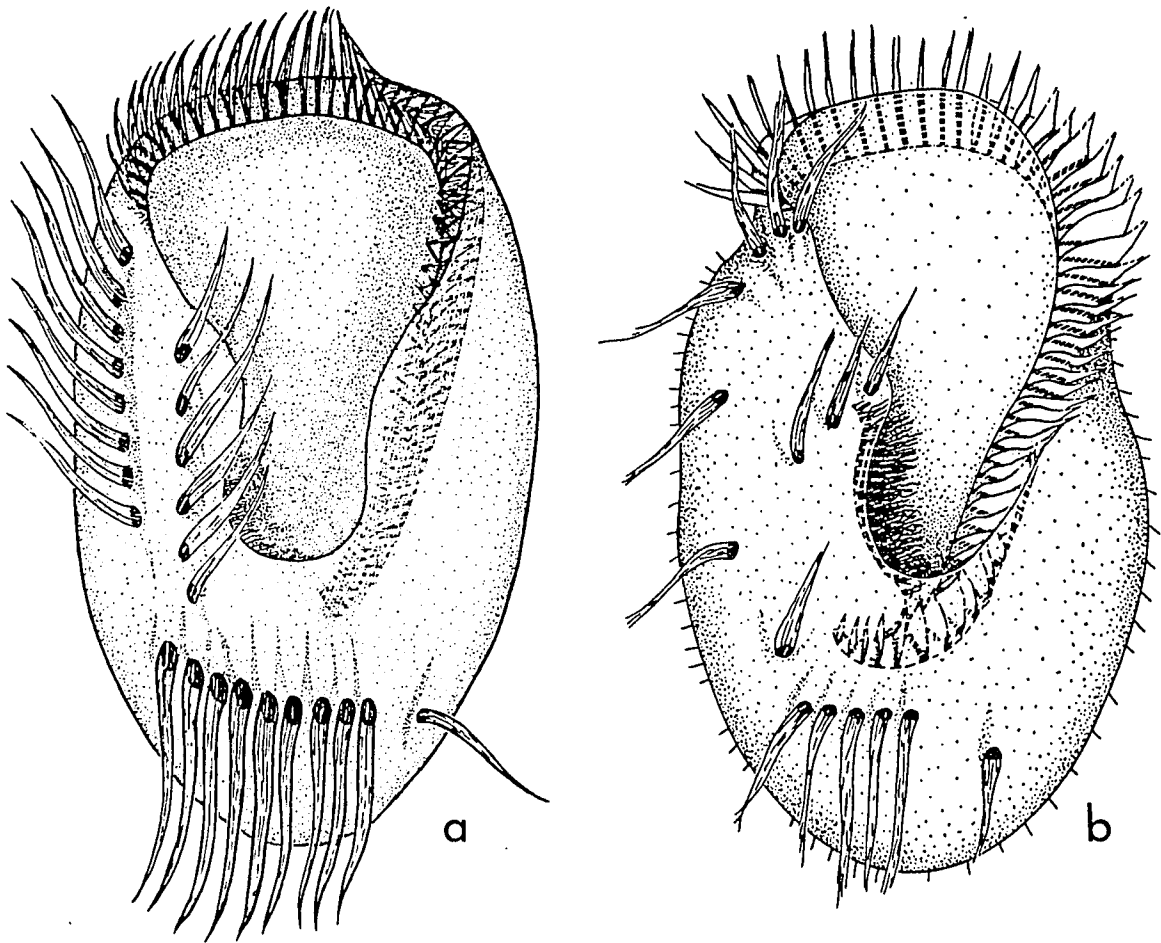


Figure XXV.

FIG. XXVI. Diagram of Paraeuplotes, Discocephalus and Swedmarkia

- a. Paraeuplotes tortugensis Wichterman, 1942
(redrawn from Wichterman, 1942)
- b. Discocephalus ehrenbergi Dragesco, 1960
(redrawn from Dragesco, 1960 and Wicklow, 1978)
- c. Swedmarkia arenicola Dragesco, 1954
(redrawn from Dragesco, 1954)

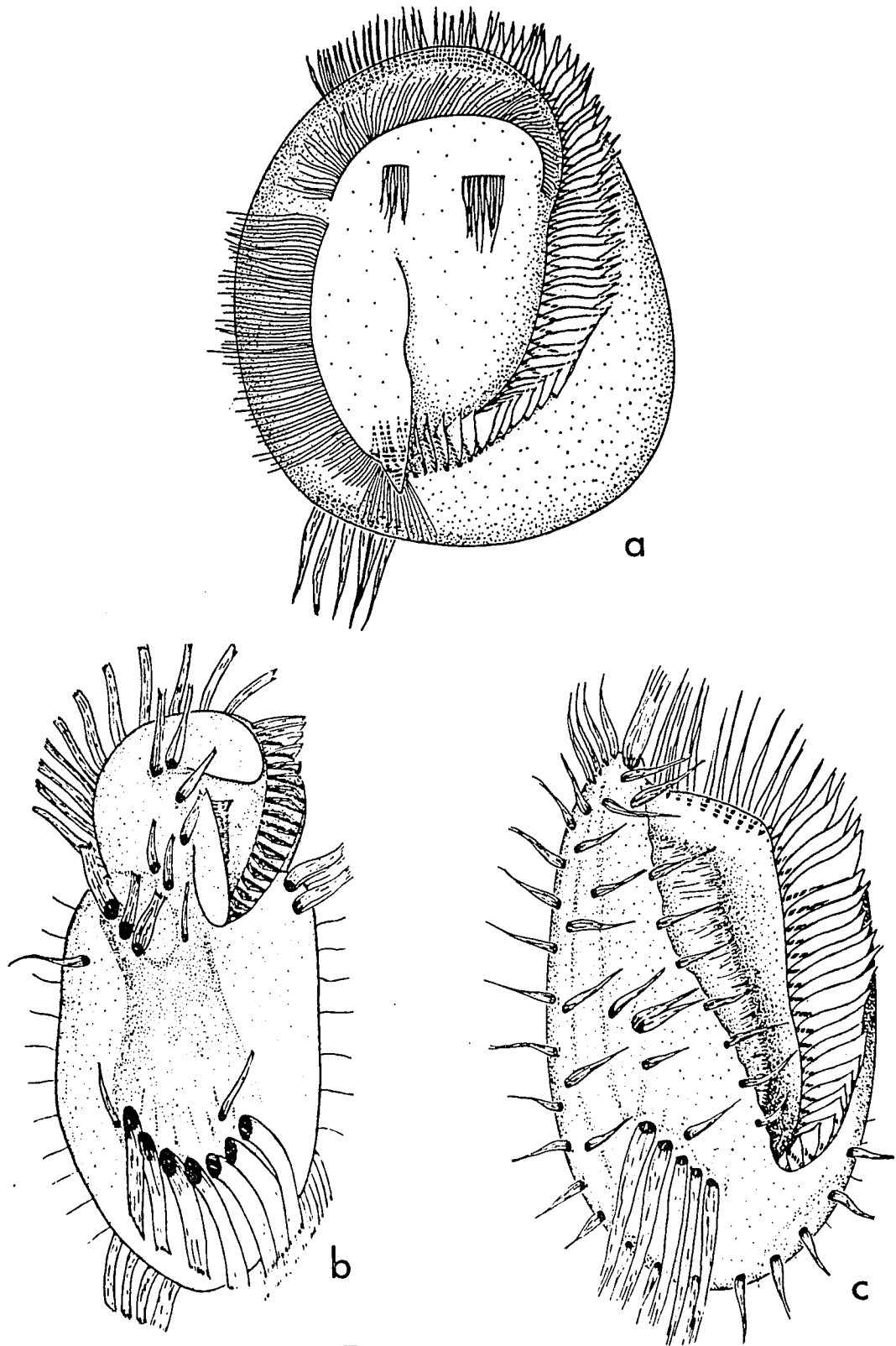


Figure XXVI.

FIG. XXVII. Diagram of Paraurostyla and Urostyla division

- a. Ventral cortical morphogenesis of division in Paraurostyla weissei
- b. Ventral cortical morphogenesis of division in Urostyla marina

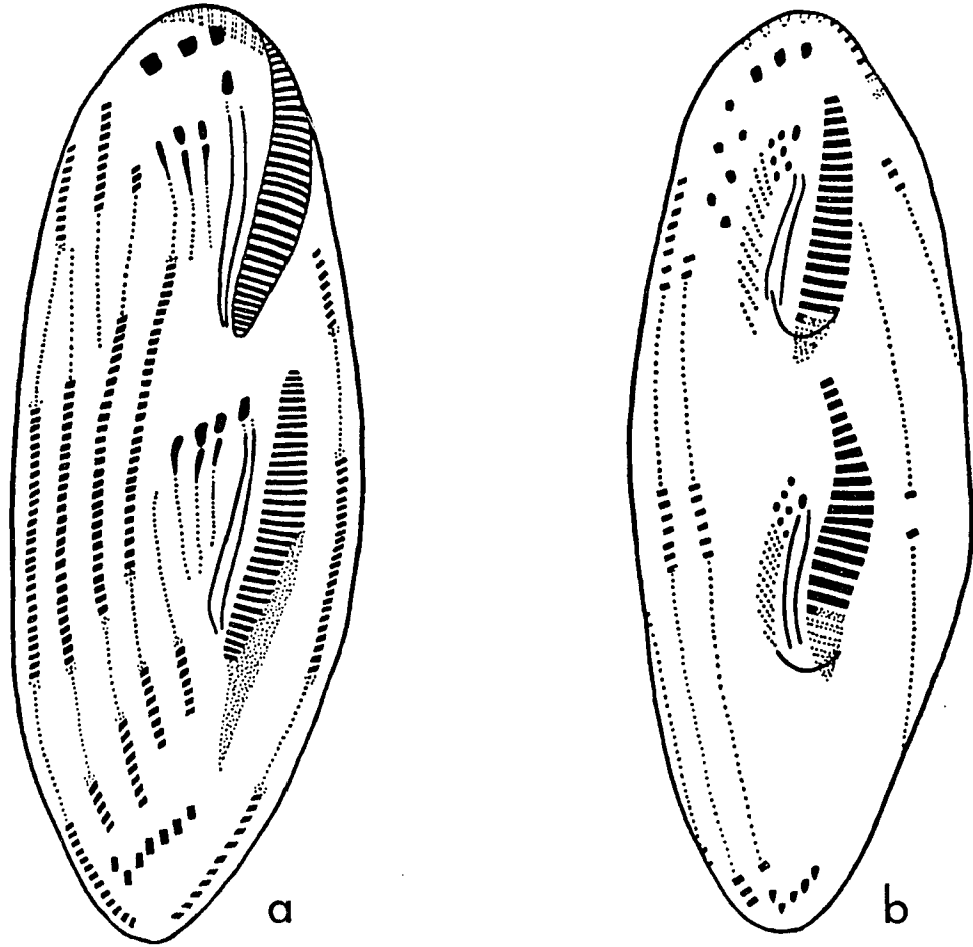


Figure XXVII.

FIG. XXVIII. Proposed phylogeny for the suborder Euplotina

Hypotrichida

Euplotina

Euplotidae

Euplotes
Certesia
Diophrys
Euplotaleos
Euplotiscus
Euplotopsis
Euplotoides

Aspidiscidae

Aspidisca
Euplotaspis
Paraeuplotes — placement of this genus in Aspidiscidae
is provisional

Gastrocirrhidae

Gastrocirrhus
Cytharoides
Euplotidium

Uronychidae

Uronychia

Discocephalus and Swedmarkia have been placed provisionally in the suborder Euplotina because of insufficient information on their cortical morphogenesis and unclear relationships with other genera.

Gastrocirrhidae

EUPLOTINA

Gastrocirrhus
Cytharoides
Euplotidium

Euplotidae

Euplotaleos
Euplotoides

Aspidiscidae

Paraeuplotes
Aspidisca
Euplotaspis
Euplotes

Certesias

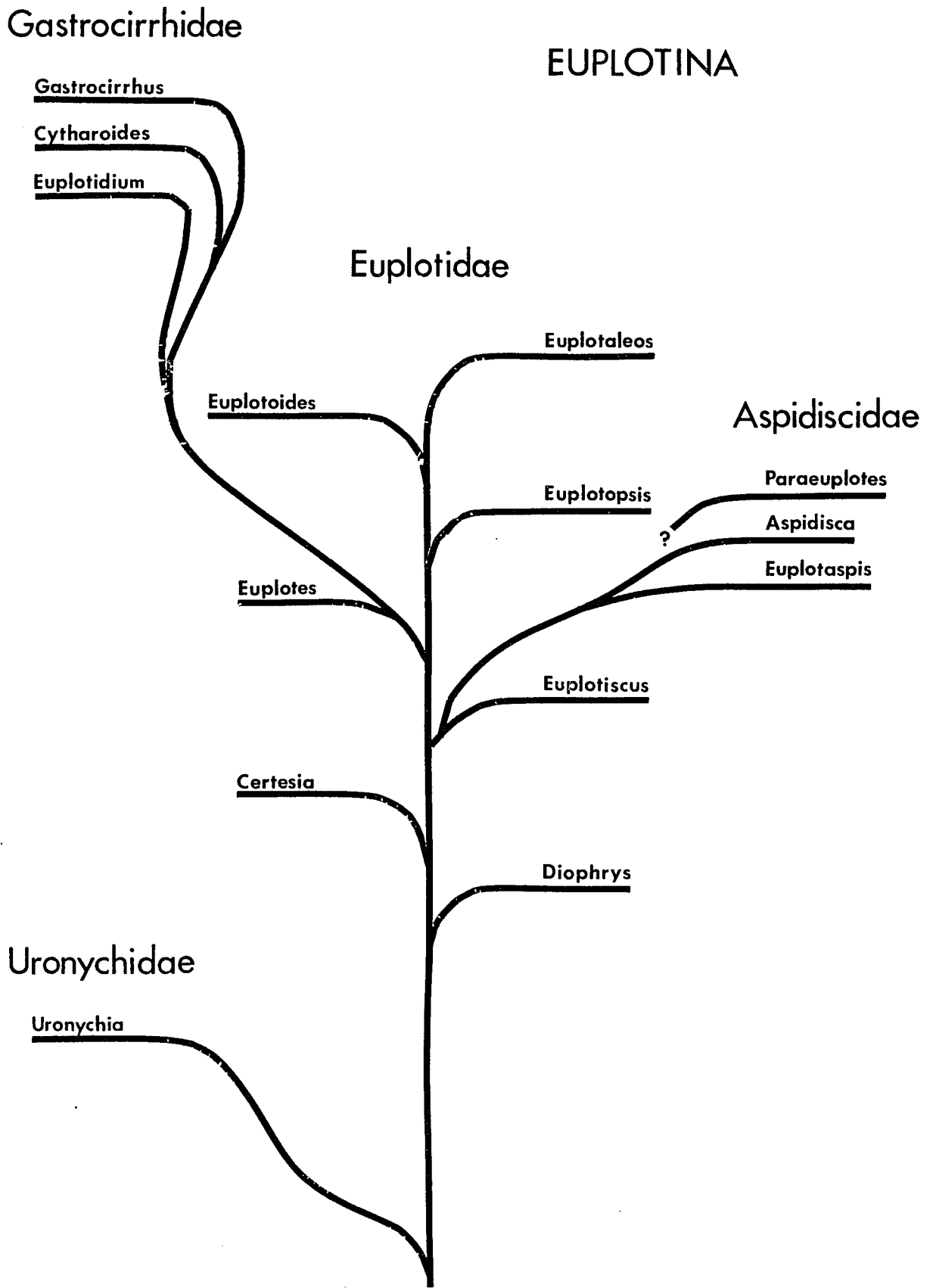
Euplotiscus

Diophrys

Uronychidae

Uronychia

Figure XXVIII.



SUMMARY

Cortical morphogenesis of division, particularly development of the buccal ciliature (Borrer, 1979b) within the order Hypotrichida, has proven useful in the study of taxonomic relationships (Borrer & Evans, 1979; Grimes, 1976; Grimes & L'Hernault, 1978; Jerka-Dziadosz, 1972; Jerka-Dziadosz & Frankel, 1969; Tuffrau & Fryd-Versavel, 1977). The present study proposes a number of major taxonomic revisions on one group of hypotrichs which has its own unique pattern of cortical morphogenesis separating it at the subordinal level from other hypotrichs. This group forms the new sub-order called Euplotina. Unifying morphogenetic and cortical characteristics of the Euplotina include (1) the opisthe oral primordium developing de novo just posterior to the parental adoral zone of membranelles with continuing development occurring in a subsurface pouch, (2) the oral primordium not donating kinetosomes to any developing cirral primordia, (3) the cirral primordia for frontoventral and transverse cirri forming separately and apart from other primordia or parental structures, (4) the left marginal cirral primordia developing lateral to the parental left marginal row, (5) the parental AZM becoming the proter AZM, (6) a well-developed argyrome system (7) no right marginal cirri, (8) pair formation during conjugation is ventral-surface-to-ventral surface, and (9) cyst composed of two membranes and formed without all kinetosomes being resorbed.

The sub-order Euplotina is divided into four families and from 14-16 genera as outlined in Fig. XXVII. 1) Aspidiscidae: flat, disk-shaped animals with reduced paroral and endoral membranes, AZM entirely on the ventral surface, no left marginals or caudal cirri (rudimentary caudals in Euplotaspis), long frontoventral and transverse cirral primordia, and includes the genera Aspidisca, Euplotaspis and, tentatively, Paraeuplotes. 2) Gastrocirrhidae: animals with a large anteriorly opening buccal cavity, no left marginal or caudal cirri (rudimentary left marginal cirrus in Euplotidium) and includes the genera Gastrocirrhus, Cytharoides, Euplotidium, and, tentatively, Swedmarkia. 3) Uronychidae: a new family where the animals have large left marginal cirri, large, bent caudal cirri, well-developed two-part buccal membrane, development during division of a proteroral primordium and includes the single genus Uronychia. 4) Euplotidae: presence of both left marginals and caudal cirri with a large ventrally opening buccal cavity and includes the genera Diophrys, Certesia and 51 species included in the genus Euplotes, now divided into 5 separate genera: (1) Euplotiscus: 10 frontoventral cirri, single dorsal argyrome with all 6 species being marine; (2) Euplotes: 10 frontoventral cirri, double dorsal argyrome with most of the 17 species being marine, (3) Euplotopsis: 9 frontoventral cirri in pattern I, double to complex dorsal argyrome with most of the 15 species being marine; (4) Euplotoides; 9 frontoventral cirri in pattern II, double dorsal argyrome with all 7 being freshwater

species; and (5) Euplotaleos; 9 frontoventral cirri, dorsal argyrome with long, longitudinal polygons between a double system, with a single marine species.

It is suggested that the main line of evolution within the sub-order Euplotina has been through the family Euplotidae (Diophrys – Certesias – Euplotiscus – Euplotes – Euplotopsis – Euplotoides – Euplotaleos). The family Uronychidae (Uronychia) branches early from an ancestor of the entire sub-order. The family Aspidiscidae (Euplotaspis – Aspidisca) branches from a Euplotiscus-like organism while the family Gastrocirrhidae (Euplotidium – Cytharoides – Gastrocirrhus) branches from a Euplotes-like organism.

The outline of possible evolutionary trends should be considered a directional guide only for further development and refinement of taxonomic relationships. Many other approaches are needed to test this hypothetical evolutionary scheme. One of the most important areas for continued study will be on different aspects of the cytoskeleton ultrastructure. A better understanding of evolutionary trends should be achieved by studying the ultrastructure of the endoral and paroral membranes, particularly in Diophrys, Uronychia, Certesias, Euplotaspis, Euplotiscus, and Euplotoides. The dorsal bristle structure and associated cytoskeletal features in Diophrys, Aspidisca, Euplotaspis, Uronychia and Euplotiscus should also be investigated. Many other

studies such as the morphogenesis of the macronucleus during division (i. e. *Aspidisca*; *Euplotaspis*) or the morphogenetic process of excystment or the ultrastructure of cysts should help in understanding the evolutionary trends within the sub-order Euplotina.

As pointed out in the discussion, several genera need to be studied in considerable depth using the methods of silver and protargol staining associated with TEM and SEM microscopy so as to assess the number and patterns of ventral cirri, patterning of dorsal argyrome and structure of other discernable cortical characteristics. This is especially true in the genus *Diophrys* and *Aspidisca* where such information should clarify evolutionary development within these genera and possibly show that they could be divided into several genera as the genus *Euplotes* has in the present paper. Such studies should first address variability in diagnostic cortical structures used in clonal populations as a function of different environmental factors and as seen in different wild populations.

In addition to these detailed studies the cortical morphogenetic process of division and cortical structure of members of the family Gastrocirrhidae should be studied. Studies show the cortical structure of several described species of *Euplotidium* to be quite different with a study on buccal ciliature development proving useful in describing the taxonomic relationships within this genus. *Paraeuplotes* and *Swedmarkia* have been provisionally placed in the family Aspidiscadae pending

a study of cortical morphogenesis of division.

This study shows that the use of cortical morphogenesis in conjunction with other aspects of protozoan biology; e. g. cortical structure, habitat, is useful in the development of evolutionary schemes. While this evolutionary scheme will undergo further refinement, the logic used in its development offers direction for future research.

APPENDIX I

Checklist and index of species/synonyms¹

Species	Investigator and Date	Later Identification
<u>Coccudina keronina</u>	Bory 1826	<u>E. patella</u>
<u>Euploea charon</u>	Ehrenberg 1830	<u>E. charon</u>
1. <u>Euplotes aberrans</u>	Dragesco 1960	
<u>E. aculeatus</u>	Ehrenberg 1838	<u>Aspidisca aculeata</u>
*2. <u>E. aediculatus</u>	Pierson 1943	
3. <u>E. affinis</u>	(Dujardin 1841) Kahl 1932	
*4. <u>E. alatus</u>	Kahl 1932	
5. <u>E. amieti</u>	Dragesco 1970	
6. <u>E. antarcticus</u>	Fenchel & Lee 1972	
<u>E. appendiculatus</u>	Ehrenberg 1838	<u>E. charon</u>
7. <u>E. apsheronicus</u>	Agamaliev 1966	
*8. <u>E. balteatus</u>	(Dujardin 1841) Kahl 1932	
9. <u>E. balticus</u>	Kahl 1932	
*10. <u>E. bisulcatus</u>	Kahl 1932	
<u>E. carinata</u>	Stokes 1885	<u>nomen nudum</u> <u>Verschaffelt 1930</u>

¹Junior synonyms are unnumbered.

*Species cultivated in my laboratory.

Species	Investigator and Date	Later Identification
23. <u>E. latus</u>	Agamaliev 1967	
<u>E. leticiensis</u>	Bovee 1957	<u>E. aediculatus</u>
<u>E. longipes</u>	Claparède & Lachmann 1858	<u>E. vannus</u>
24. <u>E. magnicirratus</u>	Carter 1972	
<u>E. marioni</u>	Gourret & Roeser 1886 (referred to by Kahl 1932, in error; was never described)	
*25. <u>E. minuta</u>	Yocom 1930	
*26. <u>E. moebiusi</u>	Kahl 1932	
*27. <u>E. muscicola</u>	Kahl 1932	
28. <u>E. muscorum</u>	Dragesco 1970	
*29. <u>E. mutabilis</u>	Tuffrau 1960	
*30. <u>E. nana</u>	Jones & Owen 1974	
31. <u>E. neapolitanus</u>	Wichterman 1964	
32. <u>E. novemcarinata</u>	Wang 1930	
<u>E. octocarinatus</u>	Carter 1972	<u>E. patella</u>
33. <u>E. octocirratus</u>	Agamaliev 1967	
<u>E. paradoxa</u>	Kent 1869	insufficiently described
34. <u>E. parkei</u>	Curds 1974	
*35. <u>E. patella</u>	(Müller 1773) Ehrenberg 1831	

Species	Investigator and Date	Later Identification
<u>E. caudata</u>	Meunier 1910	<u>E. vannus</u>
*11. <u>E. charon</u>	(Müller 1773) Ehrenberg 1830	
*12. <u>E. crassus</u>	(Dujardin 1841) Kahl 1932	
*13. <u>E. crenosus</u>	Tuffrau 1960	
14. <u>E. cristatus</u>	Kahl 1932	
*15. <u>E. diadaleos</u>	Diller & Kounaris 1966	
16. <u>E. dogieli</u>	Agamaliev 1967	
*17. <u>E. elegans</u>	Kahl 1932	
*18. <u>E. eurystomus</u>	Wrzesniowski 1867	
<u>E. excavatus</u>	Claparède & Lachmann 1858	<u>Diophrys</u> sp.
<u>E. extensus</u>	Fresenius 1865	<u>E. vannus</u>
<u>E. gabrieli</u>	Gourret & Roeser 1886	<u>E. vannus</u>
19. <u>E. gracilis</u>	Kahl 1932	
*20. <u>E. harpa</u>	Stein 1859	
21. <u>E. indentatus</u>	Carter 1972	
22. <u>E. inkystans</u>	Chatton in Tuffrau 1960	
<u>E. labiatus</u>	Ruinen 1938	<u>E. alatus</u>

	Species	Investigator and Date	Later Identification
*36.	<u>E. plumipes</u>	Stokes 1884	
37.	<u>E. polijanskyi</u>	Agamaliev 1966	
38.	<u>E. polycarinatus</u>	Carter 1972	
	<u>E. psammophilus</u>	Vacelet 1961	<u>Euplotidium</u> <u>psammophilus</u>
*39.	<u>E. quinquecarinatus</u>	Gelei 1950	
*40.	<u>E. raikovi</u>	Agamaliev 1966	
41.	<u>E. rariseta</u>	Curds, West & Dorahy 1974	
42.	<u>E. roscoffensis</u>	Dragesco 1966	
43.	<u>E. rotunda</u>	Gelei 1950	
	<u>E. salina</u>	Yocom 1930	<u>E. crassus</u>
44.	<u>E. strelkovi</u>	Agamaliev 1967	
	<u>E. striatus</u>	Ehrenberg 1838	<u>E. vannus</u>
	<u>E. subrotundus</u>	Perty 1852	<u>E. affinis</u>
	<u>E. taylori</u>	Garnjobst 1928	<u>E. crassus</u>
*45.	<u>E. tegulatus</u>	Tuffray 1960	
	<u>E. terricola</u>	Penard 1922	Not considered a member of the genus <u>Euplotes</u>
46.	<u>E. thononensis</u>	Dragesco 1960	
*47.	<u>E. trisulcatus</u>	Kahl 1932	
	<u>E. truncata</u>	Meunier 1910	<u>E. vannus</u>

<u>Species</u>	<u>Investigator and Date</u>	<u>Later Identification</u>
<u>P. longiremus</u>	Dujardin 1841	<u>E. charon</u>
<u>P. patella</u>	Dujardin 1841	<u>E. patella</u>
<u>P. radiosa</u>	Dujardin 1841	<u>E. charon</u>
<u>P. scutum</u>	Dujardin 1841	<u>Diophrys scutum</u>
<u>P. subrotundus</u>	Dujardin 1841	<u>E. affinis</u>
<u>P. vannus</u>	(Müller 1786) Bory 1826	<u>E. vannus</u>
<u>Trichoda charon</u>	Müller 1773	<u>E. charon</u>
<u>T. cimex</u>	Müller 1773	insufficiently described
<u>T. lyncaster</u>	Müller 1786	<u>Aspidisca lyncaster</u>
<u>T. lynceus</u>	Müller 1773	<u>Aspidisca lynceus</u>
<u>T. patella</u>	Müller 1773	<u>E. patella</u>
<u>T. silurus</u>	Müller 1773	insufficiently described
<u>T. transfuga</u>	Müller 1786	<u>Uronychia transfuga</u>
<u>Uronychia paupera</u>	Daday 1907	<u>E. eurystomus</u>

APPENDIX II

Five genera containing species originally included in Euplotes

Each description includes a diagnosis and the number and type species. Species are numbered and alphabetical after the type species. Junior synonyms are indented following their senior synonym. Euplotiscus, Euplotopsis, Euplotoides, Euplotaleos, and Euplotistus are new generic names which will be formally erected in a future publication (Hill, 1980b).

Genus Euplotes

Ehrenberg, 1830.

- 10 frontoventral cirri
- double dorsal argyrome
- 17 species; 15 marine, 1 euryhaline, 1 freshwater
- 2 species found in digestive tract of sea urchins

Type by monotypy: E. charon (Müller, 1773).

1. E. charon (Müller, 1773) Ehrenberg, 1830

Trichoda charon Müller, 1773

Ploesconia charon (Müller, 1773) Bory, 1826

Euploea charon Ehrenberg, 1830

E. appendiculatus Ehrenberg, 1838

Ploesconia charon Dujardin, 1841

P. radiosa Dujardin, 1841

P. longiremus Dujardin, 1841

E. balteatus Burkovsky, 1970

2. E. alatus Kahl, 1932

E. labiatus Ruinen, 1938

3. E. antarcticus Fenchel & Lee, 1972
4. E. balteatus (Dujardin, 1841) Kahl, 1932
Ploesconia balteata Dujardin, 1941
5. E. crenosus Tuffrau, 1960
6. E. harpa Stein, 1859
Ploesconia cithara Dujardin, 1841
7. E. indentatus Carter, 1972
8. E. inkystans Chatton in Tuffrau, 1960
9. E. magnicirratus Carter, 1972
10. E. moebiusi Kahl, 1932
11. E. neopolitanus Wichterman, 1964
12. E. octocirratus Agamaliev, 1967
13. E. polycarinatus Carter, 1972
14. E. quinquecarinatus Gelei, 1950
15. E. rariseta Curds, West & Dorahy, 1974
E. moebiusi Kahl, 1932 in Borrer, 1963
16. E. trisulcatus Kahl, 1932
17. E. tuffraui Berger, 1965

Genus Euplotiscus

- 10 frontoventral cirri
- single dorsal argyrome
- 6 species, all marine

Type by original designation: Euplotiscus vannus (Müller, 1786) Hill, 1980 n. comb.

1. Euplotiscus vannus (Müller, 1786) Hill, 1980 n. comb.

Kerona vannus Müller, 1786
Ploesconia vanus (Müller, 1786) Bory, 1826
Euplotes vannus (Müller, 1786) Minkjewicz, 1901
E. striatus Ehrenberg, 1838
E. longipes Chaparède & Lachmann, 1858
E. extensus Fresenius, 1865
E. gabrieli Gourret & Roeser 1886
E. marioni Gourret & Roeser 1886
E. caudata Meunier, 1910
E. truncata Meunier, 1910
E. worcesteri Griffin, 1910

2. Euplotiscus balticus (Kahl, 1932) Hill, 1980 n. comb.

Euplotes balticus Kahl, 1932
E. vannus var. balticus Kahl, 1932

3. Euplotiscus crassus (Dujardin, 1841) Hill, 1980 n. comb.

Ploesconia crassa Dujardin, 1841
Euplotes taylori Garnjobst, 1928
E. violaceus Kahl, 1928
E. salina Yocom, 1930
E. crassus Kahl, 1932
E. crassus var. minor Kahl, 1932

4. Euplotiscus cristatus (Kahl, 1932) Hill, 1980 n. comb.

Euplotes cristatus Kahl, 1932

5. Euplotiscus minuta (Yocom, 1930) Hill, 1980 n. comb.

Euplotes minuta Yocom, 1930

6. Euplotiscus mutabilis (Tuffrau, 1960) Hill, 1980 n. comb.

Euplotes mutabilis Tuffrau, 1960

Incertae sedis:

- Euplotiscus roscoffensis (Dragesco, 1966) Hill, 1980 n. comb.

Euplotes roscoffensis Dragesco, 1966

Genus Euplotopsis

- 9 frontoventral cirri in pattern I
- double to complex argyrome
- 15 species; 9 marine, 2 euryhaline, 4 freshwater

Type by original designation: Euplotopsis affinis (Dujardin, 1841) Hill, 1980 n. comb.

1. Euplotopsis affinis (Dujardin, 1841) Hill, 1980 n. comb.

Ploesconia affinis Dujardin, 1841

P. subrotundus Dujardin, 1841

Euplotes subrotundus Perty, 1852

E. affinis (Dujardin, 1841) Kahl, 1932

E. affinis var. tricirratus Kahl, 1932

2. Euplotopsis apsheronicus (Agamaliyev, 1966) Hill, 1980 n. comb.

Euplotes apsheronicus Agamaliyev, 1966

3. Euplotopsis bisulcatus (Kahl, 1932) Hill, 1980 n. comb.

Euplotes bisulcatus Kahl, 1932

4. Euplotopsis dogieli (Agamaliyev, 1967) Hill, 1980 n. comb.

Euplotes dogieli Agamaliyev, 1967

5. Euplotopsis elegans (Kahl, 1932) Hill, 1980 n. comb.

Euplotes elegans Kahl, 1932

E. elegans forma littoralis Kahl, 1932

E. elegans forma littoralis Dragesco, 1960

6. Euplotopsis gracilis (Kahl, 1932) Hill, 1980 n. comb.

Euplotes gracilis Kahl 1932

7. Euplotopsis latus (Agamaliyev, 1967) Hill, 1980 n. comb.

Euplotes patella forma latus Agamaliyev, 1967

8. Euplotopsis muscicola (Kahl, 1932) Hill, 1980 n. comb.

Euplotes muscicola Kahl, 1932

9. Euplotopsis muscorum (Dragesco, 1970) Hill, 1980 n. comb.
Euplotes muscorum Dragesco, 1970
10. Euplotopsis nana (Jones & Owen 1974) Hill, 1980 n. comb.
Euplotes nana Jones & Owen 1974
11. Euplotopsis parkei (Curds, 1974) Hill, 1980 n. comb.
Euplotes parkei Curds, 1974
12. Euplotopsis poljanskyi (Agamaliiev, 1966) Hill, 1980 n. comb.
Euplotes poljanskyi Agamaliiev, 1966
13. Euplotopsis raikovi (Agamaliiev, 1966) Hill, 1980 n. comb.
Euplotes raikovi Agamaliiev, 1966
14. Euplotopsis strelkovi (Agamaliiev, 1967) Hill, 1980
n. comb.
Euplotes strelkovi Agamaliiev, 1967
15. Euplotopsis zenkewitchi (Burkovsky, 1970) Hill, 1980
n. comb.
Euplotes zenkewitchi Burkovsky, 1970

Incertae sedis:

- Euplotopsis aberrans (Dragesco, 1960) Hill, 1980 n. comb.
Euplotes aberrans Dragesco, 1960
- Euplotopsis novemcarinata (Wang, 1930) Hill, 1980 n. comb.
Euplotes novemcarinata Wang, 1930
- Euplotopsis rotunda (Gelei, 1950) Hill, 1980 n. comb.
Euplotes rotunda Gelei, 1950
- Euplotopsis thononensis (Dragesco, 1960) Hill, 1980 n. comb.
Euplotes thononensis Dragesco, 1960

Genus Euplotoides

- 9 frontoventral cirri in pattern II
- double dorsal argyrome
- 7 species, all freshwater

Type by original designation: Euplotoides patella (Müller 1773) Hill, 1980 n. comb.

1. Euplotoides patella (Müller, 1773) Hill, 1980 n. comb.

Trichoda patella Müller, 1773
Kerona patella Müller, 1786
Coccudina keronina Bory, 1826
Himantopus charon Ehrenberg 1833
Ploesconia patella Dujardin, 1841
Euplotes patella (Müller, 1773) Ehrenberg, 1831
E. charon var. marina Quennerstedt, 1867
E. carinata Stokes, 1885
E. paradoxa Kent, 1880
E. patella var. alatus Kahl, 1932
E. patella var. lemanii Dragesco, 1960
E. variabilis Stokes, 1887 in Borrer, 1972

2. Euplotoides aediculatus (Pierson, 1943) Hill, 1980 n. comb.

Euplotes aediculatus Pierson, 1943
E. leticiensis Bovee, 1957
E. eurystomus Tuffrau, 1960
E. eurystomus Carter, 1972

3. Euplotoides amieti (Dragesco, 1970) Hill, 1980 n. comb.

Euplotes amieti Dragesco, 1970

4. Euplotoides diadaleos (Diller & Kounaris, 1966) Hill, 1980 n. comb.

Euplotes diadaleos Diller & Kounaris, 1966
E. patella var. alatus Kahl, 1932

5. Euplotoides eurystomus (Wrzesniowski, 1867) Hill, 1980 n. comb.

Himantophorus charon Müller, 1786
Euplotes eurystomus Wrzesniowski, 1867

- E. patella var. eurystomus Wrzesniowski, 1870
E. plumipes Stokes, 1884 in Borrer 1972
E. variabilis Stokes, 1887
Uronychia paupera Daday 1907
E. patella forma variabilis Kahl, 1932
E. plumipes Tuffrau, 1960 Stokes, 1884 in
 Tuffrau, 1960
E. plumipes Carter, 1972 Stokes, 1884 in Carter, 1972
E. plumipes Stokes 1884 in Hill & Reilly, 1978

6. Euplotoides plumipes (Stokes, 1884) Hill, 1980 n. comb.

Euplotes plumipes Stokes, 1884

7. Euplotoides woodruffi (Gaw, 1939) Hill, 1980 n. comb.

Euplotes woodruffi Gaw, 1939

Genus Euplotaleos

- 9 frontoventral cirri
- dorsal argyrome with long, longitudinal polygons between double system
- the single species is marine

Type by original designation: Euplotaleos tegulatus (Tuffrau, 1960) Hill, 1980 n. comb.

1. Euplotaleos tegulatus (Tuffrau, 1960) Hill, 1980 n. comb.

Euplotes tegulatus Tuffrau, 1960

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